











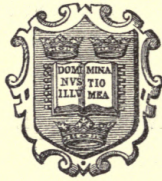


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FORMS OF ANIMAL LIFE

*G. ROLLESTON AND W. H. JACKSON*

London  
HENRY FROWDE



OXFORD UNIVERSITY PRESS WAREHOUSE  
AMEN CORNER, E.C.



# FORMS OF ANIMAL LIFE

*A MANUAL OF COMPARATIVE ANATOMY*

*WITH DESCRIPTIONS OF SELECTED TYPES*

BY THE LATE

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LINACRE PROFESSOR OF ANATOMY AND PHYSIOLOGY  
IN THE UNIVERSITY OF OXFORD

*SECOND EDITION*

REVISED AND ENLARGED BY

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NEW COLLEGE

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Oxford

AT THE CLARENDON PRESS

M.DCCC.LXXXVIII

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Διὸ δεῖ μὴ δυσχεραίνειν παιδικῶς τὴν περὶ τῶν ἀτιμοτέρων ζώων ἐπίσκεψιν.  
ἐν πᾶσι γὰρ τοῖς φυσικοῖς ἔνεστί τι θαυμαστόν . . . . καὶ πρὸς τὴν ζήτησιν περὶ  
ἐκάστου τῶν ζώων προσιέναι δεῖ μὴ δυσωπούμενον ὡς ἐν ἅπασιν ὄντος φυσικοῦ  
καὶ καλοῦ.—ARISTOTLE, De Part. Anim. i. 5.

Παντὸς προσθεῖναι τὸ ἐλλείπον.—ARISTOTLE, Ethic. Nicom. i. 7.

38943

MUSEUM, OXFORD:

March 5, 1870.

## PREFACE TO SECOND EDITION.

THE present edition of 'Forms of Animal Life' was taken in hand by the late Professor Rolleston in the Long Vacation of 1879. The work was carried on with prolonged interruptions, incident to a life of many and varied engagements, until he left England in December 1880. By that time he had completed the descriptions of Preparations 1-9; three new Plates (Pls. IV, VII, IX) had been engraved under his direction, and he had compiled notes upon them, which have been employed in the descriptions printed in this volume.

Soon after beginning his work, the Professor asked me to undertake a joint authorship of the book. The part then assigned to me was to rewrite the descriptions of a certain number of the Preparations, the general accounts of *Urochorda*, *Arthropoda*, parasitic *Vermes*, *Coelenterata* and *Protozoa*, as well as of several minor classes. He read my account of *Protozoa*, and settled that it should form a model for the accounts of all other groups. As now printed it has been so far modified as to accord with the recent progress of knowledge.

When Professor Rolleston went abroad he put me in possession of his plans for the rest of the work, handed his papers to me, and expressed a hope that, if he were disabled from completing the new edition, I might be the person to do it in his stead. It is almost needless for me to add that in fulfilling this sacred trust I have endeavoured to carry out his wishes, which were mainly three: (1) to enlarge the descriptions of the Preparations and accounts of the various classes of animals, and bring them to the standard of contemporary knowledge; (2) to add to each class or group a brief classification; and (3) to give as full a bibliography as space would permit.

The method I have adopted to meet the last requisition is to cite the most important and recent authorities which, when consulted, will in most cases give the names of all other accounts worth reading, so as to form

a really very complete index to the state of present knowledge. These authorities write chiefly in foreign languages, and I need scarcely remark that every modern anatomist must also be a modern linguist. Literature, though not everything in Science, is yet indispensable, and as Professor Rolleston observed in the preface to the first edition of his book (pp. viii-ix):—

‘In some cases even the beginner will find it necessary to consult some of the many works referred to in the descriptions of the Preparations and in the descriptions of the Plates; but the bibliographical references have been added with a view rather to the wants indicated in the words “Für Akademische Vorlesungen und zum Selbststudium,” so often prefixed to German works on Science, than to those of the commencing student.’

The debateable points of Phylogeny are not treated at any length. Professor Rolleston, having tried one experiment, particularly desired that they should be omitted on account of the great space their adequate discussion must needs occupy.

One alteration in the arrangement of the volume had been contemplated by the Professor, but left unsettled, and has now been carried out in consequence of the opinion of Professor Huxley in its favour. The descriptions of the Preparations, those of the Plates, and the general account of the Animal Kingdom, have changed places. The two former stood last in the first edition, but take precedence in this. The new arrangement tallies better with the order in which Professor Rolleston wished the several parts to be studied, as stated, loc. cit. pp. vii-viii:—

‘It is recommended that in all cases the study of the described Preparation or specimen should precede that of the accounts in the Introduction (i. e. *General account of the Animal Kingdom, Ed.*) of the Class and Sub-kingdom (i. e. *Phylum, Ed.*) to which it belongs, and that the study of the Plates should be taken up only after the attainment of a considerable familiarity with actual specimens by the practice of dissection.’

The Plates, however, illustrate the Preparations, and are therefore placed as the second section of the book<sup>1</sup>.

<sup>1</sup> A few changes in the Preparations have been made. Some have been added, e. g. those relating to the Rabbit; the Privet Hawk Moth has been substituted for the Death's Head which is difficult to procure; similarly, the Dog's Tapeworm and its *Cysticercus* replace the Bladderworm of the Sheep (*Coenurus*). The skeleton of the Common Fowl, two dissections of a Caterpillar, the angular Sea Cucumber, and the Bugle Coralline, have been omitted. The Preparations were made by Charles Robertson, Esq., Demonstrator of Anatomy in the University Museum; the greater part

Although the Professor contemplated the above-mentioned changes, he desired to retain the 'distinctive character' of the book. This character, as he himself said, *loc. cit.* pp. v-vi :—

'Consists in its attempting so to combine the concrete facts of Zootomy with the outlines of systematic Classification as to enable the student to put them for himself into their natural relations of foundation and superstructure. The foundation may be made wider, and the superstructure may have its outlines not only filled up, but even considerably altered by subsequent and more extensive labours; but the mutual relations of the one as foundation, and of the other as superstructure, which this book particularly aims at illustrating, must always remain the same.'

Another observation may be quoted, *loc. cit.* p. vi :—

'It is hoped that this work, though written with a view chiefly to the needs of University students of Comparative Anatomy, and with special reference to the application of that branch of science as an engine of instruction, may in some measure meet the requirements of the now not inconsiderable number of persons who are attracted to the study by seeing the important bearings which it has upon questions not only of theoretical and philosophical, but also of practical interest.'

It would have been more agreeable to my own feelings if this second edition had been issued at an earlier date. But the great length of time which has elapsed since the publication of the first—full seventeen years—has brought with it so many and such vast changes in Comparative Anatomy that great labour and consequent delay became inevitable. I may mention that scientific periodicals on the general subject and its branches have since 1870 been almost doubled, not only in number, but also in bulk; and one whole science—that of Comparative Embryology—has been formulated and now constitutes the foundation of all Anatomy. Any worker placed single-handed under such conditions, is at a great disadvantage even with all the modern paraphernalia of abstracts. And I have to add a lesson learnt by personal experience, that in most cases the best abstract available cannot by any means stand in the place of the original paper. Among other causes of delay my own employment as a teacher must be taken into account, and there have also occurred

of them were exhibited by him as a 'Zoological series with Dissections in illustration,' in the Educational Department of the Great Exhibition of 1862.

Thirteen woodcuts have been added in the text, and three new Plates (Pls. IV, VII, IX). Of the old plates, one (Pl. IX of the first edition) has been cancelled. The woodcuts 1-5 and the three new plates have been drawn by Julian Drummond, Esq., the present Radcliffe Artist; the plates of the first edition were drawn by his predecessor, George Crozier, Esq.

many unforeseen interruptions. Under these circumstances it is my pleasant duty to thank the Delegates of the University Press for their kind forbearance on the question of time.

My warmest thanks are due to Sir H. W. Acland, K.C.B., F.R.S., for the use of a room belonging to his own suite in the University Museum, and for a free and extensive command of all requisite literature in that rich storehouse of scientific books, the Radcliffe Library, without which my task could never have been accomplished. To Professor Moseley, F.R.S., Dr. Rolleston's successor in the Linacre chair, I render my best thanks for an unlimited employment of the anatomical collections under his charge, and the loan of his own MS. notes on the *Anthozoa Zoantharia*. I have also to record a debt of gratitude to my early and constant friend, Professor Westwood, who has given me much assistance by way of access to specimens and pamphlets on the difficult phylum *Arthropoda*. In kind compliance with my request, Professor Ray Lankester, F.R.S., liberally allowed me to copy two figures of his own construction (Woodcut 13, A, B, and 1, 2, 3, 4); and Professor Kitchin Parker, F.R.S., furnished valuable information, at the time unpublished, relative to points in the development of the Vertebrate skull, and also granted permission for the use of two figures (Woodcuts, 6 and 7) illustrating the skull of the common Frog. I have to thank Mr. C. Robertson, who was conversant with Professor Rolleston's wishes, for assistance on various points, and Mr. G. C. Bourne for several suggestions and for other help; nor must I by any means omit Professor W. B. Spencer of Melbourne University, and Mr. G. H. Fowler, to whose most timely and friendly care I am entirely indebted for the addition of the Index.

The compilation of this book, though laborious in the extreme, has been attended by its pleasures. But the crowning pleasure of all can only befall me if its publication gains the sympathy of those who are competent to judge the nature of the task, and the book itself proves a real aid to students in this most fascinating science of Comparative Anatomy.

WM. HATCHETT JACKSON.

MUSEUM, OXFORD :

September 24, 1887.



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## LIST OF ABBREVIATED TITLES.

The following works which are continually quoted are referred to in the text by letters only. It is hoped all other abbreviations will explain themselves. It may be well to mention that 'SB.' and 'Dk.' stand respectively for 'Sitzungsberichte' and 'Denkschriften.'

- A. M. A. = Archiv für Mikroskopische Anatomie, Bonn.
- A. N. = Archiv für Naturgeschichte, Berlin; often cited in literature as Wiegmann's or Troschel's Archiv.
- A. N. H. = Annals and Magazine of Natural History (various series), London.
- A. Sc. N. = Annales des Sciences Naturelles, Zoological section (various series), Paris.
- A. Z. Expt. = Archives de Zoologie Expérimentale et Générale (two series), Paris.
- C. R. = Comptes Rendus des Séances hebdomadaires de l'Académie des Sciences, Paris.
- J. L. S. = Journal of Linnean Society, Zoological section, London.
- J. Z. = Jenaische Zeitschrift für Naturwissenschaft, herausgegeben von der Med. Nat. Gesellschaft zu Jena.
- M. J. = Morphologisches Jahrbuch, eine Zeitschrift für Anatomie und Entwicklungsgeschichte, Leipzig.
- Ph. Tr. = Philosophical Transactions of the Royal Society, London.
- P. R. S. = Proceedings of Royal Society, London.
- P. Z. S. = Proceedings of Zoological Society, London.
- Q. J. M. = Quarterly Journal of Microscopical Science, London.
- Tr. L. S. = Transactions of Linnean Society (two series), London.
- Tr. Z. S. = Transactions of Zoological Society, London.
- Z. A. = Zoologischer Anzeiger, Leipzig.
- Z. W. Z. = Zeitschrift für Wissenschaftliche Zoologie, Leipzig; often cited in literature as Siebold and Kölliker's Zeitschrift.

## ADDITIONS AND CORRECTIONS.

- Page 131. Labial tentacles, Thiele, Z. W. Z. xlv. 1886. Pericardial gland (also in *Gastropoda*), Grobben, Z. A. ix. 1886; x. 1887.
- pp. 144-5. There are ten stigmata, the abdominal being eight, not seven as stated. The testes and their ducts are paired.
- p. 146. Studies in Comparative Anatomy, iii; the Structure and Life-history of the Cockroach, &c., Miall and Denny, London and Leeds, 1886. Translucent white spots on head, Carrière, Z. A. ix. 1886, p. 496.
- p. 177. Development of *Astacus*, Reichenbach, Abhandl. Senck. Ges., xiv. (1), 1886.
- p. 186. Green gland; Grobben, A. M. A., xxx. (2), 1887.
- p. 206, l. 17. There are several species of *Monocystis* inhabiting the Earthworm. Bergh mentions (Z. W. Z. xlv. p. 308, note 2), in his paper on the genitalia and their development in *Lumbricus*, that an ovarium or a pair of ovaries may be present in somite xiv in addition to the ordinary pair in somite xiii. Two pairs of ovaries are present in other Earthworms also; see Beddard, P. Z. S. 1887, pp. 388-9.
- p. 212. Giant fibres or neurochord, Leydig, Z. A. ix. 1886.
- p. 226, 8 lines from bottom: add that, the three lateral nerves spring from the principal ganglion on each side.
- p. 250, 12 lines from bottom: the cells collect *round* not *in* the canals and ampullae. The error is due to a mistake in an abstract, the only account accessible at the time.
- p. 258, *ad fin.* The *Amoebulae* of *Pelomyxa* probably belong to a parasite; cf. p. 900, note 1.
- p. 302. Tongue of Bee, Breithaupt, A. N. 52, ( ), 1886; Graber, Z. A. x. 1887.
- p. 343 and note. Pineal eye of Lizards, Spencer, Q. J. M. xxvii. 1887; of Fishes (*Cyclostomi*), Beard, Nature, xxxvi. 1887, p. 246.
- p. 347. Ear-ossicles of *Mammalia*. For other views, see a paper by Dollo, in Q. J. M. xxiii. p. 579, and Baur, Q. J. M. xxviii. p. 169. It seems to me that embryological evidence is conclusive in favour of the view in the text; see the plates to W. K. Parker's paper on the Skull of *Mammalia*, Ph. Tr. 176, 1885.
- p. 349, 10 lines from top. There are five visceral clefts in some *Lacertilia* and *Ophidia*, as in *Chelonia* (Rathké), according to van Bemmelen, Z. A. ix.
- p. 352, 10 lines from top. The pulmonary artery of *Lacerta*, *Tropidonotus*, and the Hen is the VIth aortic arch as in *Amphibia*, the Vth aborting. Id. *ibid.*
- pp. 370, 371. Selenka, *Didelphys Virginiana*, Studien über Entwickelungsgeschichte der Thiere, i., Wiesbaden, 1886; Caldwell, Embryology of *Monotremata* and *Marsupialia*, P. R. S. xlii. 1887.
- p. 446. On the *Salpa* chain, see Brooks, Studies Biol. Lab. Johns Hopkins Univ., iii. pt. 8, 1887.

p. 483. On the asymmetry of *Gastropoda*, Bütschli, M. J. xii. 1887.

p. 509. Add the following definitions of Thysanura and Collembola:—

1. *Thysanura*. Rings of the thorax similar; abdomen with ten somites, elongate, terminated by 2-3 appendages usually jointed; rudimentary abdominal limbs sometimes present; antennæ long, many jointed; maxillary palpi 7-jointed, labial 4-jointed; e.g. *Campodea*, *Lepisma*, *Machilis*.

2. *Collembola*. Prothorax small, meso- and meta-thorax not clearly segmented, or the pro- concealed by the meso-thorax; abdomen with six somites, very often globular, with a ventral adhesive tube and a terminal forked springing organ; antennæ 4-8 jointed, palpi absent; e.g. *Smynturus*, *Podura*.

p. 519. *Peripatus Capensis*. Sedgwick has shown (Q. J. M. xxvii. 1887) that the coelomic cavities of the somites persist as small vesicles in the appendages, that the nephridia are the developed tubular portions of these cavities which obtain external openings, and that the nephridia of the 3rd somite give origin to the salivary glands. The coelome, so-called, of the adult, is a system of vascular spaces (=metacoel, p. xxix, *post*) developed independently of the cavities of the somites. The generative cells are derived from the endoderm in the 6th-20th somites, pass into the dorsal parts of the true coelomic cavities of the same somites, which unite to form the generative glands; the generative ducts are developed from the coelomic cavities of the 21st somite; their openings are therefore nephridial. There are no cilia in this species.

p. 526. The Malpighian tubes of spiders (*Araneidae*) have been shown to be, as in some *Amphipoda*, appended to the mesenteron, not to the proctodæum; see Loman, Tijdschrift der Nederl. Dierk. Vereen. (2), i. p. 109.

p. 562. Hamann, Beiträge zur Histologie der Echinodermen, pt. 3, Anat. etc., der Echiniden und Spatangiden, Jena, 1887. *Dorocidaris*, etc., Prouho, A. Z. Expt. (2), v. 1887.

p. 576. Mémoire sur l'Organisation, &c., *Antedon rosacea*, Perrier, Nouvelles Archives du Musée, Paris (2), ix. 1886.

p. 578. Catalogue of *Blastoidea*, Geol. Department Brit. Mus., Etheridge and Carpenter, 1886.

p. 588. For *Echinoderes*=*Kinorhyncha*, see Reinhard, Z. W. Z. xlv. 1887.

p. 612. Nephridia etc. of *Polychaeta*, J. T. Cunningham, Q. J. M. xxviii. (2), 1887.

pp. 621, 622. The so-called sexual organs of *Priapulidae*, are both nephridial and sexual, the two parts opening on opposite sides into the main canal. The sexual part is developed last. Schauinsland, Z. A. ix. p. 574.

p. 694. Sollas has shown that the coecal processes of the shell in *Waldheimia cranium* lodge a sensory cell beneath the periostracum, which is connected by a fibril to a nerve-ganglion cell in the mantle. Sc. Proc. Roy. Dublin Soc. v. 1886, p. 318.

p. 711. *Cephalodiscus* proves to be an Enteropneustan, a near ally of *Balanoglossus*. The epistome or buccal-shield is the proboscis, and contains a coelomic cavity opening by two dorsal pores. It is followed by a collar with a right and left coelomic cavity, opening each by a pore, and extending into the six arms of each side. The body has also a right and left coelomic cavity. The nervous system is ectodermal, and principally massed on the dorsal aspect of the collar, but extends on to the proboscis and the arms. There is a pair of gill-slits overhung by an

opercular fold, and a diverticulum homologous with the 'notochord' of *Balanoglossus*. See Harmer, Appendix to M'Intosh on *Cephalodiscus*, Challenger Reports, xx. 1887.

p. 716. *Polyparium* (not as printed, *Polypodium*) *ambulans*; See Korotneff, Z. W. Z. xlv. 1887 (transl. A. N. H. (5), xx); Ehlers, *ibid*.

p. 732. Classification of Alcyonaria; see Studer, A. N. 53 (1), 1887.

p. 811. *Hyalospongiae*. F. E. Schulze, 'Hexactinellidae,' Challenger Reports, xxi. 1887.

## ERRATA.

Page 53, line 12 from bottom, *for* and *read* end.

p. 55, line 2 from bottom, *for* interclavicular *read* interclavicular.

p. 59, line 20, *for* vertebrae *read* vertebra.

p. 61, line 20 from bottom, *for* long-oblique *read* long, oblique.

p. 91, line 4, *for* (S. O.) *read* (E. O.).

p. 112, line 24, *for* 1871 *read* 1817.

p. 113, line 21 from bottom, *for* ganglia *read* ganglion.

p. 168, line 6 from bottom, *for* five *read* fine.

p. 199, line 11 from bottom, *for* *Acanthrodrilus* *read* *Acanthodrilus*.

p. 232, line 20, *for* *Staphylocystes* *read* *Staphylocystis*.

p. 243, lines 20, 21, *for* *Ophridium* *read* *Ophrydium*.

p. 249, line 15 from bottom, *for* Abth. ii. *read* Abth. i.

p. 250, line 12 from bottom, *for* in the *read* round the.

p. 253, line 20 from bottom, should *read* A. N. H. (5): vii. 1881; *gemmule of Carterella*, ix. 1882; x. 1882; *fossil spicules*.

p. 273, line 16, *for* metanaphros *read* metanephros.

p. 302, line 2, *for* labral *read* labial.

p. 337, last line, p. 338 line 1, *for* ali- *read* prae-, and *for* prae-, ali-

p. 376, line 18, *for* and *read* or.

p. 462, line 20, *for* arteries *read* veins.

p. 465, line 18, *for* *Cirroteuthidaei* *read* *Cirroteuthidae*.

p. 475, line 13 from bottom, *for* *Enthyneura* *read* *Euthyneura*.

p. 482, line 12 from bottom, *for* skull *read* shell.

p. 483, line 17 from bottom, *for* large or *read* large and.

p. 485, line 2, *for* exterior *read* anterior.

p. 490, line 5 from bottom, *for* hollow-jointed, *read* hollow, jointed.

p. 500, line 22, *for* into *read* by.

p. 515, line 11 from bottom, *for* class *read* order.

p. 530, line 4, *for* *Tyroglyphidae* *read* *Tyroglyphidae*.

p. 536, line 5 from bottom, dele commas after *Phyllopora* and *Branchiopoda*.

p. 584, note, line 8 from bottom, *for* arms *read* anus.

p. 647, line 7 from bottom, *for* peristallic *read* peristaltic.

p. 658, line 16 from bottom, *for* viscuall *read* visual.

p. 716, line 17, *for* *Polypodium* *read* *Polyparium*.



## GENERAL INTRODUCTION.

THERE are two kingdoms, an Animal and a Vegetable, to one of which everything that lives may be assigned with more or less certainty. The contrast between the higher or multicellular animals and plants is too great and constant both in an anatomical and physiological sense to leave room for doubt. An animal possesses the power of locomotion ; it has a compact form, a special digestive organ for the reception of solid food, and it is unable to utilise Carbon dioxide as a source of carbon for the production of carbohydrates ; it has organs of special sense with a nervous system, specialised contractile cells or muscular tissue, complex excretory products, and in the majority special organs of excretion, lymph or blood, with circulatory organs, &c. Its tissue cells, with few exceptions, are not isolated or all but isolated by closed and firm cell-envelopes. Supposing that it is fixed, its other characteristics remain ; if it takes on a branched or plant-like mode of growth, examination shows that it consists of a connected multitude of typical animals, each one perfect in itself. A few instances are known in which chlorophyl bodies are present ; and it appears probable that they enable the organism to utilise Carbon dioxide for the preparation of starch under the influence of light. Whether, however, the chlorophyl bodies are in all these instances intrinsic parts of the organism is a matter of dispute (pp. 242-5). A typical multicellular plant, on the other hand, is either branched, and it then consists of a root with a stem, bearing a number of repeated organs, the leaves, which are subject to modification, or it is compact and its cells very similar one to another. It is fixed ; it has chlorophyl bodies, which under the influence of light enable it to utilise Carbon dioxide as a source of carbon ; it is able to build up protoplasm and therefore derive tissue elements from the Carbon dioxide of the air, ammonia, nitrates and mineral constituents of the soil ; it is devoid of digestive organs, of special sense organs, nervous system, excretory organs, special contractile tissue. Its tissue cells become isolated completely or all but completely by closed and firm cell-envelopes. It may require for food partly elaborated material or fairly complex organic compounds in solution, and may then

be devoid of chlorophyl bodies, but its other characters remain unchanged. If it has a motile initial stage the course of development proves its plant-like nature. In those rare instances, i.e. in Insectivorous plants where solid food is digested and the products of digestion utilised, the process of digestion is carried on externally to the organism, and absorption takes place by the outer surface.

What is true of multicellular animals and plants is true, within limitations, of unicellular. There are of course in a unicellular animal no specialised systems of organs such as the digestive, for example, but power of locomotion remains, and the natural irritability, automatism and contractility of the protoplasm are very strongly developed. Solid organic food is ingulfed within the protoplasm and is broken down, giving rise to fat, albumen, glycogen or other starchy bodies as in higher animals; it also leaves generally a faecal residue, and there is reason to think that complex and sometimes crystalline excretory products are formed. But the organism may in some cases utilise organic food in solution, in other words it is saprophytic, e.g. some *Flagellata*, and probably the *Mycetozoa*; in other cases, e.g. the Flagellate *Euglena*, owing to the presence of chlorophyl bodies, nutrition becomes holophytic or completely plant-like. In these instances recourse can be had only to considerations of structure, life-history, comparison with other forms, or the behaviour of the doubtful organism under altered conditions of life. Good examples of these considerations may be drawn from *Flagellata* and *Mycetozoa*. The position however of some few forms, e.g. the *Volvocina*, remains a matter of doubt, and they are claimed by botanists and zoologists alike. Their nutrition is holophytic, and their structure is paralleled in undoubted vegetable organisms<sup>1</sup>.

However complex in structure a multicellular animal or plant may be, it can be traced without exception to an origin from a single cell. Many animals, the whole group known as *Protozoa*, and many plants never attain a higher degree of morphological complexity than a single cell. But in some *Protozoa*, at any rate, that cell possesses highly developed vital energies and a corresponding specialisation of parts. In its simplest aspect a cell may be defined as a mass of protoplasm (cytoplasm) containing one or more nuclei. It has been shown that non-nucleated masses of protoplasm, derived from nucleated, are in the *Protozoa* capable of growth in size, but they have no power of reproduction. On the other hand, there are a few *Protozoa* (certain *Proteomyxa*) which appear to

<sup>1</sup> See Maupas, C. R. 88, 1879, p. 1274.

consist really of non-nucleated protoplasm, capable not only of growth but reproduction. They may be distinguished as 'cytods' from the cell to which a nucleus is essential. It is possible however that the elements of the nucleus are in these cases disseminate. Protoplasm, or 'the physical basis of life,' is a substance of complex chemical composition containing Nitrogen, Carbon, Oxygen and Hydrogen, with Sulphur, Phosphorus, Sodium and Potassium. From the physical point of view it is viscid, of variable refrangibility, more or less doubly refractile, colourless, hyaline in its purest condition. It appears sometimes to be structureless, but as a rule it is more or less vesicular, consisting of a denser substance (mitome) enclosing droplets of a more fluid character (enchylema, paramitome), and it is endowed with certain physiological properties, the sum of which constitute life. It is contractile, irritable, possessed of automatism, able to convert other protoplasm or less complex compounds, sometimes organic only, sometimes only inorganic, into its own substance. And this nutrition not only maintains the *status quo*, but if over sufficient for that purpose leads first to the storage of superfluous material in the shape of fat, albumen and starchy bodies; and secondly, causes a positive increase of bulk, with which is connected the power of reproduction in its most primitive form—a division of the mass into two similar parts. But all these powers are exercised at the cost of a chemical transformation or degradation of the protoplasm itself, in part respiratory, i. e. oxydative. The products of this degradation, Carbon dioxide and various nitrogenous compounds, are useless to the organism, and are excreted. The whole of the vital properties enumerated can be exercised only while the protoplasm is saturated with water. One of the consequences of the vital energies of protoplasm is that as a substance it can never be obtained in a chemically pure condition, which is only approached when it is starved. Otherwise it is laden with the products of progressive and regressive metamorphosis. It may be added that the protoplasm of a cell often gives origin by conversion to an external or internal cell-skeleton, the characters of which, both chemical and physical, are extremely variable<sup>1</sup>.

The nucleus of a cell is a structure sharply marked off from the protoplasm. In its simplest state it is homogeneous and more or less

<sup>1</sup> See the introductory chapter in Foster's 'Textbook of Physiology,' and on the movements, &c. of protoplasm, Engelmann, 'Die Protoplasma- und Flimmerbewegung,' in Hermann's Handbuch der Physiologie, i. 1879, p. 343 et seqq., the first part of which is translated in Q. J. M. xxiv. 1884. On the structure and physiology of ciliated cells, see also Engelmann, Pflüger's Archiv für Physiologie, xxiii. 1880.

rounded, but capable sometimes of changes of shape. It consists principally of a substance termed nuclein from a chemical point of view, or chromatin from its marked physical peculiarity, that of readily absorbing, and to a much greater degree than the rest of the cell, various kinds of stains such as carmine. But this simple structure is rarely retained. The nucleus is limited externally by a nuclear membrane, its chromatin is disposed in very various ways, as a reticulum, a much coiled thread, in fragments as a lining to the nuclear membrane and one or more central spots. To nodal thickenings of the thread, &c., or to the fragments of chromatin, the term nucleolus is generally applied. The intervals between the chromatin elements are occupied by a nuclear fluid, composed of a protoplasm (caryoplasma), which may be resolved like the protoplasm of the cell (of which it is a part) into a denser and more fluid portion. As this protoplasm takes up stains but slightly, it is frequently designated achromatin. The structure of the nucleus is not always the same at all periods of its life; it may be at first homogeneous, but as a rule assumes one of the more complex forms.

The process of division of the cell may be comparatively simple or complicated. The division of the protoplasm is preceded, or accompanied, by division of the nucleus. The latter process may be direct or amitotic, the nucleus simply elongating, and being split by a constriction. Or it may be indirect or mitotic, the achromatin being disposed in lines parallel to the long axis of the nucleus, making the figure of a spindle, and the chromatin grouped at the centre of the spindle, dividing into parts which move in opposite directions to either pole of the spindle, whilst a constriction splits the nucleus in two. It is rare for the chromatin to be grouped in two masses on the equator and the split of the nucleus to take place through its poles. The figures seen in the process are spoken of as karyokinetic. It has been found that the typical mitotic and amitotic modes of divisions are connected by intermediate phases, at least in some tissue cells. The nuclear membrane is dissolved in mitosis and reconstituted round the new nuclei<sup>1</sup>.

<sup>1</sup> The denser mitome of the nucleus and the body of the cell may give rise to an equatorial plate, or the former may do so, and not the latter. This plate, which is common in plants, but has only been detected in certain tissue-cells of *Arthropoda*, may evanesce, or fission may take place through its median plane. It may be noted that the mitome of the cell-body is frequently arranged in radii during the nuclear changes, and that a clear spot, the polar spot or corpuscle, may appear at each pole of the spindle. For the structure of the cell, see Carnoy, 'La Biologie cellulaire,' Lierre, Fasc. i. pt. 2, 1884; for cell-division (cytodieresis) in *Arthropoda*, Id. 'La Cellule,' Lierre, i. 1885-6, and the summary of both papers by A. Bolles Lee in Q. J. M. xxvi. 1886, p. 481; cf. also Flemming and Carnoy in Z. A. ix. 1886. For the fission of the giant-cells, &c. in the medulla of bone, see Denys, 'La Cellule,' ii. (2), 1887.

The single cell from which a multicellular animal is developed is known as an ovum. It may be derived from an epithelium or sub-epithelium, ectodermic or endodermic (*Coelenterata*); or from a special organ, the ovary, furnished with a duct and developed usually in the mesoblast, sometimes from special cells set apart at a very early stage of development, e. g. in some *Insecta*, perhaps in rare instances from the endoderm (some *Turbellaria*). It may be naked, or provided with one or more envelopes, derived from itself, from surrounding cells, or special glands<sup>1</sup>. It may be hyaline, or it may be filled to a greater or less extent with nutrient material, derived by its own vital energies from the lymph-plasma of the body, from the products produced by the regressive changes of surrounding cells (granulosa cells) of the ovary, rarely from other cells. This nutrient reserve-material may be distinguished as food-yolk or deutoplasm from the protoplasm with which it is mixed<sup>2</sup>. Or the nutrient material may be derived from a special gland, the vitellarium, and be inclosed with the ovum in the egg-shell to be utilised as the ovum segments (some *Turbellaria*, *Trematoda*, *Cestoda*)<sup>3</sup>. In one phase of the life-history of the digenetic *Trematoda*, the Sporocyst or Redia, the reproductive cell is one of a number of cells filling the central part of the body and lining the body walls. These cells may perhaps be regarded as collectively making up an undifferentiated ovary, i. e. as cells from which, in another phase, the immature Fluke, the reproductive organs are derived.

As soon as the ovum has attained its definitive size, it very generally, probably universally, gives origin to two polar bodies, or globules, or directive vesicles. The ovular nucleus (germinal vesicle or vesicle of Purkinje with nucleolus or germinal spot) approaches the surface, undergoes karyokinetic changes, and finally one moiety is extruded with a very small amount of protoplasm. After a brief period of rest the phenomenon is repeated. The polar globules may themselves divide again, and the

<sup>1</sup> An egg-shell must be carefully distinguished from structures inclosing a number of ova like the cocoons of the Leech and Earthworm, which are secreted by the surface of the body.

<sup>2</sup> An ovary in which every ovarian cell becomes an egg, may be termed panoistic; one in which some only become eggs, others giving origin to secondary yolk or an egg-membrane, meroistic. The terms are Brandt's, and were originally applied by him to Insectan ovaries.

<sup>3</sup> There can be no doubt that a vitellarium is essentially a part of an ovarium. Certain Rhabdocoela prove this point remarkably well; see von Graff, *Monographie der Turbellarien*, i. Rhabdocoelida, Leipzig, 1882, p. 138, on the 'Keimdotterstock.' Granulosa cells, yolk cells, epithelium cells connected with the egg, have very generally a similar origin to the egg itself. See A. Thomson, 'Recent researches on Oogenesis,' *Q. J. M.* xxvi. 1886, p. 602, with lit. given p. 606, and a paper by Korschelt, 'Über die Entstehung, etc. der versch. Zellenelemente des Insekten-ovariums,' *Z. W. Z.* xl. 1886.

nucleus or nuclear moiety they contain pass through mitotic changes<sup>1</sup>. In some *Rotifera*, *Crustacea*, and *Insecta* one polar body only is formed, and the ovum then proceeds to segment. Such ova are termed parthenogenetic, and the process parthenogenesis. But in the vast majority of multicellular animals it is necessary for the ovum to be impregnated, i.e. it must fuse or conjugate with another cell, the spermatozoon, just as in some unicellular animals a temporary or permanent conjugation between two individuals is requisite from time to time to perpetuate the race. The spermatozoon is typically a flagellate cell, with or without the addition of a vibratile membrane; it is rarely amoeboid; sometimes of very various shapes even in the same class (*Turbellaria*); motile, except in *Crustacea* and a few other Arthropods<sup>2</sup>. It is produced by the repeated fission of a cell, or of part of a cell, belonging to a testis, an organ homologous with the ovary. During its evolution, a process analogous to the formation of polar bodies in the ovum, or homologous with it, is supposed to occur very generally<sup>3</sup>. The testis may co-exist with the ovary in the same

<sup>1</sup> The formation of polar globules is certainly due to cell-fission; the fact that the nucleus undergoes mitotic changes during their appearance is sufficient to prove the point. They may themselves divide again, and their nuclear fragment show mitosis: see especially Trinchisi, 'Evoluzione nei Molluschi,' *Atti Acad. Lyncei*, (3), vii. 1879, Pls. 1 and 8. But they are commonly degenerate in structure. For recent observations see A. Thomson, 'Recent Researches on Oogenesis,' *Q. J. M.* xxvi. 1886, p. 591, with lit. p. 605. Their significance is a difficult question. If a spermatozoon enters the ovum, e.g. in an *Asterias* before they are formed, no union between the male and female pronuclei takes place until the process is completed. A single polar body is found in parthenogenetic ova (Weismann, *SB. Natf. Ges. Freiburg*, i. B., iii. (1), 1887), a fact that disproves the view that the bodies are a male element which must be got rid of before impregnation, or a safeguard against self-fertilisation. See the views of Weismann, *Nature*, xxxvi., p. 607, and Minot, *American Naturalist*, xiv. 1880, p. 106; cf. Balfour, *Comp. Embryology*, i. pp. 61-4, and E. van Beneden, 'Recherches sur la fécondation,' *Arch. de Biologie*, iv. 1883, especially pp. 482, 527, 603 et seqq. Compare with the account given by the last-named, Carnoy, on the germinal vesicle and polar globules in *Ascaris megaloccephala*, 'La Cellule,' *Lierre*, ii. (1), 1886; in sundry Nematodes, *Id. op. cit.* iii. 1887, and *ibid.* in the appendix to the 'conférence.' For views connected with the import of the nucleus, &c. to the doctrine of Heredity, see Weismann, 'Die Continuität des Keimplasma's,' *Jena*, 1885, summarised by Moseley, *Nature*, xxxiii. 1885-6, p. 154; *Id.* 'Die Bedeutung der sexuellen Fortpflanzung,' &c., *Jena*, 1886, similarly summarised, *Nature*, xxxiv. 1886, p. 629; also Kölliker, 'Die Bedeutung der Zellkerne,' &c., *Z. W. Z.* xlii. 1885, summarised in the *American Naturalist*, xix. 1885, p. 1222; *Id.* 'Das Karyoplasma,' &c., *Z. W. Z.* xlv. 1886; O. Hertwig, 'Das Problem der Befruchtung,' &c., *J. Z.* xviii. 1885, and the chapters on the reproduction of plants in Vines, *Physiology of Plants*, Cambridge, 1886, or the corresponding lectures in Sachs, 'Physiology of Plants,' transl. by Marshall Ward, Clarendon Press, 1887; also Geddes, 'Theory of Growth,' &c., *Proc. Roy. Soc. Edinburgh*, 1886.

<sup>2</sup> The immobility of the spermatozoa of *Crustacea* and some other Arthropoda is somewhat doubtful. The spermatozoon of *Cypris* becomes active when transferred to the female; and that of the Cladoceran *Polyphemus* shows amoeboid motion (Zaccharias, *Z. W. Z.* xli. 1885).

<sup>3</sup> For the accessory globule of the spermatozoa, see E. van Beneden and Julin, *Bull. Acad. Roy. Belg.* (3), vii. 1884, p. 322; Brown, *Q. J. M.* xxv. 1885, pp. 350-1, 357; and A. Thomson, 'Recent Researches on Oogenesis,' *Q. J. M.* xxvi. 1886, pp. 596-8. The accessory globule has been supposed to get rid of a female element in the developing spermatozoon and thus to be homologous with a

animal, which is then said to be monoecious or hermaphrodite; or it may be lodged in another animal of the same species, in that case said to be dioecious or of separate sexes. In hermaphrodite animals the testis may ripen at a different time to the ovary, a phenomenon known as successive hermaphroditism, and in most instances certainly a safeguard against self-impregnation, e. g. in the hermaphrodite *Gastropoda*. Some hermaphrodites, however, are self-impregnating, such as *Cestoda*, some *Trematoda*. The Nematode genus *Angiostomum* is a unique example of an organism, which though anatomically a female, is yet a self-impregnating hermaphrodite. The actual process of impregnation is, briefly stated, first the penetration of the spermatozoon into the ovum, either through its envelope at any spot, or by a special aperture, the micropyle, secondly the fusion of the protoplasm of the two cells, which is perhaps an unessential feature, followed thirdly by fusion of the nuclei, often termed the male (spermatozoal) and female (ovular) pronuclei. The two pronuclei approach each other, and the granules of the surrounding protoplasm are arranged round each of them, so as to form a star or aster with a pronucleus as a centre. This aster is most pronounced on the aspects of the pronuclei turned to one another. The ovum has now become an oosperm, and it speedily undergoes fission or segmentation and gastrulation.

What is generally considered, but perhaps wrongly, to be the most primitive mode of segmentation is seen in an oosperm, which is alecithal, i. e. devoid, or nearly so, of food-yolk. The nucleus divides with mitosis, and a constriction splits the oosperm into two equal or sub-equal halves or blastomeres. Each half then divides again into two, and so on. The two first divisions take place in a vertical plane, the third in a horizontal, the fourth in a vertical, and the fifth in a horizontal, and then regularity is lost. In many instances, however, a regular sequence of stages is not recognisable. The result of segmentation is the formation of a hollow sphere, the blastula or blastosphere, the cells or blastomeres being disposed in a single layer round a central cavity filled with an albuminous liquid, the blastocoele or segmentation cavity. In many instances the blastocoele is absent, or nearly so, and the term morula is then used instead

polar globule. Such a value can hardly be assigned to the various forms of blastophores, nucleated and non-nucleated, seen in spermatogenesis. The male cell is incapable of further development, i. e. of parthenogenesis in animals where it is highly specialised; so, too, in the higher plants, but in certain of the lower male parthenogenesis appears to occur, see Vines, 'Physiology of Plants,' p. 674; cf. Weismann, 'Continuität des Keimplasma's,' Jena, 1885, cap. ii. p. 70, on the significance of polar bodies, and cap. iii. p. 88, on the essential character of parthenogenesis; Id. Nature, xxxiv. 1887, p. 607.

of blastosphere<sup>1</sup>. The cells of the blastosphere are frequently (p always) dissimilar at opposite poles, one set typically smaller and more clear, the other larger and more granular. The latter undergo invagination or *embolé*, that is to say they sink inwards, obliterating more or less completely the blastocoele. The result is an invaginate, or embolic Gastrula, an ovate or spherical body composed of a double layer of cells, an outer epiblast (=ectoderm), an inner hypoblast (=endoderm), separated or not by a space, the remnant of the blastocoele, and continuous at the blastopore or Gastrula mouth. The central cavity into which the blastopore leads is the archenteron<sup>2</sup>.

Instances of typical or equal segmentation are met with in most groups of multicellular animals, but the process is commonly modified by the accumulation of food-yolk; the blastocoele may be absent or only slightly indicated, and transformation into a Gastrula is sometimes carried out by an invagination, sometimes by a modified form of invagination known as overgrowth or *epibolé*, that is to say the epiblast grows round the hypoblast or yolk. The food-yolk may accumulate at one extremity of the oosperm, or in its centre; to these two types the terms telolecithal and centrolecithal are respectively applied. A telolecithal ovum may segment completely but unequally, the hypoblastic cells being larger and dividing more slowly, or its segmentation is partial and confined to a disc at one pole, a large amount of yolk remaining unsegmented; nuclei appear in it, however, at the pole of segmentation, a certain amount of protoplasm becomes segregated round them, and cells are thus added to the blastoderm or segmented area. The extremes are connected by transitional forms. Centrolecithal ova are confined to *Arthropoda*. The central aggregation of the yolk may be present from the first, or take place during segmentation. The yolk is in the latter case always massed at the central ends of the blastomeres, which may or may not fuse, whilst in the former case the furrows between the blastomeres are superficial, i. e. do not penetrate to the centre of the oosperm. The central mass of yolk thus left either does not segment at all or does so at a late period, and the masses to which it gives origin are non-nucleate. The blastomeres may be equal or unequal, their formation may be simultaneous or successive, and is very often preceded by a multiplication of

<sup>1</sup> The term 'morula' is also applied to solid masses of cells produced by segmentation and not yet definitively arranged in Gastrula-fashion.

<sup>2</sup> The blastocoele is sometimes open by one or more pores to the exterior, e. g. in the amphiblastula of *Sycon* (*Sycandra*). It would have been better if the term blastopore had been restricted by usage to such openings, and some such term as 'gastropore' applied to the Gastrula mouth.



nuclei. Indeed in *Peripatus* cells are never distinctly delimited, the result being a syncytium<sup>1</sup>. The Gastrula is derived either by invagination or by differentiation of the yolk-cells.

In some *Coelenterata* the Gastrula stage is attained either by immigration of cells from one or various points of the blastosphere into the blastocoele, with subsequent differentiation of the immigrant cells, by delamination of the inner ends of the blastospherical cells, or by a mixture of the two processes. See p. 746, note 1, pp. 752, 764, 800. The variations observable in closely allied genera, make it probable that the phenomena *as observed* in these cases are of secondary origin, due perhaps to a precocious formation of the endoderm. The name 'parenchymula' or 'parenchymella' has been applied to the form where the central cavity is filled with cells.

There can be no doubt that segmentation and gastrulation, processes which take place in every life-history or ontogeny, represent ancestral stages in the evolution or phylogeny of multicellular animals. But at the present time there is no such thing known as a sphere or blastosphere leading an independent life and reproducing its kind, its component cells united by a bond indissoluble without entailing death on each cell. The same statement is true of the Morula and of the Gastrula. The claims of the *Mesozoa* to represent a Gastrula are excessively doubtful; those of Haeckel's *Gastreae*, at present inadmissible. See pp. 817-8.

Putting the *Mesozoa* aside, the vast majority of multicellular animals may be classified as *Metazoa*. The growth of the individual is complicated by the formation of tissues and systems of organs. Sensory and nervous tissue, contractile tissue, supporting or connective tissue, localised reproductive tissue, are differentiated in connection either with the epiblast s. ectoderm, and hyoblast s. endoderm of the Gastrula, or in part independently of them. Two main divisions of *Metazoa* are recognisable, the *Coelenterata* and *Coelomata*.

The typical characters of the *Coelenterata* are as follows. The fundamental symmetry of the Gastrula is as a rule retained; the vertical axis passing through the blastopore persists; if an anterior and posterior extremity are distinguishable they are equal; and the same is true of a right and left side. The blastopore may close, or not be developed; the archenteron, except in *Porifera*, opens by a single principal aperture, which is either a perforation of the two embryonic layers, or a distinct involution of the epiblast known as stomodaeum, which may assume a

<sup>1</sup> This may be a very primitive condition; cf. Sedgwick, Q. J. M. xxvii. 1886, pp. 515-30.

digestive function (*Ctenophora*). There appears between the ectoderm and endoderm a gelatinous lamella—the mesoglaea, which may be structureless, partly fibrillate, or invaded by cells derived from one of the two epithelia. Sensory and nervous cells are epithelial or sub-epithelial; the same is true of the contractile cells, which may, however, become imbedded in the mesoglaea. The generative products are sub-epithelial and localised. But a differentiation of the mesoglaeal cells may occur, principally in *Porifera*. Reproduction by division of the organism is rare; by buds or outgrowths of the ecto- and endoderm jointly, common; by the division of a single mesoglaeal cell, or the growth of mesoglaeal cells plus endoderm cells confined to *Porifera*. See pp. 713-6; 804.

The typical characters of the *Coelomata* contrast with those of the *Coelenterata* as follows. The fundamental symmetry of the Gastrula and the vertical axis passing through the blastopore do not persist. As a rule equal right and left sides are distinguishable; but the anterior and posterior parts of the body, if the permanent mouth, as is most natural, is taken as a point of reference, are not equal, the former being relatively small, and constituting a more or less distinct head. The archenteron, the mesenteron of the adult, communicates with the exterior by a mouth, and as a rule by an anus. The blastopore may become obliterated in its centre, and its two ends may coincide with the position of the future mouth and anus as in *Peripatus*; it may close from behind forwards, or *vice versa*, and then the mouth or anus correspond respectively to the part left open; it may close and leave no trace; or it may never be found at all as in *Insecta*. The permanent mouth and anus of the adult are generally, perhaps always, formed by a more or less pronounced ingrowth of ectoderm, either at the open part of the blastopore, or independent of it. In the latter case it is a question how far the ingrowth coincides with the obliterated part of the blastopore, or the spot where it might be expected to be. To the oral and anal ingrowths, the terms stomodaeum and proctodaeum are applied. Instead of a mesoglaea, there is a cellular mesoblast or mesoderm. Its cells in all cases lie or come to lie between the epi- and hypoblast. They are formed at an early period in the ontogeny, and as a matter of fact are derived in several ways the mutual connection of which is disputed. They may have a single or a double source. As to the former, the cells arise (1) as immigrants (mesenchyme cells), from the walls of the blastosphere, or from its endodermal pole as in *Nemertea*; (2) from the walls of the archenteron close to the blastopore, e. g. many *Crustacea*; (3) from cells specialised at an early period at the blastopore,

e. g. the pole-cells of *Chaetopoda* ; (4) from the primitive streak behind the blastopore in *Peripatus*, the same streak in *Insecta* or Spiders, which may be partial or complete homologues of the streak in *Peripatus*<sup>1</sup> ; (5) from the walls of diverticula of the archenteron or enterocoelic pouches as in *Balanoglossus*, *Sagitta* and *Brachiopoda*. When it has a double source it may be (1), *supra*, combined with enterocoelic pouches as in *Echinodermata*, or with pole-cells as in *Thalassema* ; (3) *supra*, combined with enterocoelic pouches as in *Amphioxus* ; (2) or (4), *supra*, combined with cells derived from the hypoblast as in most *Vertebrata*. Whatever significance these facts may have, the mesoblast gives rise to the muscular, connective and skeletal, blood and lymph tissues, and very generally to the genital and excretory cells. In *Vertebrata*, *Cephalochorda*, *Arthropoda*, some *Vermes*, e. g. *Chaetopoda*, it is broken up into a series of paired segments, sometimes, as in many *Crustacea*, obscurely marked, giving rise in the adult to a metamerism or serial segmentation, the primitive origin of which is a matter of doubt. In connection with the mesoblast or its segments is the cavity, or series of cavities, known as body cavities or coelome, which are not homologous throughout the *Coelomata*. In some *Vermes* a coelome is absent, or represented by irregular spaces or gaps in the mesoblastic tissues, as in *Turbellaria*, *Trematoda*, and *Cestoda*, but in other *Coelomata* it is probable that it falls under one of the following heads. (1) It is an *archicoele*, or remnant of the blastocoele as in the vascular system of *Nemertea*, the head cavities of some segmented *Vermes*, e. g. *Polygordius*, some *Chaetopoda*, the body cavity of *Rotifera*, and *Dinophilus*(?). (2) It is a system of channels and spaces excavated in the mesoblast *secondarily*, e. g. the principal portions of the coelome, or the vascular spaces in *Peripatus*, and perhaps in *Mollusca*, or the whole of it in *Arthropoda* in general. To this type the name *metacoele* might be applied<sup>2</sup>. (3) It is an *enterocoele*, i. e. the persistent cavity of diverticula of the archenteron (*supra*), as in *Amphioxus*, *Balanoglossus*, *Sagitta*, *Brachiopoda*, and *Echinodermata*. There remain the coelomic cavities of *Vertebrata*, the isolated nephridial pouches and genital ducts of *Peripatus*, the series of cavities in segmented *Vermes*, the pericardium, nephridial, and perhaps genital cavities of *Mollusca*. In these instances they are now usually regarded as *entero-*

<sup>1</sup> See on the primitive streak, Sedgwick, Q. J. M. xxiv. p. 79, and xxvii. p. 530; Haddon, Introduction to the Study of Embryology, 1887, p. 41 ; and the various references given in the Index vol. ii. of Balfour's Comparative Embryology.

<sup>2</sup> Sedgwick uses the term pseudocoele, but it would apply equally well to an archicoele, or to a schizocoele, if there is such a thing, supposing his definition of a coelome to be accepted (Q. J. M. xxvii. p. 533).

*coeles* abbreviated in development, a view which has most probability so far as the *Vertebrata* are concerned, and if a distinctive name is applied to them, *crypt-enterocoele* might be suggested; or they may be simply *splits* in the mesoblast, not derived from enterocoeles, and the well-known term *schizocoele* may be retained for them. Whatever value is attached to the coelome, the result of its presence is in most instances a division of the mesoblast into two portions, one applied to the body-wall, the other to the mesenteron, for which when the separation takes place in the embryo, the names somato- and splanchno-pleure are used. It remains only to state that the epiblast gives origin in the adult to the epi- or hypo-dermis, to exo-skeletal structures, to glands, to organs of special sense and the nervous system, to the stomo- and procto-daeum and organs derived from them; the hypoblast to the intestinal or mesenteric epithelium, to the epithelia of glands or other outgrowths derived from the mesenteron, such as the lungs, thyroid, thymus, and the notochord of the *Chordata*. Reproduction by fission, or by gemmation in which the three layers are always (?) implicated, is not common; but the power of reproducing lost parts is met with in *Coelomata* as high in the scale as *Lacertilia*<sup>1</sup>.

The connection between the *Coelenterata* and *Coelomata* is probably only that of descent from a common form of ancestor, unless it be supposed that the larval Coelomates with enterocoelic diverticula have sprung from Gastrulae common to them and the *Anthozoa*.

The classes of *Coelenterata* as they now exist are specialised; it is possible that two phyla may be indicated, one which has given origin to the *Porifera*, the other to the three remaining classes. Among the *Coelomata* are found groups, the relations of which are absolutely uncertain, e.g. *Brachiopoda*, *Polyzoa*. Certain phyla, or lines of common descent, may be indicated in other cases with confidence. These are (1) the *Chordata* with which *Balanoglossus* and *Cephalodiscus* are allied, if they are not actually to be considered as Chordates; and (2) the *Echinodermata*, both of which are related to ancestors with enterocoelic pouches; (3) the *Mollusca*, descended from a trochosphere-ancestor common to them and most Vermes; (4) the *Arthropoda*, segmented animals which

<sup>1</sup> For views on the various points touched on in the foregoing account, see Sedgwick, 'On the origin of Metameric segmentation,' &c., Q. J. M. xxiv. 1884; Id. 'The Development of the Cape Species of *Peripatus*,' op. cit. xxvii. 1886, pp. 515-40; Caldwell, 'Blastopore, Mesoderm, Metameric Segmentation,' Q. J. M. xxv. 1885; Hubrecht, 'The relation of the *Nemertea* to the *Vertebrata*,' Q. J. M. xxvii. 1886. On the Mesoblast see also, Kleinenberg, 'Die Entstehung des Annelids aus der Larve der *Lopadorhynchus*,' Z. W. Z. xlv. 1886; Hubrecht, on *Lineus*, Q. J. M. xxvi. 1886; Salensky, on *Pilidium*, Z. W. Z. xliii. 1886; Metschnikoff, on the wandering cells of Asterids and Echinids, Z. W. Z. xlii. 1885, p. 656.

probably have two separate lines of descent, one including *Arachnida* and *Crustacea*, with an ancestor represented possibly by a *Nauplius*-form; the other *Insecta*, and *Myriapoda* with *Peripatus*, the latter indicating perhaps an ancestry related to the segmented *Vermes*. There remain (5) the majority of *Vermes*, an assemblage of apparently very diverse forms; the remarks on pp. 583-4, and the enumeration of classes, pp. 585-6, may suggest possible connections.

The task of unravelling the phylogeny of the subdivisions of *Metazoa* is one beset with extreme difficulty. The records of Geology have established such points as the pedigree of the Horse, the derivation of Birds from extinct Reptilians; they show the extreme antiquity of some living types, e.g. Insectans, Scorpions, Elasmobranchs in Silurian strata, the great prevalence in ages past of forms now extinct or almost extinct, their replacement in other instances by derived types. Other phenomena speak to vast changes: the present geographical distribution of many terrestrial and aquatic animals; mimicry, migration, social habits; the degeneration which has so evidently befallen certain types, due to a sedentary mode of existence, to minute size, to adaptation for a parasitic life, i.e. one dependent on the living tissues or vital processes of another animal or plant for sustained nurture, whether it be external or internal, ecto- or endoparasitism; Alternation of Generations, first discovered by Chamisso in *Salpa*, and by Steenstrup in Hydroids, Trematodes, &c., whether in the form known as metagenesis, i.e. the alternation of asexual and sexual individuals, or as heterogamy, i.e. the alternation of parthenogenetic and sexual races, or in one instance (*Angiostomum*) of an hermaphrodite and self-impregnating individual with bisexual individuals; the occurrence of prolonged metamorphoses, such as are seen in many *Arthropoda*, and the shortened metamorphoses of the early ontogeny of most animals; the degradation of an individual into an organ—a rare occurrence—exemplified in the avicularia and vibracula of *Polyzoa*, or the converse phenomenon of parts of an individual becoming elevated into the semblance of a number of individuals, the most probable interpretation to be put on the strobila of *Cestoda*. Nor has natural selection left untouched the record written on the pages of the life-history of any animal; it has falsified it in various ways at every stage—the ovum, its segmentation, the embryo. Special embryonic organs may attain a great prominence; normal embryonic phases may be slurred over, or perhaps extinguished. It is often hard to say what is ancestral, what acquired, to distinguish between structures which may be inherited or independently evolved.

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## DESCRIPTIONS OF PREPARATIONS.

### I. COMMON RAT (*Mus decumanus*),

Dissected so as to show its craniospinal nervous axis in its entire length as well as portions of most of the organs of vegetative life.

A RED injection has been thrown into the veins ; and the left halves of the walls of the craniospinal, thoracic, abdominal, and pelvic cavities, as well as the greater part of the integument in the facial region and the greater part of the left lung, have been removed so as to show *in situ* the organs previously concealed by these structures.

Of the encephalic nerve-centres we see most anteriorly the olfactory lobes : next to them the cerebral, separated from each other by the longitudinal fissure in which is lodged the longitudinal sinus : next the cerebellum bounded off anteriorly from the posterior border of the cerebral lobes by the diverging lateral sinuses, into which the longitudinal sinus divides. The presence of the lateral sinuses prevents us from seeing the corpora quadrigemina which would otherwise be visible in the middle line, owing to the divergence there from each other of the cerebral lobes. The medulla oblongata, which is, like the cerebellum, of considerable width, comes into view between the two occipital condyles, from which point down to the second dorsal vertebra, recognizable by its long spine carrying an ossicle articulated to its apex, the medulla spinalis is of much greater thickness than it attains posteriorly. It is seen in the lumbar region to break up into the cauda equina.

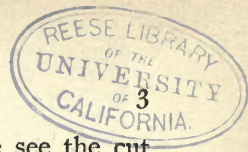
In the dorsal region, a black bristle has been passed under the aorta where it underlies the bodies of the vertebrae, and this position relatively to the craniospinal canal superiorly, as also to the digestive tract next inferiorly, and the heart most inferiorly, is held by the aorta in all vertebrata. The singleness of the aortic trunk in the adult state is characteristic of all warm-blooded animals ; but mammals, as is seen here, differ from birds in having the single trunk arching from the heart over the left and not over the right lung's root. Behind and to the right of this black bristle from before backwards are to be seen, firstly, the fourth lobe of the right lung in its pleural cavity resting on the diaphragm below, and in relation above with the heart, and on the left with the phrenic nerve ; secondly, the oesophagus, a lowly vascular tube the small calibre of which is correlated with the working of the dental apparatus in these creatures ; thirdly, the third

lobe of the right lung placed far back and to the right, and, like the lungs of all mammals, freely suspended in its pleural cavity and bearing no impressions on its exterior from the different bony constituents of the thoracic cavity ; fourthly, the vena azygos of the left side between the aorta and the vertebral column, passing up to arch over the root of the left lung, and join the vena cava descendens of that side ; and fifthly, the spinal cord. The complete diaphragm, forming a dome-shaped floor, with the heart and lungs in relation with its convex, and the liver, stomach, spleen, and kidney in relation with its concave surface, is eminently characteristic of Mammalia, that of the Crocodylina alone approaching this grade of development. The upper part of the pericardial sac has been removed, and the two ventricles (less distinctly separated from each other than in many mammals) and the left auricle are brought into view. The anterior surface of the heart is more equally shared in by the two ventricles than is the case in many mammals, in which the right ventricle forms nearly the entire anterior aspect of the organ. The left vena cava descendens, a trunk which is found in most Rodents, except the Guinea Pig and Agouti, is seen to pass in front of the root of the left lung in company with the phrenic nerve round to the back of the heart to end in the right auricle. The vena azygos of the left side is seen to join it just above the root of the left lung, and at a point some way above this, the vein from the fore-leg, which is in relation with the nerves going to that limb, is seen passing up to join another vein, which, from its being placed superficially to the sternomastoid muscle, we know to be the homologue of the external jugular of anthropotomy. The external jugular is the main trunk by which the blood from the interior of the skull returns to the heart in the Rodents and many of the lower Mammalia, and by its confluence with the vein from the anterior limb the vena cava descendens is constituted. Internally to the external jugular, just above its confluence with the subclavian vein, is seen a part of the hibernating gland ; externally to it lies the submaxillary ; above this again we see the parotid with its duct ; and above the parotid, the facial portion of the lacrymal gland sending up a duct, under which a piece of blue paper is placed, to enter the orbit and join there with the duct of a second portion of the lacrymal gland, which is placed within the orbit, and anteriorly to the duct of the extra-orbitally-placed portion. Within the orbit we see the Harderian gland in relation with the third eyelid<sup>1</sup>.

<sup>1</sup> For a fuller description of these glands, see Description of Plate I, which represents a dissection somewhat different from that which we have of these organs in this preparation. The lacrymal gland is somewhat similarly bilobed in the human subject, consisting of a palpebral and an orbital part. See Hirschfeld et Leveillé, *Neurologie*, 1853, Pl. 76, fig. 4. In man however there are between twelve and fourteen minute lacrymal ducts instead of a single one as here. But the macroscopic Harderian gland and duct of the Rodentia and mammals lower than Primates except the Chiroptera do not similarly represent the minute Meibomian glands with separate ducts on the free edge of the eyelids ; for both sets of glands coexist in Rodentia.



COMMON RAT.



In the middle line of the body inferiorly to the heart we see the cut surfaces of the six sternal bones, and in the angle intercepted between the lowermost of these and the diaphragm, we see some lobules of fatty tissue set in the process of serous membrane which connects the apex of the pericardium with the sternal bones and with the diaphragm. From these structures a vein passes back along the pericardium to end in the vena cava descendens of the left side.

In the angle between the inferior surface of the diaphragm and the lumbar muscles, the two psoas muscles and the quadratus lumborum of the left side, we see the smooth-surfaced kidney, which by this external character, as also by the internal one, of the separation of its cortical or secretory from its medullary or excretory parts, characterizes the class Mammalia. The spleen is in relation with it on the right; to the right of the spleen we have the left end of the stomach, which is less vascular and glandular than the pyloric half, here concealed and overlapped by the left lobe of the liver. From the inferior or convex margin of the stomach the curtain-like *omentum*, a process of peritoneum found, thus developed, only in mammals, hangs down over the left cornu of the uterus, which is distended with embryos, and over portions of the intestines. Immediately below the kidney and the spleen, the left ovary and Fallopian tube and the upper end of the left cornu uteri are situated. A fibrous band, under which a black bristle is placed, and which is the remnant of the ligament by which the Wolffian body in the foetus was kept in relation with the diaphragm, attaches the ovary and tube to the peritoneal covering of that muscle. Below the upper end of the left cornu uteri is seen the caecum, which is of less size and complexity than that of Rodents with rootless molars and less varied and nutritious food than these omnivorous members of the order, or than that of those, such as the Squirrels, which live on seeds and have, like most *Muridae*, rooted molars. It tapers off superiorly into the large intestine, which however in many Rodents is not, when compared with the small intestine, as much inferior in length and larger in calibre and thicker in its walls as its name and the homology of anthropotomy might lead us to expect. Below the caecum we see the cut ends of the veins from the hind-limb, and lower still we see a bristle passed underneath the ureter as it passes forwards to enter the base of the conically contracted bladder. The vagina, rectum, and bladder have, each of them, separate and independent outlets; into those from the two latter organs black bristles have been passed. The flat nail on the rudimentary thumb; the presence of tactile vibrissae above the eyes as well as upon the snout; and of hairs of great coarseness along the mesial dorsal region; the absence of hair from a small area, bifid, as usual in Rodents, in which are the orifices of the nostrils, and which is called the 'muffle;' and its presence between the annulate scales on the tail; are points worthy of notice.

For the relations held by the cerebrum and cerebellum to each other and to the tentorium, see Turner, Proceedings Royal Society of Edinburgh, March 3, 1862.

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For the histology of the Hibernating Gland, see Hirzel and Frey, *Z. W. Z.* xii. 1862. For that of the Harderian, in Mammals, see Wendt's Monograph, *Die Hardersche Drüse*, 1877; and in Birds, see MacLeod, *Bulletin Acad. Royale Sci. Belgique*, 1879, pp. 797-810.

For a figure and account of the *ligamentum diaphragmaticum* in the foetal state, see Kölliker's *Entwicklungsgeschichte*, p. 961, Fig. 587, 1879; and *Tr. Z. S.* vol. v. p. 286, 1863.

For an account of the perforation of the clitoris by the urethra in the Cape Mole, see Hunterian Catalogue of the Physiological Series contained in the Royal College of Surgeons, vol. iv. p. 2745; for a similar arrangement in *Talpa* and *Stenops* and *Lemur*, see *loc. cit.* 2810, 2811, 2812.

For the use of the word 'muffle,' see Waterhouse's *Nat. Hist. Mammalia*, vol. i. p. 50; vol. ii. pp. 7, 8; Sundevall's *Linne's Pecora*, Germ. Transl. 1848, pp. 41-43.

## 2. SKELETON OF COMMON RAT (*Mus decumanus*).

THE skeletons of many of the lower Mammalia bear a general resemblance to those of certain quadrupeds lower in the scale of life in such points as the nearness of the level at which their trunk is carried by their limbs to that of the ground on which they move; and in the maintenance by the long axis of their head, of much the same direction as that of the long axis of their entire trunk. But they invariably present the following distinctive characters, which are as peculiar to the Mammalian class as any of the points furnished by the soft parts, such as the blood-cells, the hairy integument, or the mammary glands. In every Mammalian skeleton each half of the lower jaw is made up of a single mandibular bone on each side, which at birth at least, if not, as it is here, throughout life, is distinct from its fellow of the opposite side, and articulates by a convex facet with the squamosal element of the cranial wall; and the vertebrae in the trunk always differ from those of the different lower Vertebrata in one or more or all of the following points: either in the ankylosis of their several elements, or in the size of their neural canal, or in the shape of the articular ends of their centra, or in the means whereby in the recent state these articular ends are brought into relation with each other. In the vertebra of a young mammal the neural arch may not have ankylosed with its centrum; but in all such cases two discoid epiphyses belonging to the articular ends of the centrum would also remain unankylosed, as they fuse

with it at a later period than the neural arch, and they furnish a mark as distinctive of the Mammalian class as any other connected with the vertebrae. Some mammals have an opisthocoelian ball and socket articulation between the centre of their vertebrae; and the crocodiles resemble the mammals in having interarticular fibrocartilaginous discs to connect their ball and socket centre-joints instead of synovial joints; but in such cases the greater size of the neural canal or the absence of neurocentral sutures, or the absence of sutures between the body and the lateral processes, would enable us, without having recourse to a microscopic examination of the bony tissue, to identify a vertebra as having belonged to a mammal. In all mammals, except the Cetacea, the maximum number of phalanges in any one digit is limited to three; in nearly all, the number of cervical vertebrae is neither more nor less than seven; and the number of the lumbar vertebrae is never less than two. There are very rarely any vertebrae with unanchylosed ribs anteriorly to the first dorsal vertebrae. The jaws are ordinarily dentigerous, but teeth are never found elsewhere than upon the mandibular, maxillary, and intermaxillary bones; the grinding teeth very frequently have more than a single root or fang, a method of implantation never observed in any other class.

The most distinctive character of the Rodent order is the possession of the pairs of scalpriform incisors in the upper and lower jaws, from which their name is taken. There is a single pair of incisors in the upper jaw in all Rodents, except the *Leporidae*, which are hence called '*Duplicidentati*,' as having two pairs placed one behind the other, the hinder pair being the smaller. In the lower jaw there is a single pair only in all living Rodents, without exception. The upper incisors form a larger segment of a smaller circle, the lower a smaller segment of a larger circle. The peculiarities of their growth, which goes on uninterruptedly during the life of the creature from a persistent pulp, and of their functions, entail changes of great importance in the conformation both of the skull and of particular bones. The intermaxillaries, in relation with which the upper incisors are first developed, and which form a great part of their permanent sockets, are larger in relation to the rest of the skull and of the animal than in perhaps any other mammals;—they form the whole, or nearly the whole, of the sides and under surface of the bony snout, and in all living Rodents, as in the Elephants, they interpose between the nasals and the maxillaries, whilst failing themselves to reach the lacrymals. The maxillary bone gives origin on the concave surface of its malar process to a large part of the masseter muscle, but a more deeply placed part of the muscle passes behind or inside of that process and takes origin from the sides of the snout. The presence of this deep head to the masseter is peculiar to but by no means constant in Rodents, varying with the infra- or ant-orbitally placed canal through which it passes. It co-operates, by passing round the back of the malar

process of the maxillary as round a pulley to an insertion just below the socket of the mandibular premolar, very strongly with the temporal muscle in moving the lower jaw in a vertical direction, and bringing its incisors into play upon those of the upper jaw ; whence probably the inverse ratio which has been observed to obtain between the temporal and the antorbital fossae is to be accounted for. The masseter muscle arises from nearly the whole length of the malar arch, which is made up ordinarily of the malar process of the maxillary, of the malar bone, and of the malar process of the squamosal, and sometimes of the lacrymal also. It is by the contraction of those of its fibres which pass backwards on to the posterior edge of the lower jaw, aided by that of the pterygoids, that the anteroposterior movement of the lower jaw with its molar series upon that of the upper jaw is effected. The glenoid cavity has, to allow of this movement, its long axis running anteroposteriorly as in all Rodents except *Leporidae*, and as in the *Mesotheriidae* ; whilst the unbroken molar series and the absence of canines are characteristic of the entire order without any exception. Some involution of the angle of the lower jaw, which resembles that observable in the Marsupialia, and the considerable size of this portion of the bone are points worthy of note as being present in many Rodents. Though the malar arch has a downward, rather than, as in Carnivora, an outward curve, still the interzygomatic diameter is in all Rodents the widest transverse cranial diameter. The temporal is never separated from the orbital fossa ; the cranial cavity is always much compressed from side to side on a level with the optic foramina, so as frequently to leave an interorbital fenestra by the fusion of the two foramina into one, at a point a little behind that at which the olfactory chamber succeeds the cerebral internally.

The length of the tail and the number of the caudal vertebrae vary much within the limits of this order, just as the external concha of the ear and the characters of the integumentary system do. But, in spite of the very various special habits of the animals belonging to this order, the two pairs of limbs almost invariably present the same ratio of development *inter se*, the hind limbs being the stronger and longer pair. The tibia and fibula are ankylosed here and in *Leporidae*, but not in *Sciuromorphi* nor *Hystri-comorphi*. There is, however, little tendency to ankylosis in the skeleton of the Rodents ; in this specimen the posterior pair of sacral vertebrae are not ankylosed with the anterior, with which the ilia articulate, and the mandibular bones never throughout the order ankylose, as they do in Proboscidae, Suidae, and Perissodactyla, at the symphysis, in spite of the great afflux of blood which their permanently growing incisors bring into them. In the trunk we observe that the spines of the dorsal vertebrae, from the largely developed spine of the second dorsal to that of the tenth inclusively, point backwards, whilst those of the six lumbar vertebrae and of the two last, the thirteenth and the twelfth, dorsal, point forward towards

the vertical spine of the eleventh dorsal, which has been called in consequence the 'anticlinal' vertebra. The anterior dorsal vertebrae diminish progressively in size as they are placed nearer to this vertebra, whilst the vertebrae placed posteriorly to it, and markedly the transverse processes of the lumbar vertebrae, increase in size as we pass backwards from it towards the sacrum. Well-marked and distinct anapophyses and metapophyses are developed on the anticlinal vertebra, and are to be seen on the succeeding vertebrae nearly or quite up to the sacrum. The direction of its spine relatively to those of the other vertebrae in front of and behind it, causes it to be the point of greatest mobility in the trunk. Points of less striking proportions, but more or less distinctive of, and universal in, the order are presented in the skull by the presence of an interparietal bone; by a vacuity in the skull walls for the blood to pass out from the lateral sinus, either as here by a conjugate foramen between the squamosal and the periotic, or by a foramen in the squamosal itself, the so-called 'canalis temporalis'; by the development of the post-auditory process of the squamosal into a lamina of bone, which may reach as far back as the occipital, but serves always to keep the tympano-periotic, with which it never anchyloses, in place; and, finally, by the smallness of the angle formed by a line drawn from the posterior edge of the supraoccipital on to the basicranial line. The depth of the symphysis pubis, and the oblique forward direction of the transverse processes in the lumbar region, are points probably correlated functionally with the strength of the hind limbs. The large size of the abdominal relatively to the thoracic cavity may be connected with the multiparous character of the order generally. The spine of the second dorsal vertebra has a small ossicle articulated to its apex, and pointing forward, much as in the long-necked grazing mammals the ligamentum nuchae is placed along the dorsal and cervical regions. The two first cervical vertebrae are, as is usual in mammals, much the largest in the series, and they contrast, as in all placental mammals, with the other cervical and also with all the other moveable vertebrae, in having, when adult, the centre of the first fused with that of the second, and in being connected with each other and the skull by cartilages and synovial membranes without fibro-cartilaginous discs. The first rib has its head articulated to the bodies, and its tubercle to the transverse processes of both the last cervical and the first dorsal vertebra. There are two lateral episternal bones between the first of the six sternal bones, the so-called 'manubrium,' and the clavicle, one on each side, but there is no central cervical prolongation of the sternum as in *Lepus*.

In the carpus there is the same number of bones as in that of man, for though the scaphoid and lunar are fused into one bone, the scapho-lunar, as they are also in Carnivora and Chiroptera, a bone, the *os centrale*, exists between it and the *os trapezium*, *os trapezoides*, and *os magnum* in the second row of carpals, which is not represented by a distinct bone in the

human carpus, nor in those of Ungulata, Cetacea, Chiroptera, Edentata, Marsupialia, and Monotremata, but only in those of Rodentia, Insectivora, and Simiadae exclusively of the Chimpanzees. As in all mammals, though in no amphibian a single bone, the os unciforme, supports the two outer metacarpals. In this enumeration the ulnar sesamoid bone, or 'os pisiforme,' is not reckoned as a carpal bone, nor any bone of similar function in connection with the tendons on the volar side of the hand.

In Rodentia we find two more bones in the tarsus than in the human subject, the os scaphoides being double, and an accessory bone present on the inner side of the inner os cuneiforme.

For general anatomy, Krause, *Die Anatomie des Kaninchens*, Leipzig, 2nd ed., 1884; and T. J. Parker, *Zootomy*, London, 1884, p. 301.

For an account of the position of the anticlinal vertebra in the order Rodentia and elsewhere, see Giebel, *Beiträge zur Osteologie der Nägethiere*, 1857, p. 35, or *Abhandl., Nat. Verein für Sachsen und Thüringen*, i. p. 223, *ibique citata*; or *Die Säugethiere*, 2nd ed. 1859, p. 6.

For the general characteristics of Mammalian vertebrae, see Professor Owen, *Descriptive Catalogue of the Osteological Series of the Royal College of Surgeons*, vol. i. pp. 7, 8, 1853.

For the nomenclature of the several elements of a vertebra, *ibid.* p. xlv.

For the Pro-atlas of Amniota, see Albrecht. *Z. A.* iii. 1880; and *Bull. Mus. Roy. d'Hist. Nat. Belg.* ii. 1883.

For the Osteology of the Rodentia, see Cuvier's *Ossemens Fossiles*, 2nd ed., 1823, vol. v. pt. i. pp. 4, 14, 44. Waterhouse, *Mag. Nat. Hist., N. S.*, vol. iii. 1839, A. N. H. 1841, 1842, takes the conformation of the lower jaw and of the anterior portion of the zygomatic arch as furnishing a basis for classifying the order in the three sections, *Murina*, *Hystricina*, and *Leporina*. In Johnston's *Physical Atlas*, 1856, *ad Pl.* 28, he divides the order into four families, *Muridae*, *Sciuridae*, *Hystricidae*, and *Leporidae*. See H. N. Turner, *P. Z. S.* 1848, p. 63. J. F. Brandt, *Untersuchungen über d. craniologisch. Entwicklungstufen der Nager d. Jetztzeit*, *Mémoires de l'Académie Imp. des Sciences de Saint Pétersbourg*, ser. vi. tom. vii. pp. 127-336, 1855, laying weight (p. 141) on the form and general contour of the brain-case, the characters of the base of the cranium, the direction of the pterygoid processes, the conformation of the palate with the *foramina incisiva*, and of the *ossa lacrymalia*, divides the order Rodents *s. Glires* into four suborders, *Myomorphi*, *Sciuromorphi*, *Hystricomorphi*, and *Lagomorphi*. For later views, see E. R. Alston, *P. Z. S.* 1875, 1876, and *infra*, pp. 43-45.

For the resemblances between the skeleton of the Rodents and that of the Elephant, see Cuvier, *l. c.* i. pp. 10-12.

For the differences between the skeleton of the Rodents and that of the Aye Aye, *Chiromys madagascariensis*, see De Blainville, *Ostéographie*, Fasc. iii. 1841; Professor Owen, *Tr. Z. S. v.* 1863, pp. 79-83; Professor Peters, *Berlin Abhandl.* for 1865, pp. 89-92.

For the microscopic characters of the teeth of the Rodents, and their classificatory value, see J. Tomes, *Ph. Tr.* 1850, pp. 553-561, and C. S. Tomes, *Manual of Dental Anatomy*, pp. 332 and 339. For the resemblance of the

microscopic character of the molar enamel of all Rodents (except *Leporidae* and *Hystricidae*) to that of the Proboscideans, see Trans. Odont. Soc. vol. iii. p. 239, 1871.

For the classificatory value of the ossicula auditus, see A. Doran, Tr. L. S. 1878, p. 418.

For other characters of the order Rodentia, see Waterhouse, Natural History of the Mammalia, vol. ii. pp. 1-9, 1848; De Quatrefages, Considérations sur les caractères zoologiques des Rongeurs, Paris, 1840; Milne-Edwards, Recherches sur les Mammifères, i. 1868, pp. 29, 30.

For those of the *Myomorphi*, see Osteological Catalogue, Royal College of Surgeons, vol. ii. Preparations 2223-2245; Waterhouse, Mag. Nat. Hist., *l. c.* p. 92; Brandt, *l. c.* pp. 152, 156, 300; Peters, Monatsber. Ak. Berlin, 1867.

For the Carpus and Tarsus and Shoulder-girdle, see Gegenbaur's Untersuchungen zur Vergleichenden Anatomie, Hft. i. ii. 1864, 1865; for the shoulder-girdle and sternum, see also Götte, A. M. A. xiv. 1877; Ruge, M. J. vi. 1880; Hoffman, Niederländ. Archiv für Zool. v. 1879-82. For the carpus, see Leboucq, Arch. de Biol. v. 1884; carpus and tarsus, Baur, Z. A. viii. 1885.

For the 'Canalis Temporalis,' or 'Foramen jugulare spurium,' see Otto, Nova Acta, xiii. pt. i. p. 27; Luschka, Dk. Wien. Akad. xx. 1862, p. 204; and Kölliker, Entwicklungsgeschichte, p. 929, 1879.

For the means whereby the vertebral centra are articulated in the different classes of vertebrata, see Rathke, Entwicklungsgeschichte der Wirbelthiere, mit einem Vorwort von A. Kölliker, 1861, p. 130.

### 3. SKELETON OF WILD RABBIT (*Lepus cuniculus*, var. *fera*).

THE skeleton of the Rabbit differs from that of the Rat and many though not all other *Glires Myomorphi*, not merely in such points as its larger absolute size, the incompleteness<sup>1</sup> of its clavicles, the absence save in rudiment of a hallux, the unguiculate character of its pollex, the number and rootlessness of its molars, and the smaller number of its caudal vertebrae, but in many points of greater morphological importance than any of these. Some of these latter points show that the suborder *Lagomorphi* is more closely allied than the *Myomorphi* to certain lower forms of Vertebrata; others indicate more clearly than is seen in the *Myomorphi* that a certain affinity exists between the Rodentia *s.* Glires and the large Ungu-

<sup>1</sup> The older zoologists (e. g. Fischer, Synopsis Mammalium, 1829, pp. 286, 366; Catalogue of the Royal College of Surgeons, Part iii. 1831, pp. 79, 87) divided the order into the two sections of *Glires clavicularis completis, saepe validissimis*, and *Glires clavicularis nullis aut imperfectis*. The inadequacy of this basis of classification may be judged of by the fact that the tail-less Hares (*Lagomyes*), which form a subfamily, as shown by Pallas, Glires, p. 28, closely allied to the true Hares, have complete clavicles. In the Rabbit no trace of the clavicle is visible at birth (see Parker, Shoulder-Girdle, Pl. xxv. Figs. 1, 2, pp. 207-210; Flower, Osteology of Mammalia, p. 229), though it becomes developed before adult life. In the human subject, on the other hand, the clavicle ossifies before any other bone in the developing foetus.

late Mammalia; whilst others may have their connecting character expressed by saying that the distinctive peculiarities of the Rodent type are not so sharply pronounced in this as in the other suborder already mentioned, or indeed in either of the two other suborders of Glires, the *Hystricomorphi* and the *Sciuromorphi*.

Among the last of these three sets of peculiarities may be mentioned the shape of the articular surface furnished by the squamous bone for the lower jaw. This surface is transversely, not, as usually in Rodents, antero-posteriorly elongated; and it permits consequently of a much greater lateral movement of the jaw, correlated with which we find the molars above and below not with horizontal but with concave and alternately sloping grinding surfaces. The presence of six incisors in the upper jaw of young, and of four in that of adult *Lagomorphi*, is a third, the smaller size of the sockets for the lower incisors a fourth, point indicating less specialization in this suborder.

In the relatively small extent to which the temporal muscle is developed, in the great extent to which the lower jaw is developed behind the plane of its articular process, in the presence of a diastema between the anterior scalpriform teeth and the molar series, and in the keel-shaped praesternum prolonged into the cervical region as a 'proosteon,' the *Lagomorphi* and most if not all other Rodents resemble many Ungulata, both Artiodactyle (such as *Sus*) and Perissodactyle (*Equus* and *Tapirus*). In the reduction of the independence and importance of the fibula the *Lagomorphi* and the *Myomorphi* resemble each other and many or most Ungulata, and differ from all other Rodents, with some apparent exceptions, e. g. *Pteromys* and *Castor*. In the length and slenderness of a process given off by the squamosal posteriorly to the articular surface furnished by it to the lower jaw, which process not being ankylosed, as in many other mammals, to the tympano-periotic, nevertheless clamps it into fixed relations with the other skull-bones adjacent to it, the skulls of the *Lagomorphi* and many other Glires resemble those of some Perissodactyle Ungulata, whilst the presence of a third femoral condyle, and of an internal alisphenoid canal for the external carotid artery, are points in which they strikingly resemble all living Perissodactyla. On the other hand, a curious illustration of the combination in these Rodents of peculiarities which become separated in other divisions of the class Mammalia is furnished to us by the ischium of the *Lagomorphi*, which closely resembles the ischium both of the Ruminant and non-Ruminant Artiodactyles in what is considered to be a distinctive peculiarity of at least the latter of these two divisions of animals, viz. in the presence on the outer side of the bone a little way in front of its upper and posterior angle of a well-marked outstanding forwardly-curving process of bone. The exposure in the dry skull of the turbinated bones in the nasal cavity by the deficient ossification of the lateral walls of that chamber is



another point on which weight may be laid as connecting the *Lagomorphi* with some at least of the true Ruminants, e.g. *Capra* and *Cervus*.

As points of degradation in the *Lagomorphi* as compared with higher mammals we may note in the Rabbit and Hare the absence or great retardation of any anchylosis to each other of the basicranial bones, the sutures between the basioccipital and basisphenoid and between the basisphenoid and presphenoid remaining open not only when the occipital and interparietal bones are fused, but even after these bones have become abundantly fenestrated by senile absorption<sup>1</sup>; the vertical and transverse perforations in the basisphenoid communicating with the pituitary fossa; the small antero-posterior length of the palatal plates of the palatine and maxillary bones leaving the stalked leaf-shaped end of the vomer exposed behind them, and the anterior end of the same bone exposed in front of them, when the dry skull is looked at along its base-line; the development of the 'foramina incisiva' into wide fissures continuous with the latter of the two sets of vacuities just spoken of; the persistence of open fontanelles in the occipital bone, in the interspace between that bone, the squamous, and the tympano-periotic, in the space, that is, which corresponds to the 'asterion' of Professor Broca, and in the interspace between the two last-named bones below the backwardly-running bar of the squamous; and probably also the singular fenestration or vacuolation of the anterior and upper part of the maxillaries. To these points, dependent upon a deficiency of ossification, may be added the involution of the angle of the lower jaw, which represents, though but rudimentarily, the inversion of that part of the jaw in the Marsupials; and the fusion of the optic foramina into a single mesial foramen bounded inferiorly by the presphenoid much as in Birds.

Other points worthy of note in the Rabbit's skeleton, either as compared with those of most Rodents of other suborders, or as compared with those of other mammals, are presented to us in the imperfect differentiation of the coronoid from the ascending ramus of the lower jaw; in the approach to horizontality in the symphysis of that bone; in the large size and backward direction of the tympanic process of the tympano-periotic; in the small size of the infra-orbital canal and of the anterior part of the malar process of the maxillary, and the large size of the free backwardly-projecting process of the malar bone proper; in the presence of large supra-orbital processes attached in the middle and projecting freely at either end of their length; in the fixed attachment of the upper lamellae of the ethmoid to

<sup>1</sup> The persistence of patency in the sutures of the *basis cranii* appears to possess considerable morphological value, but this cannot be said of the sutures of the roof of the skull. For example, the interparietal anchyloses very early in the Subungulate *Hystricomorphi*, but it does the like also in *Sciurus*, whilst it remains distinct for a long while in *Myoxus*, *Castor*, and the *Murini*, as well as in the *Lagomorphi*.

the nasal, constituting 'naso-turbinal' bones; the loose often lost attachment of the much convoluted inferior turbinals to the maxillaries<sup>1</sup>; in the formation by the posteriorly expanded vomer of a floor to the true olfactory portion and of a roof to the lower narial or respiratory portion of the nasal cavity; in the wide interval between the pterygoids and the tympanic bulla, and in the presence in this last bone of a *canalis caroticus*. The pitted appearance of the interparietal bone, of the upper part of the occipital bone in apposition or fused with the interparietal, and of the upper arch of the first cervical vertebra, is worthy of note as suggesting a comparison with *Lophiomys*, and with the rugose<sup>2</sup> zygomatic and frontal bones in the Paca (*Coelogenys paca*). In aged specimens this pitting almost amounts to fenestration. The anchylosed tibia and fibula are specially noteworthy.

The imperfection of the clavicles in the Rabbit and Hare prepares us for their entire absence as reported to exist in some few of the Subungulate *Hystricomorphi*, and contrasts with their complete development in some families of the same suborder (*Chinchilloides*, *Spalacopodoides*), as also in the entire suborders *Myomorphi* less *Lophiomys*, and *Sciuromorphi*, and even in the subgenus of the suborder *Lagomorphi* represented by the tail-less Hares, *Lagomys*. The presence of a backwardly and downwardly projecting process of the acromion is similarly a peculiarity observable in the *Lagomorphi* and certain *Hystricomorphi*, whilst it is absent in many Rodents, though present in other orders of Mammalia, and notably in the Elephant.

The non-development of fangs confers the same privilege of perpetual growth on the molars of the *Lagomorphi*, the true Cavies, and the Chinchillas, which is enjoyed by the incisors of all Rodents. The white colour and the shortness of the incisors again are points of similarity between the Hares and the Cavies. The number of molar teeth is greater in the Hare and Rabbit than in any other Rodents, being  $\frac{6}{2}$  as against  $\frac{5}{2}$  in the allied subfamily *Lagomys*, against  $\frac{4}{2}$  in *Hystricomorphi* and *Sciuromorphi*,  $\frac{3}{2}$  in *Myomorphi*, and  $\frac{2}{2}$  in *Hydromys*. The vacuity in the lower jaw, posteriorly to the socket for the last molar tooth, and the vertical upgrowths from the tubercles of the second to the eighth pair of ribs, are peculiarities in the skeleton of the *Lagomorphi*.

In the ossa ilii the glutæal surfaces are much more extensive than the iliac, a line drawn forwards from the tubercle for the short head of the

<sup>1</sup> The maxillo-turbinals are more complexly and finely convoluted in the Rabbit than in the Hare, the subterranean habits of the former of these animals creating a greater need for warming the inspired air. Similarly, as remarked by Professor Flower (*Osteology of Mammalia*, p. 183, second edition, 1876), in the Elephant, where the inspired air is sufficiently warmed by having to pass along the elongated proboscis, the maxillo-turbinals are wholly aborted.

<sup>2</sup> See Flower *Osteology*, p. 156; and Waterhouse, *History of Mammalia*, ii. p. 369, who suggests that periodical deposition analogous to that of the horns of deer causes this. Compare the strange account of *Lepores cornuti* given by Schreber, *Säugethiere*, i. Taf. cclxxxiii. B; Pallas, *Novae species Glirium*, p. 14, *ibique citata*.

rectus just above the acetabulum along a faintly-marked and rounded ridge represents the acetabular border of other Rodents, such as the Beaver, and shows the limit of the respective surfaces. The incisura acetabuli through which the blood-vessels and nerves enter for the supply of the hip-joint is reduced in size, and the rim of the acetabulum is interrupted only by a linear fissure. The symphysis of the pubis is deep.

The skull of the tame Rabbit differs from that of the wild in having the roof of its brain-containing portion much flatter as measured either from before backwards or from side to side than is the case in the very distinctly arched calvaria of the wild variety. The lateral boundaries of the same cavity as constituted by the squamous are much more wall-sided than in the wild race, and instead of curving gradually into a vaulted vertex they are defined or delimited off from it by largely-developed anteroposteriorly running ridges. The height of the occipital foramen is less relatively to its breadth, its upper and lower borders not being emarginated into secondary curves as in the wild variety. The length of the entire skull is considerably greater relatively to its breadth, though not relatively to the size of the entire body. This may be double that of a wild specimen, whilst the absolute breadth of the skull may be identical in the two subjects of comparison, and the absolute length may be less than 30 per cent. greater in the tame than in the wild variety.

The lines and processes of the cranium and lower jaw are less sharply defined and sculptured than in the wild variety, and the surface of the cranial bones generally is inferior in gloss and polish. The same applies to the bones of the trunk and limbs in many domestic animals as compared with animals of the same species in a wild state, and indeed is usually more clearly appreciable than in the case of the two varieties here compared with each other.

For the possession of rootless molars by other Rodents (*Octodon*, *Capromys*, most *Arvicolae*); for that of molars with short roots or with roots incomplete or late to be developed, by the Agouti, by the Paca s. Spotted Cavy, by the Beaver and the Porcupine; for that of rooted molars by the true Mice and the Squirrels, see Owen, *Odontography*, p. 401; and by Leporidae in their milk dentition, see Hilgendorf, *Monatsber. Ak. Wiss., Berlin*, 1876, p. 673.

For the presence in *Leporidae* of a perfect investment instead of, as in all other living Rodents, merely an anteriorly placed plate of enamel on the incisors, see Hilgendorf, *l.c.* But preparations made by Mr. C. S. Tomes suggest that this perfect investment exists only in the enamel membrane of the developing tooth.

For numerous other points of similarity between the Hares and the Cavies, see Waterhouse, *History of the Mammalia*, ii. p. 156, 208; Buffon, *cit.* Pallas, *l.c.* p. 29.

For the Shoulder-Girdle of the Rodents, see Parker, *Shoulder-Girdle*, 1868, pp. 207-210; and for the mesial prolongation of the praesternum in *Lepus* and

*Cavia* into the cervical region, see Plates xxiv and xxv; and for the same prolongation in Ungulata, see Pl. xxix. *l. c.*

For a detailed comparison of the osteological differences between tame and wild Rabbits, see Darwin, History of Plants and Animals under Domestication, i. pp. 120-136, 2nd ed. 1875.

#### 4. CERVICAL, DORSAL, LUMBAR, SACRAL, AND CAUDAL VERTEBRAE OF RABBIT (*Lepus cuniculus*).

GREAT mobility is secured by the particular arrangements observable in the region where the two upper cervical vertebrae articulate with each other and with the skull, and in the region of the lower dorsal and upper lumbar vertebrae. On the other hand, the transverse processes of the lower cervical vertebrae and the imbricated neural spines of the upper dorsal vertebrae prevent the possibility of any great range of movement between any two of the constituent segments of those portions of the spinal column.

The cervical vertebrae are seven in number, as almost invariably in the Mammalian class; the numbers of the dorsal and lumbar series are variable, but twelve and seven, the numbers of the dorsal and lumbar vertebrae respectively in the Rabbit, are very common numbers for those series throughout the class. The number of the caudal vertebrae is the most variable, that of the lumbar next, that of the dorsal less than that of the lumbar, that of the cervical the least variable of these four sets of vertebrae. As the number of the cervical vertebrae is all but invariable, the variability of the length of the cervical region depends upon variations in the length of the bodies of the seven vertebrae. The first cervical vertebra or 'atlas' is the widest from side to side of all the neck vertebrae; it has a low but broad neural arch, and superadded to it in front a smaller arch which is in the perfect condition of the parts made into a ring for the reception of the 'odontoid process' of the next vertebra by a transverse ligament. Its neural arch is overhung by the spine of that vertebra, and it does not give any point of attachment to the *ligamentum nuchae*. It contains two more or less separated canals for segments of the vertebral artery; one of them pierces the base of its broad 'transverse process' from behind forwards, the other turns more or less horizontally from without, inwards, behind and below the articular processes. This latter canal may be represented merely by a groove in the Rat, and ordinarily has this imperfect character in the human subject. The former has generally a short horizontal canal leading forward from it and opening on the anterior surface of the transverse process; it is however absent in the *Leporidae*, though present in the Rat and many or most other Rodents. The second cervical or 'axis' vertebra has its spine greatly developed, both anteroposteriorly and vertically, giving attachment by it both to the muscles which move, and the

elastic *ligamentum nuchae* which supports, the head. It has no anterior articulating processes upon its neural arch in mammals, but it comes into articular relation with the atlas by means of two oblique zygapophysial surfaces developed on either side of the base and a third on the front of its odontoid process, which is the backwardly displaced and anchylosed centrum of that vertebra. It is the deepest from above downwards, and the longest from before backwards, but also the narrowest from side to side of the cervical series. The first two cervical vertebrae articulate with each other and with the occiput by means of synovial joints as the neurapophysial processes are articulated to each other throughout the rest of the trunk, where however the centra are connected by interarticular fibrocartilaginous discs containing in their central pulp remnants of the primitive chorda dorsalis. The neural spines of the third and fourth cervical vertebrae are low but long, corresponding with the long neural roof which these two vertebrae possess; the spines of the shorter neural arches of the fifth, sixth, and seventh vertebrae have more of the shape which their name implies. The lateral processes or 'cervical ribs' of these vertebrae are greatly developed; those of the atlas more or less obliquely outwards, those of the axis backwards; those of the third, fourth, fifth, and sixth, both anteriorly and posteriorly, and those of the seventh outwardly. The fourth, fifth, sixth, and seventh have prominent upgrowths developed on this process or rib which are homologous apparently with the prominent tubercles of the ribs of these creatures, or, possibly, with the metapophyses of the trunk vertebrae. This process makes up by itself almost the whole of the transverse process of the seventh cervical vertebra, the inferior, antero-posteriorly-produced, process, which is much larger in the preceding vertebrae and largest of all in the one immediately preceding, being lost in this, the last of the series. These inferior elements of the transverse processes, by bending inwards form with the vertebral bodies furrows, in which the long anterior neck muscles are lodged, a central slightly-raised line marking the line of separation of these muscles and representing the homologously-placed hypapophyses of certain lower vertebrata. The segment of bone which completes the ring of the atlas anteriorly is homologous with these hypapophysial downgrowths. The last cervical vertebra in the Rabbit has not, as it has in the Rat, any connection with the tubercle of the first dorsal rib.

Eight of the dorsal vertebrae, from the second to the ninth inclusively, have, each, two half facets on their centra, the first has one whole facet anteriorly and a half facet posteriorly, and the tenth, eleventh, and twelfth have, each of them, single whole facets placed on the anterior superior angle of the lateral aspect of their centra, for articulation with the heads of the ribs. The neural spines of the dorsal vertebrae are largely developed, their apices from the second to the ninth showing a tendency to become bifid antero-posteriorly. The tenth is the anticlinal vertebra (for which, see p. 8, *supra*),

and upon it and upon each succeeding vertebra down to the sacrum a large, as upon the ninth and eighth dorsal vertebra a small, metapophysis is developed. A small anapophysis is also seen to take origin from the base of its neural arch, and to be possessed by each succeeding vertebra up to the antepenultimate lumbar. Several of the anterior, as also of the posterior dorsal vertebrae, have low hypapophysial ridges developed subcentrally; and longer ones possessing the character of spines are developed on the three anterior lumbar vertebrae, in relation in the living animal with the crura of the diaphragm. The Hedgehog, *Erinaceus europaeus*, and the Mole, *Talpa europea*, have paired unanchylosed ossicles developed intervertebrally in the same region, like caudal chevron-bones. The lumbar vertebrae as wholes, and also most of their processes, increase in size from before backwards as far as the penultimate one; the transverse processes point obliquely forward, but form a more open angle with the long axis of the column than they do in the Rat. Behind the lumbar vertebrae we have, though not invariably, four vertebrae united to each other by anchylosis of their centra, their transverse, and their articular processes; and united to a fifth vertebra by anchylosis of the lateral processes. These five vertebrae may be taken as corresponding to the *os sacrum* of anthropotomy. The two most anteriorly placed of these five vertebrae form by their transverse processes a pouched-shaped or auricular articular surface for the ilium, the posteriorly placed convex end of which is constituted by the transverse process of the second and the two sides by that of the first. In the Beaver the second vertebra contributes a relatively much smaller proportion to this articular surface, and in the Rat and many other Rodents it scarcely contributes anything. The third and fourth of these post-lumbar vertebrae do not in any Rodent furnish any articular surface to the ilium.

The four or five anterior caudal vertebrae have largely developed subquadrate transverse processes, with their free angles, both anterior and posterior, somewhat produced. From eight to ten more rudimentary vertebrae follow upon these, the most posteriorly placed being merely bars of bone, with dilated ends corresponding to the articular aspects of the centra of other vertebrae. The caudal vertebrae of the Rabbit have no chevron-bones as have those of the the long-tailed Rodents, and of many other such animals from the Ichthyosauri to the Primates, with the exception of the Ungulata and the Proboscidea, which are allied in so many other points to Rodents.

5. UPPER HALF OF RABBIT (*Lepus cuniculus*),

Dissected so as to show some of the muscles of the head, neck, shoulder, and fore-leg<sup>1</sup>. The letters and the description correspond with those on the figure annexed.

With Figure 1.

THE skin has been removed from the front of the lower jaw backwards, the sheet of cutaneous muscle, *x*, covering the region of the neck and known in anthropotomy as the *panniculus carnosus* or *platysma myoides*, has been entirely removed on the right side, as also from the region of the thorax on both sides; the incomplete clavicle with the muscles in connection with it has been separated from its ligamentous union with the sternum and displaced to the right so as to show the subjacent nerves, phrenic and brachial, on the same side; below the level of the clavicle, portions of the *pectoral*, *c*, *d*, and the *sterno-clavicular* muscles, *g*, have been dissected and turned back. On the left side, the anterior part of the *panniculus carnosus* has been left with its two fixed insertions, *x* and *x'*, into the lower jaw, and the other, *x'''*, into the sternum, intact; the clavicle is left *in situ*, but the muscles passing down to it from the head have been cut away behind the line of the cutaneous muscle to show the *sterno-scapular* muscles, *h* and *i*, in connection with the clavicle, at *j*; and the *serratus magnus*, *o*. The deep cervical fascia ( $\beta$ ) is seen to the left of the middle line of the upper half of the neck and of the intermandibular space, at a lower level than the *panniculus carnosus*. It has been removed anteriorly to show the insertion of the *digastric* muscle. On a level with the hyoid the deep cervical fascia is raised into a convexity (*a'*) by the submaxillary gland underlying it, and it furnishes, externally and posteriorly to this area, a capsule to the parotid. This gland, however, being less convex than the submaxillary, does not cause the sheet of fascia to bulge upwards. On the opposite side this fascia has been removed in the intermandibular space; and the submaxillary gland being raised from its bed is seen to send a duct in towards the mouth in an interspace between the *internal pterygoid* and *digastric* muscles. This latter muscle is in the Rabbit, as in many other mammals, monogastric, its posterior belly being represented by a tendon, which however pierces the *stylo-hyoid* just as in man. Its muscular portion is inserted into the lower jaw on either side of the symphysis, and from the same portion of the jaw a *depressor*, *w*, of the lip passes forward. On the

<sup>1</sup> It is for various reasons advisable that the student should proceed to the preparations illustrating the splanchnology of the Rabbit before addressing himself to this somewhat complex dissection. And it will be found advantageous to immerse the upper half of the body of the animal, the heart and lungs having been removed, in spirit 10° over proof (sp. gr.° 910) for three or four days before following out the detailed anatomy of the muscles here described and figured. For making special dissections of the nerves it will be found useful to acidulate the spirit with dilute nitric acid in the proportion of one part in forty. This treatment facilitates the mechanical process of dissection in several ways, and makes it less easy to overlook the more delicate structures concerned.

outer side of each of these *depressor* muscles the *panniculus carnosus*,  $x$ ,  $x'$ ,  $x''$ , takes a fixed insertion by a band of muscular fibres, which on the right side are cut short, and on the left are seen to be continuous with the rest of the muscle. In the interval between this strip of muscle and another which passes from the *platysma* to distribute itself in the region of the mouth, the *buccinator* muscle,  $y$ , comes into view. The lobes of a somewhat variable buccal gland have been removed to show these three muscles in this region.

The tendon of the *stylo-hyoid* forms an oblique angle with its muscular belly,  $s$ , being connected with the greater cornu of the hyoid, along which it passes to be attached to the body of the bone,  $t$ . To the muscular part of the *stylo-hyoid* two nerves, from the portio dura of the seventh pair with which the glosso-pharyngeal portion of the eighth pair of cranial nerves is connected, may be seen in dissection under a lens, though not in this figure, to distribute themselves. A semilunar space has been formed in the right axilla, between  $\delta$  and  $\gamma$ , by separating the *latissimus dorsi*,  $\gamma$ , as it narrows up to its insertion on the inner side of the humerus, from the similarly narrowing *panniculus carnosus*,  $\delta$ , of the regions of the flanks and back, the '*dermo-humérien*' of Cuvier (Anat. Comp. iii. p. 597), the '*costo-alaris*' of Humphry (Observations in Myology, p. 131), which passes in front of it to be inserted into the humerus together with the tendon of the *pectoralis major*. The insertion of the homologous muscle in Birds is shown in the figure of the Dissection of the Pigeon in the shape of a tendinous slip attached to the tendon of the great depressor pectoral muscle,  $x$ . From the tendon of the *latissimus dorsi* of the left side a slip of muscle,  $\epsilon$ , the '*latissimo-condyloideus*' of Bischoff<sup>1</sup>, the '*dorso-épitrochlien*' of Duvernoy (Archiv. du Muséum, viii. p. 80), is seen to take origin and pass down at right angles to that tendon to an insertion on the inner side of the olecranic process of the ulna. On either side and behind the *latissimo-condyloideus* are to be seen the three heads of the *triceps*, with which muscle the *latissimo-condyloideus* is frequently fused. Externally and anteriorly is seen the *biceps*,  $\theta$ , here, like the similarly misnamed digastric, but a monogastric muscle. From its anterior surface, one band of fascia passes off to connect itself with the fascia enveloping the muscles of the fore-arm, another leaves the tendon of the muscle at a lower level and connects itself with the radius and the tendon of the *pronator radii teres*, thereby setting up a secondary connection with the *radius* with which it is principally connected in man, whilst its principal insertion is made into a well-marked depression just above the inner and inferior edge of the olecranic process of the ulna by a broad and flat tendon. The

<sup>1</sup> Bischoff gave this muscle the convenient name of *latissimo-condyloideus*, and was followed by Dr. H. C. Chapman, in his Memoir on the Structure of the Gorilla, Proc. Acad. Sci. Philadelphia, 1878.



muscular bellies of the *pronator* and the *flexor* muscles arising from the ulna and internal condyle of the humerus have been cut through and reflected to show this insertion of the *biceps*.

This dissection contrasts with a similar dissection of the human subject in the imperfection of the clavicles; in the absence or rudimentary condition of the *omo-hyoid*; in the presence in the neck of two additional muscles, the *acromio-basilar*, *n*, and the *cleido-occipital*, *m*; in the formation of a compound 'cephalo-humeral' muscle, as in many other mammalia, by the physiological combination of the *cleido-mastoid*, *k*, the *cleido-occipital*, *m*, and the *acromio-basilar*, *n*, with the *deltoid*, *f*; in the prolongation of the *sterno-clavicular*, *g*, and *sterno-scapular* muscles, *h* and *i*, the homologues of the *subclavius*, on to the spine of the scapula at *j*, whence they act in the way of slinging up the horizontally-carried trunk; and, finally, in the greater size of the cervical *platysma*, *x*, and the development of a cutaneous muscle,  $\delta$ , the '*dermohumérien*,' *s*, '*costoalaris*,' *s*, '*brachiolateral*,' in the regions of the back and flanks. The *cleido-occipital*, *k*, the *acromio-basilar*, *n*, and the '*latissimo-condyloideus*,'  $\epsilon$ , are more or less frequently represented by muscular varieties occurring in the human subject, and the absence of any *scalenus anticus* in the Rabbit is paralleled in man by the occasional perforation of the fibres of that muscle by the upper factors of the brachial plexus, one of which, the fifth cervical, has been observed to pass entirely in front of the muscle. The *digastric*, *u*, the *biceps*, *l*, and the *pectoralis minor*, *e*, present points of difference, stated above, in which the *Leporidae* and very many other mammals coincide with each other and differ from man. The *rectus abdominis* is very usually prolonged in mammalia lower than man up to the second or first rib, and in the rabbit up even to the base of the manubrium; when thus prolonged, it is known as the '*rectus thoracis*.' It is frequently crossed at its upper end, as here, by a muscle known as the '*sterno-costalis*,' passing downwards and covering the front of the *rectus* just as the *external oblique* does that of the *rectus abdominis*. It may be better however to speak of the *sterno-costalis* as being a lateral efflorescence of the *rectus*<sup>1</sup>.

On the other hand, the arrangement and relations of the various structures of the lowly organised mammal here figured are sufficiently similar to those of man to cast considerable light upon some even of the more intricate points of anthropotomy. Among them we may specify the occurrence of certain varieties in muscles, the relations of the deep cervical fascia,  $\beta$ , and the insertions of the *pectoral* muscle, *c* and *d*.

<sup>1</sup> For a discussion of the homologies of the *rectus thoracis* and the *sterno-costalis*, see Professor Turner, *Journal of Anat. and Physiol.* May, 1867, pp. 247-253; May, 1868, pp. 392-394; Wood, *Ph. Tr.* for 1870, pp. 110-112, vol. 160. These two muscles are not lettered in this figure, but are seen to form a triangle with part of the first rib for its base and with its apex covered by the *sterno-clavicular* muscle *g*. For a figure showing the *rectus abdominis* giving off a part of the *pectoral*, see Ecker, *Anatomie des Frosches*, 1864, p. 95.

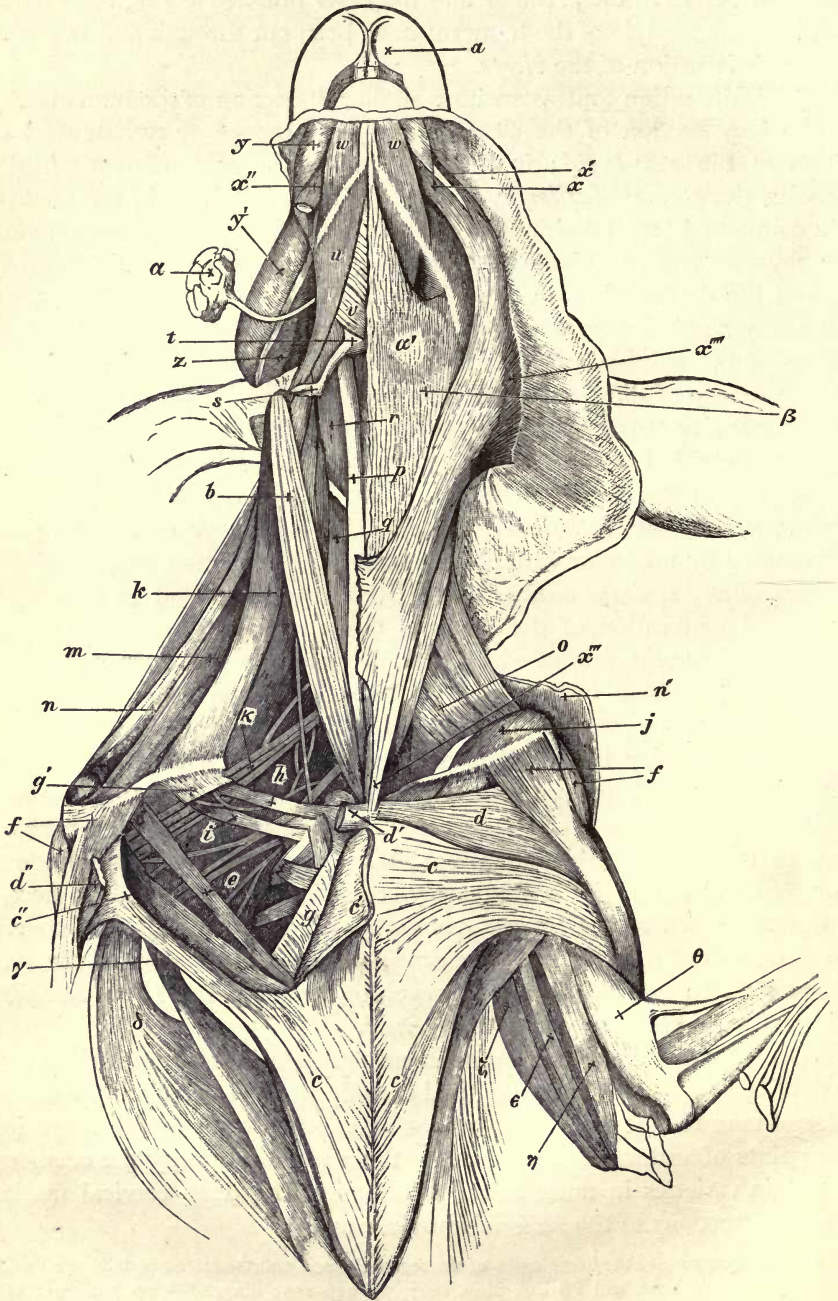


FIG. 1.—DISSECTION OF SUPERFICIAL MUSCLES IN ANTERIOR REGIONS OF HEAD, NECK, AND THORAX IN RABBIT (*Lepus cuniculus*); NEARLY NATURAL SIZE.

- a.* Bifid upper lip concealing muffle. See p. 26, *y'*, *infra*.
- b.* Sterno-mastoid muscle, arising from the prolongation of the manubrium into the neck and inserted into the mastoid.
- c.* Greater pectoral muscle of left side, arising along nearly the entire length of the sternum from the manubrium anteriorly down nearly to the leaf-shaped cartilage ending it posteriorly.
- c'*. Part of the origin of this muscle on the right side reflected.
- c''.* Pouch-like insertion of it into the humerus, the fibres from the lower part of the sternum forming the posterior, those from the upper the anterior portion of the pouch; the former passing to the inner; the latter to the outer tuberosity of the humerus, and the outwardly-looking pectoro-deltoid ridge.
- d.* Smaller pectoral muscle arising from the outer side of the keel-shaped manubrium superficially to the upper fibres of the greater pectoral, inserted together with fibres of that muscle and of the clavicular portion of the deltoid into the fascia covering the biceps, and reaching by tendon nearly to the lower end of the humerus at *d''*.
- d'*. Tendon of origin of smaller pectoral of right side cut short.
- d''.* Tendon of insertion of smaller pectoral of same side.
- e.* Third pectoral muscle, corresponding to the *pectoralis minor* of anthropotomy, as being similarly innervated, but inserted not into the coracoid, but into the head of the humerus, and only by a few fibres into the costo-coracoid membrane.
- f.* Deltoid, a bicipital muscle, its anterior head, supplied by the circumflex nerve, arising from the outer end of the clavicle and the fibrous tissues external to that insertion covering the shoulder-joint, and the posterior head arising from the apex of the acromion and the anterior edge of the metacromial process of the scapula. The external tuberosity of the humerus appears in the interval between the two muscular bellies.
- g.* Origin of sterno-clavicular muscle, from the sternum down to the level of the sixth rib, from the cartilage of which it receives some fibres, at a deeper level than that of the origins of the three pectorals, but superficially to the plane of the rectus thoracis and of the sterno-costal muscle, which are seen between the origin of the sterno-clavicular muscle and the plexus of brachial nerves to form, with the first rib, a triangle with its apex pointing downwards and inwards.
- g'*. Insertion of the sterno-clavicular muscle into the clavicle. The under fibres pass under the clavicle without being attached to it, to be inserted, together with fibres from the two muscles next to be named, into the spine of the scapula and the fascia covering the supraspinatus.
- h.* Upper sterno-scapular muscle, continuous at its origin from the manubrium sterni with the sterno-clavicular muscle, which may therefore be considered a prolongation of this muscle.
- i.* Lower sterno-scapular muscle, arising from cartilage of first rib, innervated from the same source as the two muscles, *g* and *h*, last mentioned, partially inserted like the sterno-clavicular, *g*, into the clavicle, but passing on with it and the upper sterno-scapular, *h*, to be inserted into the spine of the scapula and the fascia covering the infraspinatus muscle posteriorly.
- j.* Prolongation of the three muscles just named onwards on the left side from beneath the clavicle to the insertion just specified; the three next to be named, *k*, *m*, and *n*, having been removed to allow of this being seen.
- k.* Cleido-mastoid muscle, arising from occipital bone externally to sterno-mastoid, *b*, and inserted into the greater part of the length of the bony clavicle. It is the homologue of the cleido-mastoid portion of the human sterno-cleido-mastoid, holding the same relation to the cervical plexus. There is no sterno-maxillary as in the Horse, and in the Hyrax.
- m.* Cleido-occipital muscle, arising from the basioccipital just externally to the acromio-basilar, inserted into the outer end of the clavicle, and the head of the humerus, and becoming continuous between these two bony attachments with the fibres of the anterior portion of the deltoid.
- n.* Acromio-basilar muscle of right side, arising from the basi-occipital and inserted into the metacromial process of the scapula just anteriorly to the insertion of the anterior part of the trapezius. In most of the lower mammals this muscle arises from the atlas; in some from the axis also, thus coming to represent the upper digitations of the levator anguli scapulae in Primates. In Rodents and some Ungulata, 'by becoming amalgamated by longitudinal and lateral fusion with the *recti capitis* it may be attached to the lateral or basilar process of the occipital bone.' This is the muscle called 'levator claviculae' by Wood, pp. 88 and 94, 'acromio-basilar' by Vicq. d'Azyr, and 'acromio-trachélien' by Cuvier, in whose *Leçons d'Anatomie Comparée*, i. p. 271, ed. 2<sup>de</sup>, we find it thus spoken of: 'On le trouve dans tous les mammifères, l'homme excepté, ce

qui semblerait prouver qu'ils est une des conditions de la station quadrupède.' This would apply more correctly to the prolongation of the muscles, *g*, *h*, *i*, on to the scapula, as shown on the left side at *j*.

- n'*. Metacromial insertions of acromio-basilar and trapezius.
- o*. Anterior or cervical portion of serratus magnus of left side, exposed by the removal of the three last-named muscles. A muscular fascicle, which not rarely arises between the upper part of the origin, here seen, of the serratus and those of the scaleni, is not shown in this figure. It is a long and slender slip, and passes down vertically to join the thoracic portion of the serratus, and to be inserted with it into the posterior and inferior angles of the scapula, and appears, when compared with the omohyoid of the horse, to represent that muscle.
- p*. Sterno-hyoid muscle, arising from sternum and cartilage of first rib.
- q*. Sterno-thyroid, fused posteriorly with dorsal surface of preceding muscle.
- r*. Thyro-hyoid.
- s*. Stylo-hyoid, with its tendon running along the thyro-hyal portion of the hyoid arch at an oblique angle to its muscular belly. Within this angle lies the ninth nerve. The trunks and branches of the pneumogastric and sympathetic nerves, as also of the carotid artery, have been removed from the triangular space bounded by the sterno- and thyro-hyoids mesially, by the sternomastoid externally, and by the muscular part of the stylo-hyoid superiorly, and in the space thus bounded we see the upper part of the cleido-mastoid muscle, *m*, externally, and a part of the rectus capitis anticus major internally passing up to take origin in company with each other from the basi-occipital.
- t*. Body of hyoid bone; the longer cornu, or thyro-hyal, passes backwards in connection with the tendon of the stylo-hyoid, the anterior cornu and arch are concealed from view.
- u*. Digastric muscle, here represented by a single muscular belly, placed anteriorly and inserted into the symphysis of the lower jaw, and by a tendon taking origin from the paroccipital process and representing the posterior muscular belly of anthropotomy and the single muscular belly of the Carnivora.
- v*. Mylo-hyoid muscle.
- w*. Depressores labii inferioris.
- x*. Insertion of platysma myoides into lower jaw on left side below buccinator, anteriorly to masseter muscle.
- x'*. Fibres passing off from this cutaneous muscle to end in the moveable tissues round the mouth.
- x''*. Insertion of platysma myoides into lower jaw of right side cut short.
- x'''*. Insertion of platysma myoides into manubrium sterni.
- x''''*. Delamination of platysma myoides into two layers.
- y*. Buccinator muscle.
- y'*. Masseter muscle, with much less obliquity in its fibres than is usual in Rodents, as necessitated by the relations of the mandible and malar arch. It consists here of two strata as in the Horse, but has of course no antorbital factor as have so many Myomorphous and Hystricomorphous Rodents. It is bounded anteriorly by a stout tendinous band, which prevents the lower jaw to which it is affixed below from being separated beyond a certain distance from the jugal arch, to the freely projecting anterior angle of which it is affixed above. The mobile bifid lip compensates somewhat for this restriction on the opening of the jaws.
- z*. Internal pterygoid muscle.
- (*a*). Submaxillary gland and duct.
- (*a'*). Submaxillary gland of left side, covered by deep cervical fascia.
- (*β*). Deep cervical fascia, forming sheaths for the muscles and capsules for the glandular structures in this region. A circular bulging indicates the area where it is underlaid by the submaxillary gland.
- (*γ*). Latissimus dorsi of right side, passing beyond the tendons of the great pectoral and the 'dermo-humérien' cutaneous muscle to be inserted, together with the teres major, and underneath the tendon of the coracobrachialis, upon a well-marked facet below the inner tuberosity of the humerus.
- (*δ*). Tendon of 'dermo-humérien' muscle displaced outwards so as to leave a half-moon-shaped space between it and the tendon of the latissimus dorsi. The 'dermo-humérien' muscle joins the posterior part of the pectoralis major, *c*, and first gains a fixed attachment to the pectoro-deltoid ridge, and then, by arching over the biceps, to the inner tuberosity of the humerus.
- (*ε*). 'Latissimo-condyloideus' muscle, passing down from the tendon of the latissimus dorsi to be

inserted into the olecranic process of the ulna on a semilunar raised line a little way above its posterior angle. It here joins the triceps, to which in lower mammals it usually gives an additional head, only through fibrous expansions connecting it with the scapular head  $\zeta$ . See Nat. Hist. Rev. 1861, p. 512.

- ( $\zeta$ ). Scapular head of triceps, concealing external humeral head.
- ( $\eta$ ). Internal humeral head of triceps, exposed by removal of brachial vessels and nerves.
- ( $\theta$ ). Biceps flexor brachii, which gives off a band of fascia from the anterior surface of its muscular belly, passing on to the fascia enveloping the muscles of the fore-arm; which, secondly, gives off a narrow tendinous slip from its broad principal tendon, which connects itself with the radius and the tendon of the pronator radii teres; and which, thirdly, takes insertion by its broad principal tendon into a well-marked pit just above the inner and lower border of the ulna and below the anterior horn of its sigmoid articular surface. To show this insertion the pronator radii teres and the flexor muscles of the fore-arm have been divided and turned aside.
- ( $\kappa$ ). Brachial plexus, seen, in the absence of any fibres of the posterior belly of the omohyoid or of the anterior scalene muscle, to be crossed vertically by phrenic nerve, and to give nerve-supply to the sterno-scapular and sterno-clavicular muscles by a slender nerve arising by three roots; and to distribute other branches to the pectorals and shoulder and arm muscles. The phrenic nerve has one principal root in the neck above the level at which the formation of the brachial plexus begins; it is connected, however, very usually with the factors of this plexus by more than one nervous filament. The nerve passing to the sterno-scapular and sterno-clavicular muscles is the homologue of the nerve given to the subclavius in man. For this portion of the nervous system of the cervical region the figure and description given by Hirschfeld and Leveillé in their *Neurologie*, Pl. 40, Fig. 1, 1853, and reproduced in Quain's *Anatomy*, ed. 1882, i. p. 604, Fig. 338, may be compared. For other portions of the nerves of the cervical region, see Ludwig and Cyon, in Ludwig's *Arbeiten* for 1866, p. 148, or as reproduced in Cyon's *Atlas zur Methodik der Physiologischen Experimenten*, Taf. xvi. 1876, or with some modifications in *Handbook for Physiological Laboratory*, Pl. xciii, or in Foster's *Physiology*, 4th ed. 1883, p. 190 (ed. 3, p. 176). For the nerves in the upper part of the neck in the Rabbit, see Lovén, Ludwig's *Arbeiten*, l. c. Taf. i, and for the phrenic, Budge, *Physiologie*, 1862, p. 76. For the cervical region in the Dog, see Schmiedeberg, *ibid.* 1871, p. 56, reproduced *loc. cit.*

The literature of Comparative Myology is very extensive. Amongst the older memoirs upon this subject may be specified Douglas, *Myographiæ Comparatæ Specimen*, 1707, and the authorities cited by Otto in his *Compendium of Human and Comparative Pathological Anatomy*, translated by South, 1831, p. 245. Meckel, in 1828, devoted one volume of his *System der Vergleichenden Anatomie* to this subject. It also occupies a great part of the first volume of the second edition of Cuvier's *Leçons d'Anatomie Comparée*, published in 1835, and is treated of in certain special departments in the third and fourth volumes also. In the *Vergleichende Anatomie der Myxinoiden*, S. A. pp. 216-247, 1835, S. A. pp. 109-111, 1841, of Johannes Müller, valuable views as to the general homologies of muscles are to be found. Memoirs with similar scope but differing in results were written by Professor Goodsir in 1857-1858 (see *Anatom. Memoirs*, i. p. 451, 1856), and the subject has subsequently been treated as a whole, and also in many specialised memoirs, by Professor Humphry in successive issues of the *Cambridge and Edinburgh Journal of Anatomy and Physiology* (see his *Observations in Myology*, 1872, and especially pp. 105-188).

Cuvier's plates of the Myology of Mammals were published by M. Laurillard in 1849. The following memoirs may be mentioned as treating of the Comparative Myology of the Primates:—Ilg, *Anatomie der Sehnenrollen*, 1824; Burdach, *Beitrag zur Vergleichenden Anatomie der Affen*, 1838; Vrolik, *Recherches d'Anatomie Comparée sur le Chimpanzé*, 1841; Duvernoy, *Archives du Muséum d'Histoire Naturelle*, viii. 1855-1856; *Les Grands Singes pseudanthropomorphes*; Owen, P. Z. S. i. pp. 28-67; Church, *Nat. Hist. Rev.* 1861-1862, *Myology of Orang*;

Burt Wilder, Boston Journal of Natural History, vol. vii. 1862, Myology of Chimpanzee; Prof. Flower and Dr. Murie on the Dissection of a Bushman, Journál of Anat. and Physiol. vol. i. 1867, pp. 196-205; Pagenstecher, Mensch und Affe, Zoologische Garten, April, 1867; Bischoff, Anatomie des *Hylobates leuciscus*, S. A. 1870, pp. 7-70; Abhandl. k. Bayer. Akad. Wiss. Matth.-phys. Cl. Bd. x. Abth. 3, 1870, pp. 203-266; Champneys, Muscles and Nerves of a Chimpanzee, Journal of Anat. and Physiol. vol. vi. pp. 176-211.

Professor John Wood's papers in the Philosophical Transactions for 1869 on the Varieties of the Human Shoulder Muscles and their homologies in the Mammalia should be read in connection with the above description of those muscles in the Rabbit. Many other memoirs on Myology in its various aspects, morphological and physiological, have appeared in this country from the pens of Professors Turner, Haughton, Macalister, Mivart, and Drs. Murie, J. D. Cunningham, A. H. Young, and others in the Proceedings of the Zoological Society, the Journal of Anatomy and Physiology, and elsewhere; and abroad from those of Professors Gruber, Gegenbaur, Fürbringer, Rüdinger, and MM. J. C. G. Lücæ and Paul Albrecht. The muscles of the Rabbit are treated of in Professor Krause's monograph, Die Anatomie des Kaninchens, pp. 136-138, ed. 2, 1884, and those of the other domestic animals in Chauveau, Traité d'Anatomie Comparée des Animaux domestiques, 2<sup>nde</sup> éd.; 1871, pp. 200-347, Franck, Anatomie der Haustihere, 1871, pp. 343-478; Gurlt's Handbuch der Vergleichenden Anatomie der Haussäugethiere, ed. Leisering and Müller, ed. 5, 1873, pp. 206-329. For the masseter muscle in Rodents and its relation to the antorbital fissure, see Waterhouse, History of Mammalia, ii. p. 151, Pl. 6 a, 1848; Brandt, Mém. Acad. Imp. Sci. St. Pétersbourg, Sér. 6, Sc. Nat. Tom. vii. 1855, p. 153; Giebel, Zeitschrift, Ges. Wiss. 1865, p. 427; A. Milne Edwards, Nouv. Archiv. Muséum, iii, p. 92, 1867, *Lophiomys*; and Cuvier, Leçons, ed. 2, 1835, iv. pt. 1, p. 67, where the maxillary portion of the masseter is called 'musculus mandibulo-maxillaris.'

## 6. DUODENUM, PANCREAS, SPLEEN, AND LEFT KIDNEY, TOGETHER WITH PORTIONS OF STOMACH, OF THE JEJUNUM, OF THE LARGE INTESTINE, AND OF THE MESENTERY OF RABBIT (*Lepus cuniculus*) IN THEIR MUTUAL RELATIONS.

With Figure 2.

THE stomach, which in these animals, like the paunch of Ruminants, is never found empty after they begin to eat solid food, has been removed, with the exception of a little more than an inch of its pyloric end, *a*. As in nearly all Vertebrata, with the exception of the Ophidians, the terminal segment of the digestive tract, *h* to *k*, comes into close juxtaposition with this portion of the stomach and the duodenum<sup>1</sup>. As noteworthy points

<sup>1</sup> See Cuvier, Leçons d'Anatomie Comparée, ed. 2, 1835, tom. iv. pt. 2, p. 657: 'Dans toutes les classes des vertébrés, l'ordre des ophidiens seul excepté, le canal alimentaire a toujours une portion qui répond au gros intestin plus ou moins rapprochée de l'estomac ou du commencement du canal intestinal.' And compare the plates in Rathke's memoir, Ueber den Darmkanal des Fische, 1824, which show that this arrangement exists in most orders of Fishes as well as in air-breathing Vertebrata.

more or less distinctive of the Rabbit may be enumerated, firstly, the great distance, a foot or even as much as twenty inches from the opening, *c*, of the bile-duct, at which the pancreatic duct, *e*, opens into the duodenum

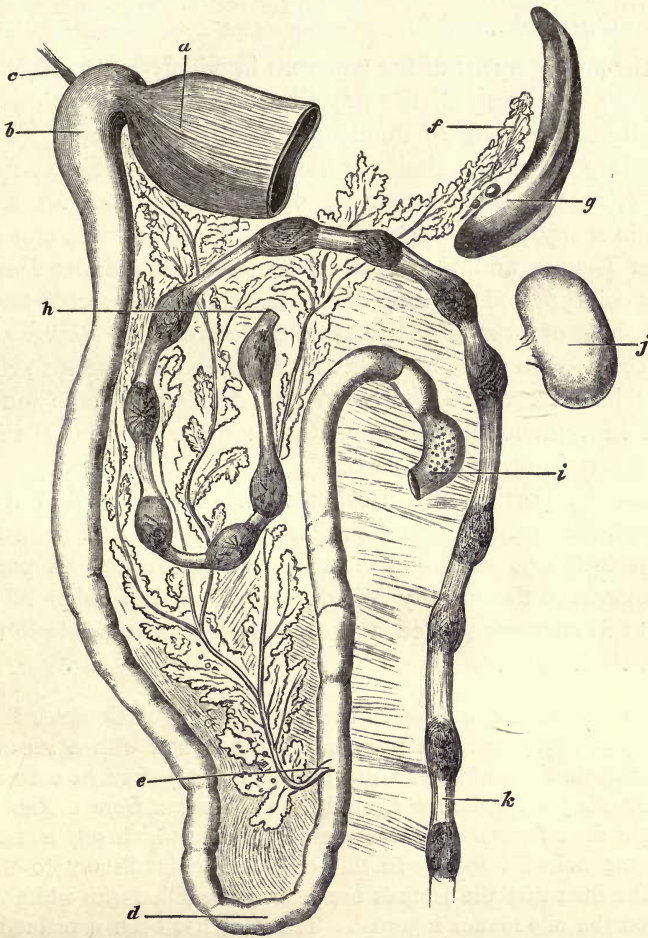


FIG. 2.—(One-half less than natural size.) DUODENUM, PANCREAS, AND SPLEEN, WITH PORTIONS OF STOMACH AND LARGE INTESTINE OF RABBIT (*Lepus cuniculus*) IN THEIR MUTUAL RELATIONS.

- a. Pyloric portion of stomach.
- b. Dilated commencement of duodenum, receiving
- c. The bile-duct.
- d. Concavity of duodenal loop, within which is contained a large part of
- e. The pancreas, to the duct of which, opening in the lower portion of the ascending limb of the loop, this line is drawn.
- f. Portion of pancreas in relation with the spleen and corresponding to the 'tail' of the organ of anthropotomy.
- g. Spleen, with two accessory splenculi.

- h.* Coil of colon supported by same lamina of peritoneum which attaches the pancreas and duodenum to each other and to the rectum. The letter points to the proximal end of the last coil described by the colon before it joins the rectum.
- i.* Peyer's patch marking point where duodenum passes into jejunum in a plane anterior to that occupied by the rectum.
- j.* Left kidney.
- k.* Rectum containing scybalæ.

secondly, the arrangement of the pancreas in widely-scattered loosely-compacted lobules, spreading all the way from the spleen at *f* down nearly to the concavity of the loop of duodenum; thirdly, the great length of this loop reminding us of the similarly long duodenum of birds; fourthly, the dilatation, *b*, at the commencement of the duodenum, an enlargement observable in many phytophagous Rodents, as *Lagostomus*, and also in the Hyrax, the Llama, and the Bottle-nose whale, *Dephinus Dalei*<sup>1</sup>. The descending colon, *k*, and the loop of duodenum are connected together by a continuous sheet of mesentery, the name therefore of *intestinum mesenteriale* cannot be confined in these animals, as it has been in others, to the jejunum and ileum; in other words, the colon and duodenum have much greater freedom of movement allowed them by the greater extent of their mesentery than in certain other Mammals.

Between the portion of the colon, shown here in section at *h*, and the segment next the caecum, shown similarly in Preparation 7 and in Fig. 3 at *f*, certain coils not shown in either figure intervene. A part of these coils corresponds to the spirally-coiled portion<sup>2</sup> of the colon of the Artiodactyla, but this correspondence is more plainly demonstrable in the Guinea Pig than in the Rabbit.

Professor Claude Bernard has, in the *Supplément aux Comptes Rendus*, tom. i. Pl. 3-4, Fig. 5, 1856, figured a pancreas of the Rabbit with a second, which is a much smaller, duct opening into the bile-duct just before its entrance into the intestine. On Pl. 7-8 *l. c.* he has figured the same organ from a Rabbit in which only the single duct figured here was present, and in which oily matter had been mixed with the animal's food. In this case it is only distally to the point of entrance of the duct that the lacteals are seen to be filled with white fluid and to have absorbed the oily matter ingested. This fact has been explained by Bidder and Schmidt, *Die Verdauungssäfte und der Stoffwechsel*, p. 256, 1852, as being due to the oily matter having been absorbed in the proximal segments of the duodenum, and having been also passed through the lacteal vessels in connection with them, and so having disappeared from view in the period of from five to six hours which they suppose to have been allowed to elapse between the ingestion of the oily matter and the examination of the duodenum. Bernard's views were controverted by other physiologists (see Schiff, Moleschott's *Untersuchungen*, ii. p. 345, 1857,

<sup>1</sup> See Owen, P. Z. S. 1839, p. 176, and Hunterian Catalogue, vol. i. 566 B.

<sup>2</sup> For a figure showing the spirally-coiled portion of the colon, the caecum, and the small intestine of an Artiodactyle, see Dr. Cobbold, *Cyclopaedia of Anatomy and Physiology*, vol. v. art. 'Ruminantia,' Fig. 361, p. 538. For several showing similar arrangements in Rodentia, see Pallas, *Novae Species Glirium*, Pl. xvii. 1778.



and Krause, *l. c.* p. 163), but in answer, Bernard appealed to the existence firstly of a second duct in the situation above specified, and secondly of certain accessory pancreatic glands either sessile upon or with ducts opening into the bile-duct (see figures, pp. 350-351, *Leçons sur les propriétés physiologiques des Liquides de l'organisme*, 1857). The second duct, however, of the pancreas in the Rabbit, though such an accessory duct does exist in several Ungulata, several Carnivora, the Elephant, and the Beaver, has been allowed by Bernard himself not to be constantly present (see *Comptes Rendus, l. c.* p. 390, and *Leçons de Physiologie Expérimentale*, 1856, ii. p. 271, in which last work it is best described as 'petit conduit pancréatique exceptionnel venant s'ouvrir dans le canal cholédoque'); and Krause, *l. c.*, suggests that a branch of the arteria gastro-epiploica dextra has been taken in an uninjected preparation for a duct. As regards the smaller accessory pancreatic glandules in connection with the bile-duct, Donders and Kuhne have remarked that they would be quantitatively inadequate to account for the emulsification of fatty matters which has sometimes been observed to have taken place in the duodenum above the opening of the pancreatic duct. On the whole, however, it seems that though some emulsification is effected independently of the pancreas, the appearances figured by Bernard, *Comptes Rendus, l. c.*, are so constant as to show that the process is very greatly helped by the secretion in question. For good summaries of the whole question, see Kuhne, *Lehrbuch der Physiologischen Chemie*, 1868, pp. 131-133, and Foster's *Text-Book of Physiology*, 4th ed. 1883, p. 295 (ed. 3, p. 279). The existence in certain animals of more than a single duct to the pancreas was first pointed out by De Graaf, in his *Tractatus Anatomico-medicus de succi pancreatici natura et usu*, pp. 16-17, 1671. The *duplex* and *triplex ductus*, however, are illustrated by him only by instances from Birds; amongst Mammals he only records the presence of a second smaller duct as having been occasionally found in Man and the Dog. See also Nuhn, *Lehrbuch der Vergleichenden Anatomie*, pp. 50-51, 1878.

## 7. CAECUM AND PARTS OF LARGE AND OF SMALL INTESTINE OF RABBIT (*Lepus cuniculus*).

With Figure 3.

THE lymphatic (or lacteal) sinuses<sup>1</sup> surrounding the Peyerian follicles in the walls of the vermiform appendix, *a*, in the dilated termination of the small intestine, *c*, and in a saucer-shaped patch of glands, *d*, in the large intestine, have been injected with Berlin blue, so as to show the relation of the lacteal vessels to the Peyerian follicles in the walls of the intestine, as also to certain mesenteric glands left in relation with it. The mesentery connecting the caecum and vermiform appendix with the segments of the small and large intestine has been cut through, and the caecum disposed so

<sup>1</sup> The lymphatic and lacteal vessels of many organs may be readily injected by the simple 'Einstichsverfahren' of Hyrtl and Teichmann. It is especially easy to obtain successful results in the case of the Peyerian glands of the Rabbit where, as in *Bos* and *Ovis*, the base of the follicles is surrounded by lymphatic sinuses, and not as in man and in the Carnivora by a reticulation of lymphatic vessels.

as to form the periphery of the preparation. The centre-point of the preparation and of the figure is occupied by a globular sac, *c*, the '*sacculus rotundus*,' the thick walls of which consist of Peyerian follicles, and represent the histologically somewhat similar termination of the small intestine in man. The small intestine dilates to form this sac after describing a siphon-shaped course internal to one formed by the commencement of the colon. A saucer-shaped patch, *d*, similar in structure to the *sacculus rotundus*, lies immediately to the right of it in the wall of the large

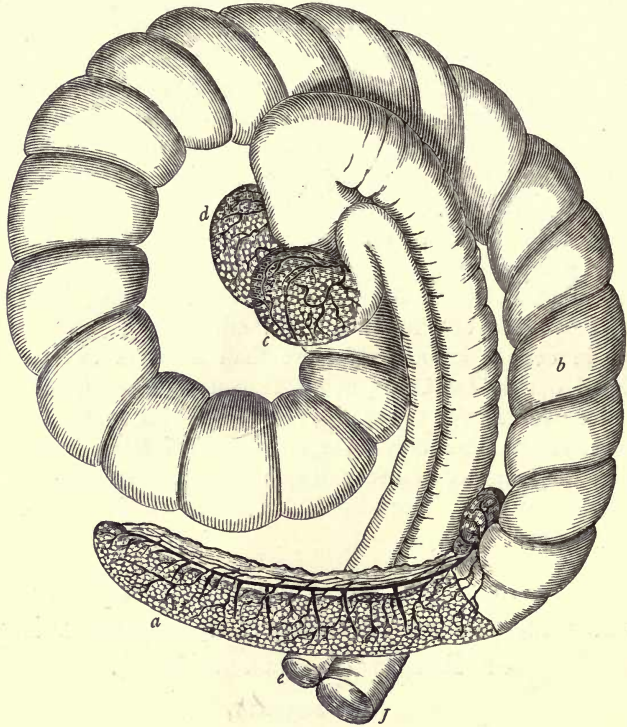


FIG. 3.—(Half natural size.) CAECUM WITH VERMIFORM APPENDIX AND PARTS OF LARGE AND SMALL INTESTINE OF RABBIT (*Lepus cuniculus*).

- a.* Vermiform appendix.
- b.* Thin-walled portion of caecum, spirally constricted in correspondence with an internally situated spiral valve.
- c.* The *sacculus rotundus*, or dilated globular end of small intestine, with thick walls consisting of Peyerian follicles.
- d.* Saucer-shaped thickening of wall of large intestine, on the internal periphery of which, not shown in this figure, the ileo-caecal valve opens.
- e.* Distal end, *i. e.* segment next caecum, of small intestine in section.
- f.* Proximal end, *i. e.* segment next caecum, of large intestine in section.

Attached to the spirally-constricted part of the caecum on its inner edge, just before it passes into the vermiform appendix, we see certain mesenteric glands into which an injection of Berlin Blue has passed, having been introduced by 'Einstichung' or puncture with a fine syringe into the lacunar spaces surrounding the Peyerian follicles of the vermiform appendix.

CAECUM OF RABBIT.

intestine, and overlies the opening of the ileocaecal valve. The caecum consists of two parts: the first of them, *b*, 14.5" in length, is wide in calibre, diminishing somewhat towards its termination, thin in its walls, and spirally constricted externally in correspondence with the spiral valve developed internally; the second, *a*, about 5.5" long and corresponding to the vermiform appendix of anthropotomy, is of much smaller calibre, but of much thicker walls, consisting mainly of Peyerian follicles; it has no internally projecting fold nor externally impressed furrows, but is mapped into well-defined spaces by the injection occupying the lacunar spaces of the Peyerian patches. This injection may be seen to have passed into some mesenteric glands attached to the spirally-constricted portion of the caecum close to its junction with the appendix. What may be called the *caput coli* lies in this preparation between the concavity of the caecum and the two Peyerian agglomerations of glands already mentioned. Its external surface is not puckered or corrugated, but from it the three longitudinal muscular bands, the so-called *taeniae coli*, take origin and give a sacculated appearance to the commencement of the colon proper. The mucous membrane of the colon is seen to be beset with villi of a granulation-like appearance, an unusual appearance in Mammalia. The inwardly projecting folds of the colon are, the spiral coils of the caecum are not, obliterated by distension. From this Preparation and Figure it may be seen that the Peyerian agminate glands may take either the form of a caecal cylinder with thick walls as in the vermiform appendix, *a*, here and in man; or that of a globular sac such as that developed here at *c* immediately proximally to the ileocaecal valve; or that of a saucer-shaped thickening of the walls of the large intestine immediately beyond that valve. In like manner the follicles, which are the essentially distinctive characteristic of the Peyerian 'patches,' are themselves found, when examined under low powers of the microscope, to be of very various shapes; those, for example, from the vermiform appendix of the Rabbit presenting the outlines of the sole of a shoe, whilst those of the Guinea-pig and of Man are subspheroidal in shape.

For a description of the caecum and the sacculus rotundus, see F. Bohm, De Glandularum intestinalium structura penitiori, Berolin. 1835, Diss. inaug., cited Frey, Z. W. Z. xiii. p. 28, 1863.

For the histology of the Peyerian glands generally, see Frey, *l. c.*, and Handbuch der Histologie et Histochemie des Menschen, ed. 5, 1876, p. 525 (lit. p. 529); His, Z. W. Z. x. p. 333; xi. p. 416; xiii. p. 455.

For the histology of a Peyer's patch in small intestine of Rabbit, see Verson in Stricker's Histology, Eng. Trans. vol. i. p. 566, fig. 108.

For that of the sacculus rotundus, see His, Z. W. Z. xi. p. 426, Taf. xxxv. Fig. 6; Frey, *l. c.* p. 65.

For that of the vermiform appendix, see Frey, Z. W. Z. xiii. p. 64, Taf. iii. Fig. 1.

For that of the Peyerian patch on the colon, where the follicles are larger than anywhere else, see Frey, *ibid.* p. 68.

For the method of injection by puncture and the use of Berlin blue, see Frey, *Z. W. Z. l. c.* p. 52, and *Mikroskopische Technik*, ed. 7, 1881, pp. 128, 132, 293, 295; and Schäfer, *Practical Histology*, pp. 144 and 157.

For the presence of villi in the large intestine, see Cuvier, *Leçons*, ed. 2, 1835, iv. pt. 2, pp. 243 and 274.

8. BLADDER, UTERUS MASCULINUS, UROGENITAL CANAL, AND RECTUM, WITH GLANDS IN RELATION WITH THEM RESPECTIVELY, OF MALE RABBIT (*Lepus cuniculus*).

With Figure 4.

THE upper half of the bladder has been removed, and the cavity of the lower half, *a*, laid open from behind, as have been also the cavities of the *Uterus masculinus*, *s.* 'Organ of Weber,' *s.* *Vesicula prostatica*, *b*, and of the urogenital canal at *d*. The right *crus penis* has been cut through at *l*, as also the left, not seen in the figure of this Preparation; and the parts removed from their connection with the pelvis. A wire has been passed from the cavity of the bladder along the urethra behind the *uterus masculinus*, *b*, into the urogenital canal, *d*, and along this canal to its outlet in the glans penis. The rectum, *c*, has been displaced to the right from the mesial plane which it naturally occupies. The walls of the bladder have been turned outwards, and the orifices of the ureters appear consequently to lie upon its anterior instead of upon its under or posterior surface as in nature.

The *uterus masculinus*, *b*, is of colossal proportions in the *Leporidae*, attaining in some cases an absolute length of as much as three inches. With the exception of the Koala, it has not been observed in any marsupial, the generative organs of which animals, however, resemble those of the Rabbit in some points, as, for example, in the absence of seminal vesicles. It bears here a striking resemblance to the upper part of the vagina of the female Rabbit, as shown at *b* in Fig. 5, p. 37, having a similar rudimentary septum developed upon its anterior wall. But the presence, not merely of a considerable interlacement of muscular fibres, but also of glandular structures in its walls, as also some other reasons, would seem to make it safer to consider this organ to represent at once both uterus and vagina. Its upper angles are slightly produced and project between the upper boundaries of the prostatic glands, *h*, and the cut short ends of the vasa deferentia. These projections, like the somewhat similarly drawn-out upper angles of the true human uterus, must be taken to represent the cornua uteri of the *uterus duplex* and *uterus bicornis*. The organ is flanked on

either side by three packets of tubular glands, two lettered *h* and *i*, and a third which, being placed between them and somewhat anteriorly, is not seen clearly in this figure. This last consists of three simple unbranched tubules, which, though said by Weber to be variable in presence, are yet usually to be found in the interval between the lower ends of the two packets, *h* and *i*, and open by three distinct orifices into the urethra, as stated by Martin St. Ange, *Étude sur l'appareil reproducteur*, p. 11, who calls them 'accessory prostates.' The larger of the two other packets of glands, *h*, is readily separable from its fellow of the opposite side, posteriorly as well as anteriorly; the smaller, *i*, interdigitates more or less intimately with its fellow on the posterior surface of this portion of the urethra, but, as in the human subject, the glandular elements of the prostate do not cross the middle line anteriorly. The characteristic concentrically laminated prostatic concretions are found in the tubuli of the smaller packet, though not in the larger; but it is in accordance with general usage to speak of both of these sets of glands as 'prostates,' the smaller as the 'anterior' and the larger as the 'posterior prostates.' The anterior prostate is divaricable into two lobes, each with a separate duct: the posterior has but a single duct: with, however, the three ducts from the accessory prostates there are six ducts opening into this portion of the urethra on either side. In the adult Rabbit the vasa deferentia open by an unusual arrangement into the *uterus masculinus* about two lines from its orifice; in the embryo the normal arrangement exists whereby the *uterus masculinus* opens a little way above these ducts. The testes have been removed in this preparation, together with the greater part of the vasa deferentia, the cut ends of which are seen passing behind the upper angles of the *uterus masculinus*. The portion of the urogenital canal which is laid open at *d* corresponds to the portion known in anthropotomy as the 'membranous,' 'muscular,' or 'interfascial' portion, and as the 'isthmus urethrae.' Though longer relatively than in our own species, it has by no means the same relative preponderance which the homologous portion of the canal has in some other Rodents, as *e.g.* *Arctomys*, and in some Carnivora, *e.g.* *Canis*.

The wire which has been passed down the urogenital canal from the interior of the bladder projects from the orifice of the urethra, which in these animals, retromingent like other Rodents, has the shape of a vertical backwardly-looking slit. The Cowper's glands, *j*, organs found in all mammals except, so far as is known, *Mustela* and *Delphinus*, with capsules of voluntary muscular fibre and ducts leading into the commencement of the spongy part of the urethra, are seen on either side of the *sinus urogenitalis*. On the left side we see at *l*, in the plane in which this canal passed under the pubic arch, one of the crura penis with the *pubo-cavernosus* and *ischio-cavernosus* muscles cut through and detached from that arch, and on the opposite side we see, at *k*, two ano-preputial glands, one much larger

than the other, and a hairless area of integument, *g*, on to which the ducts of these glands open, and which is prolonged into the fold covering the glans penis. A similar arrangement to this exists in the Tenrec. Just

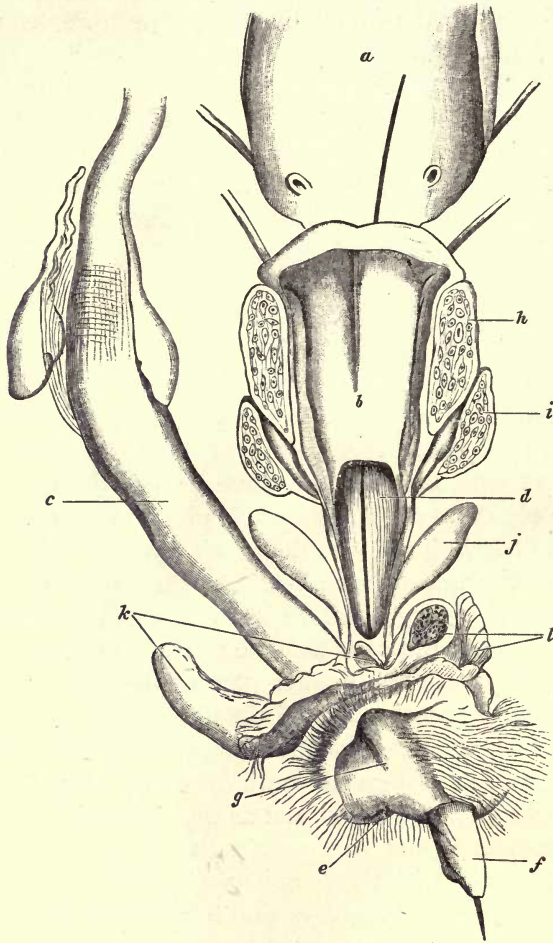


FIG. 4.—BLADDER, UTERUS MASCULINUS, AND UROGENITAL CANAL FROM ITS COMMENCEMENT TO ITS TERMINATION AT THE ORIFICE OF THE PENIS, WITH THE PROSTATIC AND COWPERIAN GLANDS OPENING INTO IT, TOGETHER WITH THE RECTUM AND ANOPREPUTIAL GLANDS OF RABBIT (*Lepus cuniculus*) SEEN FROM BEHIND.

One-third larger than the parts figured are in the period of sexual activity of an adult male.

- a.* Urinary bladder. The upper half has been removed and the cavity laid open, and the walls reflected so as to show the openings of the two ureters towards its lower end.
- b.* Uterus masculinus (in section), with prostatic glands on either side.
- c.* Rectum, with two of the cystic stages (*Cysticercus pisiformis*) of *Taenia serrata* attached to the external surface of the longitudinal muscular coat of the intestine, which has been reflected to show their connection with it.
- d.* Urogenital canal. A wire passes along it to its termination at the external orifice of the penis,

having been introduced into it from the bladder at *a*. The penial urethra conveys both urinary and seminal products in all mammals above the Monotremata, in which group it conveys seminal products only, reversing the functions of the homologous canal of those female mammals, such as the Rat and the Mole, in which there is a closed clitorid urethra.

*e*. Anus.

*f*. Penis, with vertically elongated backward-looking orifice.

*g*. Hairless patch on to which the ano-preputial glands open.

*h*. Upper prostatic glands.

*i*. Lower prostatic glands.

*j*. Cowper's glands.

*k*. Larger and smaller ano-preputial glands, rudimentary in man.

*l*. Corpus cavernosum of right side in section, with parts of the pubo-cavernosus and ischio-cavernosus muscles lying upon it.

below this area the anus opens at *e*. The rectum, *c*, has been displaced outwards and to the right so as to give an unimpeded view from behind of the organs just described. At its upper part it carries, attached to its longitudinal muscular coat, two hydatids, the cystic stage (*Cysticercus pisiformis*) of *Taenia serrata*, which takes on its cestoid or 'strobile' form in the intestines of the Dog or Fox.

A comparison of this preparation with such figures as those of the homologous organs in the human subject at pp. 419, 428, figs. 304, 310 of Quain's Elements of Anatomy, 8th ed. 1878, will show clearly the different proportions of the organs in the two subjects respectively, whilst a comparison of it with the similarly dissected and displayed preparation of the female organs of the Rabbit (see *infra*, Prep. 9, Fig. 5, p. 37, and Description, pp. 34-38) will show the close correspondence which exists between the male and female organs in this animal from the commencement of the urogenital canal outwards. The structure of the crura clitoridis and that of the crura penis are strikingly similar, especially in the very considerable thickness of their external fibrous sheath. The median septum which these sheaths form by their apposition remains distinct throughout the length of the compound organ they make up, as is the case in many mammals of the Rodent and other orders which possess a penial ossicle, whilst in the Ungulata, such as *Cervus*, *Sus*, *Tapirus*, *Equus*, and the Cetacea there is neither median septum nor penial ossicle.

An excellent article on the male generative apparatus and the anal glands of Mammals by Prof. Leydig is to be found in the Z. W. Z. ii. pp. 1-58, 1850. One of similar merit on the *Uterus masculinus*, s. *Vesicula prostatica*, by Professor R. Leuckart, is contained in the Cyclopaedia of Anatomy and Physiology, *sub voc.* 'Vesicula prostatica,' 1852. See also E. H. Weber, Abhandlungen Jablonowskischen Gesellschaft, 1846, pp. 382-385, 396, 405, Taf. v. figg. 1-3, where the generative organs of the Rabbit are figured; as also one by Van Deen, Z. W. Z. i. Taf. xx. 1849, and the work by Martin-Saint-Ange, L'Appareil reproducteur des Animaux Vertébrés, Pl. i. and ii. 1854. See also Huschke in Soemmering's Anatomie, 1844, and a good article, translated by

Prof. Peters, in Müller's Archiv, 1849, from the Swedish of F. Wahlgren. A uterus masculinus of somewhat similar proportions is figured by Pallas, 'Novae species Glirium,' 1778, from the *Arctomys bobac*, p. 117, Taf. ix. fig. 5, but in the genus *Lagomys*, judging from his figures 9 and 15, Taf. iv. B, we must suppose the two vasa deferentia to be, by a very unusual arrangement, fused into a single tube but a very short distance above the bulb of the urethra, and the uterus masculinus to be absent contrary to what Leuckart has (*l. c.* p. 1419) suggested. The organ is said to be somewhat smaller in the Hare than in the Rabbit. It is much smaller relatively in the human subject than in most Mammalia in which it has been seen; for figures, however, of a large specimen from a human embryo of 32 weeks, see Betz in Müller's Archiv, 1850, Taf. ii.

For the General Morphology of the male and female generative organs in Mammals, see Allen Thomson in Quain's Elements of Anatomy, vol. ii. 1882, p. 911, and Banks 'On the Wolfian Bodies,' 1864, *ibi citat.*; Leuckart, Zur Morphologie und Anatomie der Geschlechtorgane, aus Göttingen Studien, 1847, and *l. c. supra*; Meckel, Zur Morphologie der Harn- und Geschlechtswerkzeuge, 1848; Fredrik Wahlgren in Müller's Archiv, 1849, pp. 686-713; Rathke, Vorträge zur Vergleichenden Anatomie, 1862, pp. 135-170; Gegenbaur, Grundriss der Vergleichenden Anatomie, 1878, p. 645, where the *uterus masculinus* is taken as the homologue rather of the vagina than of the uterus. See also Watson, P. Z. S. 1878, p. 424; Young, Journal of Anat. and Physiol. 1879, p. 315; and for opening of vasa deferentia into uterus masculinus, see same two authors, on Elk, J. L. S. 1878, p. 375; on *Hyaena crocuta*, P. Z. S. *l. c.*; and Dr. Young on Koala, *l. c.*

For *Taenia serrata* and *Cysticercus pisiformis*, see Preps. 46 and 47 *post.* For figures, see P. J. van Beneden, Mémoire sur les Vers Intestinaux, Paris, 1858, p. 148, Pl. xx. And for the fact that this particular parasite affects the locality *h* as a 'point de prédilection' (much, perhaps, in the way that the stress of certain infectious diseases has preferential sites), see Martin St. Ange, *l. c.* p. 7.

For the migration of these and other *Cysticerci* from their first site in the liver, and for the recovery of the liver from the injury thus inflicted, see Leuckart, Die menschlichen Parasiten, 1879, pp. 92, 93, and 174. Flukes will similarly migrate from the liver into the peritoneal cavity.

## 9. GENERATIVE ORGANS, TOGETHER WITH THE BLADDER AND RECTUM, AND THE GLANDS IN RELATION WITH THEM, OF FEMALE RABBIT (*Lepus cuniculus*).

With Figure 5.

THE dissection has been made upon the same plan as the preceding Preparation of the urinary and generative organs of the male Rabbit, and it shows very clearly the exactness of the homology existing between the parts from the commencement of the urogenital canals, *c* and *d*, outwards. The two organs, *b* and *b'*, in the two preparations are very closely similar, and this similarity has led to the belief that the *uterus masculinus* of the



male Rabbit should be held to represent merely the vagina of the female. It is a sounder view probably to consider it, as stated above, p. 30, to represent both vagina and uterus.

The extent to which the vagina projects beyond the summit or 'superior fundus' of the bladder is a remarkable point of contrast in the adult female Rabbit as compared with the adult females of most other species of mammals, placental and other; in the newly-born female however (in which it may be remarked the parts in question are curiously similar to the analogous and homologous ones of the male at the same age), these proportions are exactly reversed, whilst in well-injected adult specimens the superior vesical arteries are sufficiently obvious to remind us of their functions in foetal life.

The junction of the uteri, *a*, to the Fallopian tubes, at *e*, is marked by the difference in calibre of the two parts of the continuous and tortuous cylinders which they make up, and by the attachment to it of the 'ligamentum rotundum' which passes down to be inserted into the pubic eminence, as also of the 'ligamentum ovarii' and the 'broad ligament'.<sup>1</sup> The two uteri are entirely distinct from their points of junction with the Fallopian tubes up to their openings by separate *ora tincae*, one on either side of the rudimentary median septum on the anterior wall of the vagina, *b*. In the Bizcacha, *Lagostomus trichodactylus*, a South American Rodent with many points of affinity to the Marsupials (see Darwin, Origin of Species, p. 379, 6th ed. 1872), what is a rudimentary septum in the Rabbit forms a perfect division in the vagina for a distance of as much as one inch beyond the *ora tincae*, constituting thus a transition towards the arrangements characteristic of Marsupialia. (See Owen, P. Z. S. Part vii. 1839, p. 77.) The uteri are similarly distinct, forming a 'uterus duplex' in *Sciurus*, *Arctomys*, *Spalax*, *Bathyergus*, *Echimys*, *Erethizon*, *Hydrochaerus* amongst Rodents, and in *Orycteropus* amongst Bruta; they fuse into a 'corpus uteri' with *cornua uteri* superadded to it at a greater or less distance from the commencement of the vagina, forming thus a *uterus bicornis*, in *Mus*, *Cavia*, *Caelogenys*, *Dasyprocta* amongst Rodents, as in most other placental Mammals; whilst even in the *uterus simplex* of *Dasypus* among the Bruta and in that of the Primates, more or less of the embryonal bifidity is retained by the production upwards and outwards of the angles of the *fundus uteri* towards the Fallopian tubes, much as are the angles of the *uterus masculinus* of the Rabbit shown in Fig. 4, *b*.

In the lower part of the vagina, a short distance above its junction with

<sup>1</sup> It is instructive to compare such a preparation as this of these ligaments with such a figure as that given by Dr. A. Farre (after Richard) in the Cyclopaedia of Anatomy and Physiology, Supplement, art. 'Uterus,' p. 598, fig. 404; or that given by Prof. Allen Thomson in Quain and Sharpey's Elements of Anatomy, ii. 1882, p. 707, fig. 608; or those by Henle, Handbuch der Menschlich. Anat. ii. ed. 2, 1873, figs. 364, 374, pp. 474, 487.

the urethra to form the urogenital canal (*c*), two valvular involutions with their concavities looking upwards are developed, and have been taken to represent the somewhat similar projections in the double vaginae of Marsupials. Similar folds exist also in the lower portions of the vagina of the Rhinoceros and some other female Mammalia; and in the upper of the Cetacea, the Suidae, and the insectivorous Tenrec. The urogenital canal, *c*, is laid open in part of its course, from the point where it commences at the junction of urethra and vagina, and is seen to be of considerable length as compared with the homologous segment in most Mammalia. This canal appears to be of the greatest relative length in the Monotremata, where the two uteri open into it separately and immediately above the openings of the ureters and below the downward opening of the bladder, that is to say, without the interposition of any vagina proper; and of the least in the Primates, where it corresponds simply to the *Vestibulum vaginae*. But the morphological value of these facts is somewhat diminished when we find that in an order with tolerably uniform internal anatomical arrangements such as the Carnivora (to say nothing of an order such as the Bruta, comprehending such widely different forms as *Dasypus sexcinctus* and *peba*, *Bradypus tridactylus* and *Cholaepus didactylus*), the length of this canal may vary as much as it does in species as closely allied as *Hyaena brunnea* (Murie, Tr. Z. S. for 1867, p. 504) and *H. crocuta* (Watson, P. Z. S. 1877, p. 376). And in orders such as that of the Rodents as illustrated by the Rabbit here, by *Hystrix* and by *Dasyprocta*, as that of the Insectivora as illustrated by *Erinaceus*, and as that of the Prosimii as illustrated by one at least of the *Lemurida* and by the Aye-aye, in which there is a urogenital canal of greater or less length, we may find precisely the opposite condition set up, that namely of entire separation of the genital and urinal canals, by enclosure of the urethra within the lower part or corpus spongiosum of the clitoris; reversing thus the arrangement which is usual in female mammals and is homologous to the condition known as 'hypospadias' in males. Thus in the females of the Norway Rat, *Mus decumanus*, as also in *Lagostomus*, *Arvicola*, *Bathyergus*, and *Myodes* amongst Rodents, *Sorex* and *Talpa* amongst Insectivora, and *Stenops*, *Tarsius*, and some but not all *Lemurs* amongst *Prosimii*, the clitoris is perforated by the urethra, and the urinary and female genital canals are entirely distinct, which is not the case here. One crus of the clitoris is seen here with its accompanying muscle as cut away from the os pubis; the bilobed termination of the organ lies concealed within the vulva, with the inner walls of which it is continuous. The ano-preputial glands, *i*, like the other organs from the commencement of the urogenital canal outwards, correspond very exactly with those of the male already described; the glands representing the Cowperian glands of the male, and known in the female as the glands of Bartholini or Duverney, are seen between the ano-preputial glands and the

crus of the clitoris, and in this specimen are smaller in size than the homologous glands in the other sex.

The ovaries, as in animals still in the breeding period of life, are tuberculated or nodular from the presence on their exterior of Graafian follicles

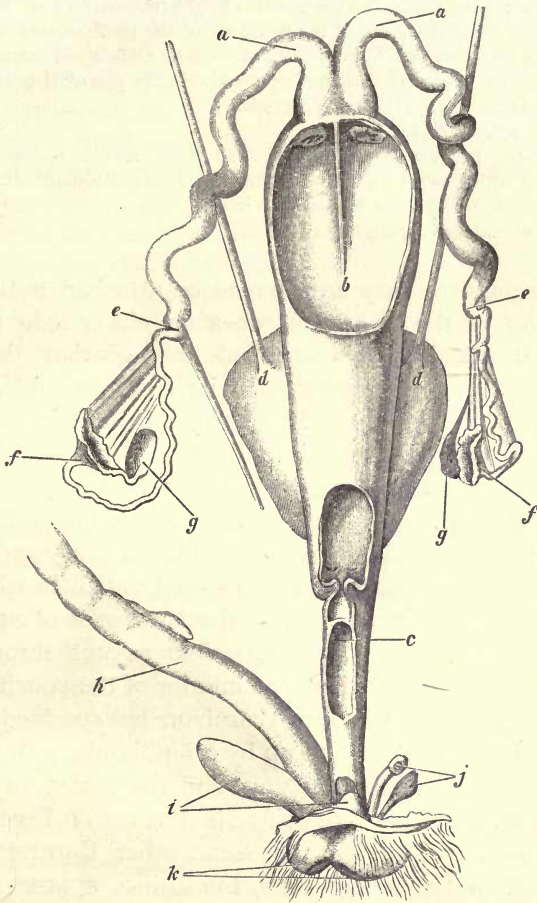


FIG. 5.—OVARIES, FALLOPIAN TUBES, UTERI, VAGINA, UROGENITAL CANAL, RECTUM, AND ORGANS IN RELATION WITH THE EXTERNAL OPENINGS OF THE TWO LATTER CANALS FROM FEMALE RABBIT (*Lepus cuniculus*). (One-half less than natural size.)

- a. The two uteri opening by distinct *ora tincae* into the single vagina.
- b. Vagina laid open from behind in two parts of its length and showing a rudimentary septum on its anterior wall in its upper segment, and two semi-lunar folds in its lower and narrower segment.
- c. Junction of urethra with vagina to form the urogenital canal, the upper half of which is laid open.
- d. Entrance of ureters into bladder; the points of entrance are drawn a little higher up than they ought to be.
- e. Junction of Fallopian tube with uterus of either side. From this point on the right a flat band,

the homologue of the 'ligamentum rotundum' of anthropotomy and of the *gubernaculum testis* in the male, passes downwards and inwards, whilst from it and the Fallopian tube beyond it, that part of the 'broad ligament' known as 'ala vesperilionis' passes to the funnel-shaped opening of that tube.

- f. Fimbriated and funnel-shaped opening of the Fallopian tube; the so-called 'Pavilion' or 'Infundibulum,' the mucous orifice looking into the peritoneal cavity inwards and backwards from the posterior aspect of the broad ligament.
- g. Ovary, connected on the right side with the pavilion by the tubo-ovarian or 'infundibulo-ovarian' ligament, formed by the drawing out of the periphery of the pavilion, and on the left with the uterus of that side by the ovarian ligament. There are no fimbriae on the infundibulum of the Monotremata, and its outer periphery is almost entire in the placental genus *Sus*, but they are present, so far as is known, in all other Mammals.
- h. Rectum, with one hydatid affixed to it.
- i. Ano-preputial glands. Between the smaller of these glands and the rectum is seen part of the gland homologous with Cowper's gland and known as the gland of Bartholini.
- j. One *crus* of the *clitoris*, with muscle in relation with it.
- k. Rectum and external outlet of urogenital canal.

with ova nearly mature; they are seen to be attached to the infundibular fimbriate opening of the Fallopian tubes on either side by one of the fimbriae of that opening, the so-called tubo-ovarian ligament, which secures that an ovum on escaping from its Graafian follicle shall readily find its way into the oviduct. The ligaments and peritoneal laminae passing from the opening of the oviduct and from the ovary to the proximal end of the uterus cause the oviduct to take a very contorted course. In some mammals, *e.g.* *Talpa*, *Canis*, *Ursus*, *Meles*, the peritoneal laminae, which here form only a widely open capsule for the ovary and infundibulum, coalesce and form an all but completely closed pouch in which ovary and opening of oviduct are both enclosed, so that an escape of an ovum into the peritoneal cavity becomes nearly impossible except through the small orifice near the uterine cornu where the interior of the pouch communicates with the peritoneal cavity. In the two carnivora last specified, even the small orifice thus left is frequently filled up by a hernia-like protrusion into it of one of the fimbriae of the infundibulum; and the ovary, a small portion of which is usually to be seen at that orifice, is thus cut off from view and from access to the peritoneal cavity. In some other Carnivora (*Lutra* and *Mustela*), at least in the young state, this orifice appears to be entirely closed by an overgrowth of peritoneal membrane.

For descriptions and figures of the organs of the human subject corresponding with those described here, see Farre, Cyclopaedia of Anatomy and Physiology, vol. v. article 'Uterus and its Appendages.'

For the general homologies of the female generative organs, see Leuckart, Rathke, and Allen Thomson, as referred to above, p. 34.

For the vagina and uterus duplex as an abnormality in anthropotomy, see Dr. J. Matthews Duncan, Journal of Anat. and Physiol. May, 1867, p. 269.

The Palaeontological history of the order Rodentia may seem to put the

affinity which has so often been alluded to as existing between them and the Ungulata into a clearer light than even the most detailed account of the anatomical resemblances which exist between the living representatives of the two groups under comparison. The most obvious, though perhaps also essentially the least important difficulty besetting such a comparison, is that which is based on the difference in size; but this is done away with by the discovery in American Miocene deposits of 'various small ruminant-like animals, some not larger than a Squirrel in size, to which the names *Leptomeryx*, *Hyphisodus*, *Hypertragulus*, have been applied.' See Flower, Proc. Royal Institution, March 10, 1876. On the other hand, the discovery in the South American Pliocene deposit of the animal known as *Mesotherium*, which was a little larger than the Capybara, and has been supposed to link the Rodents and notably the *Leporidae* to the Perissodactyle type by many connecting peculiarities, whilst retaining itself so many of the characteristics of the Rodent order as to have induced Mr. Alston, P. Z. S. 1876, pp. 73, 74, to create for its reception a third suborder, that of *Glîres hebetidentati* (see p. 44), equivalent to each of the two other suborders, those of *Glîres duplicidentati* and *Glîres simplicidentati*, into which Rodents may be divided, might seem to give as positive an illustration of the absence of any sharp circumscription in the delimitation of this group as can be asked for. The order, Tillodontia, established by Professor O. C. Marsh, would seem to bear more striking evidence still in the same direction, coming as it does from the earliest geological formation, the lower Eocene, in which Rodents are found; and combining some of the characters of Carnivores with those of both Ungulates and Rodents, as though they were survivors of some still earlier type unrepresented, as indeed are all Mammals, in any as yet explored strata of the Cretaceous age. Similar affinity has often been spoken of as existing between the Toxodontia of the Post-Tertiary South American deposits and the Rodents; but as this much later date might have led us to expect, the similarities between the two orders are by no means so clearly made out.

As regards existing Ungulata, the affinities of the Rodentia are distributed pretty evenly between the two divisions of Ungulata Artiodactyla, the non-Ruminantia *s. Bunodonta* and the Ruminantia *s. Selenodonta* (for which see W. Kowalewsky, Ph. Tr. vol. 163, pp. 69-74, 1873) and the Perissodactyla; but it must be borne in mind that though the differences between the now existing Hoofed animals thus named are very sharply defined, geological researches, especially in the American Tertiaries, have revealed to us forms in which these lines of demarcation tend to become obscured, or at least approximated. It would be easy to say, for example, that the imperfection of the orbital ring was a point of considerable importance, and united the Rodentia with the Perissodactyla; but Professor O. C. Marsh (see Introduction and Succession of Vertebrate Life in America, 1879, p. 161) states that several species of *Cervidae* from the lower Pliocene of the west of America fail to have the orbit closed behind.

A simple way of expressing the known facts may perhaps be furnished by saying that though the Rodentia with reference merely to their claws would be ranged with the Unguiculata rather than with the Ungulata of Linnaeus (see *Systema Naturae*, ed. xiii. vol. i. p. 17), they nevertheless present both in their skeleton and in their internal organs more marked points of essential affinity to

the latter than to the former of these two sets of Mammalia, and that even as regards the particular difference, such as it is, which exists between claws and hoofs, the *subungulate* character of certain South American Rodents (*Dasyprocta*, *Caelogenys*, *Dinomys*, *Cavia*, *Dolichotis*, and, notably, *Hydrochaerus*) very much reduces its value. The fact pointed out in the Description of Preparation, p. 27, note, to the effect that the microscopic character of the ultimate radicles or spongioles of the lacteal system in the Rabbit resembles that of the Ruminants rather than that of the Unguiculata, illustrates this position. On the other hand, however, Krause, Hdbk. der Menschlichen Anatomie, p. 234, 1876, has pointed out that the Rabbit, unlike the Ungulata, Horse, Pig, Ox, and Sheep, has capillary veins in the spleen instead of wide funnel-shaped orifices for the commencement of those vessels. The semi-pedunculate fashion in which the deciduous serotina is in the Guinea Pig, Agouti, and some other Rodents, attached to the wall of the uterus, and the fact that in the former at least of the animals named this structure is sometimes retained within the uterus at parturition, may appear to point to the existence of some approximation to the character of the non-deciduate cotyledonary placentation of typical Ruminants. But the springing up in later foetal life of a zone of villi, supplied by omphalo-mesenteric vessels around and exteriorly to the placental area in Rodents, though of physiological interest, as was pointed out in the Zoological Transactions for 1863, vol. v, still does not constitute, as seems to have been more recently stated, any but a physiological approximation of the Rodent to the Ruminant type of placentation.

The peculiarity of the placentae of the Guinea Pig and Agouti just alluded to, the comparative simplicity of their caecum, and the great development of the spirally-coiled portion of their colon, and the presence in them of but a single superior cava, the small number of their mammae and of their young, and the early attainment by them of the faculty of self-help, are points in which they resemble the Artiodactyla and differ from the *Lagomorphi*; but, as the Descriptions of the Preparations (Nos. 3 and 4) show, Brandt is entirely justified in pointing, *l. c.* p. 291, to numerous connecting links, *characteribus nonnullis generis Leporini cum Ruminantium ordine*.

The apparent paradox of an affinity connecting the Proboscidea (the Elephant and Mastodon) with the living Rodents, has already been alluded to, p. 8. One of the most striking of these resemblances lies in the facts that in both sets of animals the intermaxillary interposes itself between the maxillary and the nasal bones and joins the frontal without however touching upon the lacrymal bone, relations which do not exist either in the Aye-aye, or in the Hyrax, or in the Dugong, animals with incisors of somewhat similar relative proportions. But this remarkable peculiarity had not been attained to by the Pliocene genus and sub-order *Glires hebetidentati* of Alston, represented by the *Mesotherium*, in which animal the intermaxillary's nasal process is too short to prevent the maxillary from abutting upon the nasal, and fails, as in *Hyrax* alone of the animals just mentioned, to reach the frontal.

The absence of enamel from the incisor teeth or tusks of the adult Elephant, otherwise so exactly homologous with the incisors of the Rodents, might appear to constitute a difference between them and those of the Rodents, did we not know that these teeth when first cut in the Elephant have a cap of enamel, and that a



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serially homologous fact is presented to us in the possession by the American Pliocene Mastodons of a band of enamel on their tusks (see Marsh, *l.c.* p. 41).

The naked-eye structure of the molars of many Rodents, such as the Capybara, is strikingly like that of the Elephants, and the microscopic arrangement of the enamel in the same teeth in the Elephant and the Mastodon has been shown to be of the same type as that observable in all Rodents except the *Leporidae* and the *Hystricidae*. The coronoid processes of the lower jaw are small, and the relations of the molars to the malar processes of the maxillaries and of the squamous bones are the same in both orders, both the latter bones entering into the composition of the arch.

The Elephant might have been expected to have had a single superior cava, as have some of the largest existing Rodents, the South American Subungulata, and all other existing large-sized mammals. But it has, like all the Old World and all Nearctic Rodents, two. And it appears that there is some reason for holding that the Proboscidea, in contradistinction to the living Perissodactyla, and to the Artiodactylous Camel, Pig, and Deer, are an Old World type, and to be expected therefore to follow that type in such particulars as the one specified.

The Elephant however has the symphysis of the lower jaw perfectly ankylosed; it is more entirely testicondous; its brain is richly convoluted, as indeed are the brains of most existing mammals of large size except the Manatee, and its placenta is zonary.

The zonary form of the placenta similarly distinguishes the Hyracoidea from the Rodentia whilst uniting them more or less with the Proboscidea. In the structural composition of the malar arch *Hyrax* agrees with the two orders just mentioned, and differs from the Ungulata, but on an estimate such as is given by Brandt (Mem. Acad. Sci. St. Pétersbourg, 1869, Tom. xiv) of the sum total of the affinities of this animal, it should be ranked as an Ungulate with Rodentward affinities rather than as a Rodent. Brandt's own words run thus, p. 119: 'Es werden daher die Hyracen im Allgemeinen wohl am passendsten als *Ungulata gliriformia* oder *glirioidea* bezeichnet und als eine, jedoch weit mehr den Luftthieren ähnliche, Mittelform zwischen den genannten Thieren und den Glires angesehen werden können.' On another page, p. 116, Brandt suggests that *Hyrax* may connect the 'Pachyderms,' by which he in this connection means the Perissodactyla, with the Sciuromorphic Rodents specially, and also with the Lagomorphic, whilst the *Mesotherium* would stand similarly in relation to the *Lagomorphi* and the larger animals in question. Andreas Wagner indeed had expressed himself in 1844 in opposition to Cuvier, and to the same effect as Brandt, by saying that a separate family should be created for *Hyrax* amongst the Pachyderms, and that it should be considered as forming a transition towards the Rodents.

Cuvier, as is well known, in opposition to the view which trivial names, such as that of '*Marmotte bâtarde*,' given to *Hyrax*, embodied, went so far as to speak of it as being a dwarf Rhinoceros, and in his *Ossemens Fossiles*, ii. p. 127 *seqq.* 1822, he enumerates certain points of resemblance between the two animals. These points are such as the number, 20-21, of the ribs, as the transverse direction of the condyle of the lower jaw, as the absence of canines, as the shape of the nails, and as the presence of but three toes on the hind feet, and are inadequate to the support of such a view as the epigrammatically stated one just quoted. His

suggestion as to placing *Hyrax* between Rhinoceros and Tapir is less open to objection. It may be remarked that some of the peculiarities of *Hyrax*, such as the bisacculate character of its stomach, the presence of a sterno-maxillary muscle, the dilatations of its Eustachian tubes, the flatness of the roof of its skull, the perfect orbital ring, the absence of a clavicle, and of an acromion on the scapula, and the presence of a diastema between the incisors and the canines, are points which are at least as indicative of equine affinities as of connection either with the Rhinoceros or with the Rodent stock. And if on the other hand the presence of a languette on the dorsal, and of *papillae foliatae* on the lateral surface of the tongue in *Hyrax*, are points curiously reproduced in the Rabbit and the Rat, the important point of the absence of a second superior vena cava distinguishes *Hyrax* from all rodents except the *Caviidae*, and the zonular character of its placenta distinguishes it essentially from all known Rodents whatever.

Few points of real affinity connect the Rodentia with the Insectivora in addition to those more superficial peculiarities in general appearance, size, and habits, which have caused the two orders to be connected in common language. And these points are mainly such as may be characterized as indications of comparatively low organization in the scale of Mammalian life; and they are rarely constant in all the members of the two orders. Among them we may specify the not infrequent vacuolation or fenestration of the bony roof of the palate, the imperfect condition of the bony support of the tympanum, and the retention of the primitive jugular foramen. Similarly in the soft parts of both orders we find usually, if not always, cerebral hemispheres devoid of convolutions, and two superior caeae, as we do in all known Sauropsida. But irrespective of the differences in dentition, which may appear to lose some of their importance since we have been acquainted with the existence of *Apatemys* from the Middle Eocene of America, which had (see Marsh, *l.c.* p. 43) gliriform incisors combined with insectivorous molars, the digestive organs in the two orders are strikingly different, the intestinal tract being provided with a caecum in all Rodents except the *Myoxini*, whilst it is absent in all Insectivora except *Macroscelis*, *Rhynchocyon*, and the *Tupaïidae*. Both orders alike, it is true, have a discoid deciduate placenta, but in the Rodents the omphalo-mesenteric vessels take a large share in the nutrition of the foetus up to the end of pregnancy, the umbilical vesicle lines the whole of the chorion which is not occupied by the disk of the placenta proper; and this disk is never attached except to the mesometrial border of the uterine cornua; whilst in the Insectivora as in the Chiroptera the umbilical vesicle is attached, with the exception of *Sorex*, only over a limited circular area of the chorion opposite that occupied by the true placenta, the functional importance of its vessels is less, and the site of the allantoid placenta may be on any part of the uterine walls.

There can scarcely be any doubt that the Insectivora must be considered to be as ancient a form of mammalian life as the Rodentia; indisputable remains however of the order have not as yet been found lower than the Middle Eocene, whilst remains of Rodents have been identified in the lowest Eocene, the Coryphodon beds of North America. This absence of Insectivora however must be ascribed to the present imperfection of the Geological record; and it should be



added that a jaw of a small Mammal (*Dromotherium*) from the Trias of North Carolina, though supposed to have belonged to some Entomophagous Marsupial allied to *Myrmecobius*, is not definitely proved not to have belonged to a true Insectivora, and indeed that the likeness between these two sets of animals is a very strong argument for the antiquity of the Insectivora, as also for their inferiority when compared with the Rodentia, at least as regards the lowest members of each order.

This inferiority is manifested in the Geographical Distribution of the two orders. Though both alike are favoured as regards spreading over the world by the smallness of their size and their faculty of hibernation, and, in the case of certain Insectivora, of aestivation also, the Insectivora are obviously a 'failing' order, being, though represented in all the Zoo-geographical regions except the South American and Australian, still poor in numbers both of individuals and of species.

Many points, however, bear evidence to the antiquity of the Rodent type of Mammalian life, and to its alliance with still lower forms, such as the Marsupials and the Sauropsida, which is correlated with that antiquity. The imperfect ossification which leaves perforations or fenestrations in many cranial and facial bones, and allows sutures such as those of the basicranial bones and the symphysis of the jaw to remain unanchylosed, while in higher Mammals we find them continuously ossified; the retention both of bones such as the presphenoid and of processes such as the basiptyergoid in a distinctness and independence which is lost in higher forms; the small size of the coronoid process and the tendency to inversion of the angle of the mandible, the occasional persistence of the vomer in two distinct moieties, and the constant imperfection of the orbital ring, are some of such points furnished by the skeleton.

Great as are the variations observable within the limits of the order Rodentia, all living Rodents agree in the following particulars: they have the homologues of the two central incisors in both jaws furnished with permanently growing pulps, and with chisel-shaped cutting edges; these teeth are so largely developed as to have caused all the other incisors to abort either wholly, as in the *Glires simplicidentati*, or all but wholly, as in *Glires duplicidentati* or *Lagomorphi*; and the canines to abort invariably, leaving thus a diastema between the incisive and the molar series of teeth. The symphysis of the lower jaw is never anchylosed perfectly. The greatly developed incisive bones always separate the maxillaries from the nasals, but are themselves separated by processes of the maxillaries from the lacrymals. The lacrymal canal opens inside the orbit. The orbital ring is never perfect. The maxillary bone always forms a part of the jugal arch together with the malar and the squamous. The omphalo-mesenteric vessels contribute importantly to the nourishment of the foetus during the whole of intra-uterine life; the allantoid or true placenta is attached to the mesometrial part of the circumference of the uterus.

Till the discovery of the singularly aberrant *Lophiomys Imhausii*, the absence of the opposable hallux so commonly observable in Marsupials was supposed to be characteristic of all Rodents. This Rodent, in which the malars and parietals extend over the temporal fossa, as is the case in Chelonia, but in no other known Mammal, is also the known Rodent which is pedimanous. See A. Milne Edwards,

Nouv. Arch. du Muséum, 1867, p. 114. The name 'Prensiculantia' or 'Pfötler' was suggested by Illiger, Prodrômus, p. 81, 1811, after Buttmann, as a substitute for that of *Glires* upon the following grounds:—'Nota: nomen hujus ordinis a celeb. Buttmann excogitatum est ut manicularum instar manuum usus his Mammalibus familiaris indicetur, aliis e motus instrumento desumptis notis toti ordini communibus simulque characteristicis, deficientibus.'

The differences between the *Glires duplicidentati*, s. *Lagomorphi*, represented by the Rabbits, the ordinary Hares, and the Tailless Hares, and all the other living Rodents, are so great, and those which separate the three other subdivisions of the order, the *Myomorphi*, represented by the Mice, the *Sciuromorphi*, represented by the Squirrels, and the *Hystricomorphi*, represented by the Porcupines and Cavies, are so much smaller as to make it convenient to divide the order into two main divisions or Suborders: viz. the *Simplicidentati*, comprehending the three sections just mentioned, and the *Duplicidentati*, comprehending the Hares and Rabbits. Of these last the following propositions may be made in contradistinction to the *Simplicidentati*.

They have, as adults, two small incisors placed behind the two large ones in the upper jaw, these two pairs of teeth representing the anterior and the posterior of the three pairs of early life. They have a larger number of teeth,  $\frac{2}{3}$  in the molar series, than any other Rodents. The incisors are surrounded by a perfect zone, if not of enamel in the adult, at least of enamel membrane in the developing tooth. The enamel of the incisors is not divisible into two layers. The incisive and the optic foramina are, severally, confluent, and the bony palate greatly reduced. The glenoid fossa and the articular condyle of the lower jaw are less specialized to antero-posterior movement than is the case in other Rodents. The coronoid process and the sockets for the incisors in the same bone are also less specialized. Ossification is less perfect, as for example in the facial part of the maxillary and in the basicranial bones. They have a canalis caroticus in the tympanic, but no true alisphenoid canal. The fibula is ankylosed to the tibia, but articulates with the os calcis. The placenta is not disc-shaped, but consists of two or more lobes sessile on the chorion and clamped together by a saddle-shaped decidua serotina. These differences appear to place the *Lagomorphi* at a much greater distance from the group made up of the *Hystricomorphi*, the *Myomorphi*, and the *Sciuromorphi*, than any one of those sections is from any other. Of them the *Hystricomorphi*, especially as represented by the Cavies, come nearest to the *Lagomorphi*; the *Myomorphi* should be placed centrally, and the *Sciuromorphi* highest in position.

Mr. E. R. Alston, P. Z. S. Jan. 1876, pp. 73, 74, has proposed the establishment of a third Suborder, that of *Glires hebetidentati*, for the reception of the genus *Mesotherium* found in South American Pliocene deposits, and represented by an animal a little larger than the Capybara. This animal had the same number of incisor teeth placed in the same way, viz. two above and four below, as the Hyrax; they were surrounded, not merely faced, with enamel, and were not brought to a sharp cutting edge by wear, but came to present a transversely hollow blunt surface, whence the name *hebetidentati*. The mandibular condyle and the glenoid fossa were not specialized to perform the antero-posterior movements so characteristic of the *Simplicidentati*, and the three anterior and upper molar teeth were convex out-

wards as in *Toxodon*, not inwards as in typical Rodents. The massive heavy ridges on the skull give it an appearance not unlike that of the Sirenian skull when looked at from above; in some particulars, such as the great development of its paroccipitals and its palate, it resembles at once the Capybara, an exclusively South American type, and the Artiodactyla, but notably differs from both, and resembles the *Sciuromorphi* or most specialized Rodents, in possessing perfect clavicles. Professor Gervais, who has figured its skull and skeletal bones in his *Zoologie et Palaeontologie Générales*, pp. 134-139, 145, and Pl. xxii-xxv, considers its affinities to be Lagomorphous; and it resembles the Hares and differs from the Cavina in having its fibula in articular relation with the calcaneum. But it differs from all existing Rodents in having its intermaxillaries so short as to allow the maxillaries to abut upon the nasals; in having the cutting surfaces of its incisors pit-shaped like those of the Horse; and in having, as have Perissodactyla, Suidae, and Proboscidea, the two halves of the mandible anchylosed, not merely suturally joined at the symphysis. And with its other characteristics, not found to coexist in living animals, it combines the peculiarity, observable in the South American Bruta, except *Cyclothurus didactylus*, of having the ischium articulated with the caudal vertebrae.

In face of these anatomical facts recovered from the fossil remains, and bearing in mind that with them may have been combined in the living animal differences in the soft parts which would have definitely prevented us from ranking it with the Rodentia, we may hesitate to accept *Mesotherium* as constituting a third suborder of that division of Mammals. Its various affinities appear to be fairly stated by M. Serres in his fifth Memoir relating to it, *Comptes Rendus*, lxx. 1867, p. 599, in a passage which, for this reason, as also because it shows on how many sides orders, which may at first sight appear to be sharply circumscribed, may come into relation with each other, it may be well to give *in extenso*:—‘*Quelque ambiguïté que nous offre, en effet, ce singulier animal, ressemblant 1°. aux Rongeurs par la disposition de ces incisives, du mésodonte (p. 145), et par les dents uniafficulées; 2°. aux jeunes Pachydermes par la forme générale, et le rudiment des fossettes des incisives et des molaires; 3°. aux Edentés, ses contemporains, par la masse, la lourdain de sa tête et de ses membres, ainsi que par la bifurcation de la dernière phalange, enfin 4°. aux Cétacés, d’une part, par l’enfoncement de l’occiput, l’affaissement de la voûte du crâne et la petitesse de l’encéphale, qui en est la condition première, et d’autre part, par le nez large et court, un peu ouvert en dessus ce qui concorde avec l’idée de M. le Dr. Sénéchal qui pense que le *Mesotherium* était, peut-être, un animal aquatique; néanmoins, au milieu de ces conformités si diverses, celles qui le rapprochent plus particulièrement des Rongeurs et des Pachydermes dominant tellement les autres, que c’est entre ces deux ordres de Mammifères que nous croyons qu’il doit être placé comme un anneau intermédiaire qui les relie. Cet anneau serait-il, selon la pensée de Blainville, un des chaînons perdus de la série animale?’*

10. COMMON PIGEON (*Columba livia*),

Showing nervous, digestive, circulatory, and parts of respiratory and renal systems.

THE brain has been exposed *in situ* by the removal of the roof of the cranium; the integument has been removed from the right side of the front of the cervical region, as have also most of the feathers from the entire body; an opening has been made into the right side of the crop, which has been distended; the larger part of the right half of the body walls has been removed, together with the muscles and the limbs which it supported, and a red injection has been thrown into and filled the venous system.

The surface of the cerebral hemispheres is smooth; the proportion of the encephalic nervous mass to the intraspinal is much greater than in the cold-blooded Vertebrata. The backward projection of the cerebellum is very considerable. The eyes are large. The vertical third eyelid is drawn forward. The nostrils open externally as long slits overhung by a soft, bare, tumid membrane<sup>1</sup>; the external auditory meatus, which has no concha, has the feathers arranged round it like a circlet of tentacles. The great pectoral muscle, the main depressor of the humerus and the wing, is seen in section along its origin from the lower portion of the keel of the sternum, and from the furculum, the outer and lateral portions of the sternum, from which it also took origin, having been removed. Placed dorsally with reference to this muscle we see the second pectoral, the main elevator of the humerus and the wing, arising from a larger portion both of the keel and of the lateral parts of the sternum than the pectoralis major, and passing internally to the coracoid to enter the pulley-like canal, the *foramen triosseum*, formed by the clavicle or furcula, the coracoid, and the scapula. This muscle is supplied by nerves which pass in front of, whilst the great pectoral is supplied by nerves which pass below the coracoid, the first being homologous with the subclavian, the second with the anterior thoracic nerves of anthropotomy.

Whilst the tendon of the second pectoral or great levator humeri muscle, which is cut short, is seen issuing from its canal on the further side of the glenoid articular surface; on the proximal side, the humerus having been removed, we see the tendon of the biceps, homologous with the 'short head' of anthropotomy. The cut-short triangular end of the pectoralis major is seen to become partially bifid

<sup>1</sup> This membrane is sometimes called a 'cere,' but it is better to restrict the term to the denser structure similarly placed in and similarly distinctive of the *Actomorphae* and *Psittacomorphae*. Some of the *Charadrii-morphae* (Plovers), which on account of a peculiarity in the nasal bones (in which they resemble the Pigeons) were placed with them in a separate order, the *Charadriiformes*, s. *Schizorhinae*, resemble them also in the conformation of this membrane. See Coues, Key to American Birds, 1872, p. 26; Strickland and Melville, The Dodo and its Kindred, p. 46; Garrod, P. Z. S. 1873, p. 33, 1874, p. 100.

toward its apex; in the perfect condition of the parts the smaller inferiorly-placed division of the muscle gave off two tendons<sup>1</sup>, one to the long and the other to the short extensor plicae alaris anterioris; the larger division passed over a smooth facet on the humerus and over the coracoid head of the biceps to be inserted upon the inwardly-looking surface of the great triangular tuberosity of the humerus. Dorsally to the apex of the great pectoral we see a thin stratum of muscle in relation internally with the crop and homologous with the deltoid of anthropotomy. This muscle is divided into two strata by delamination. The superficial layer consists of three parts, of which the first and most internally-placed joins the long extensor of the anterior fold of the alar membrane; the second and mesially-placed joins the short extensor, whilst the third and dorsally-placed portion is inserted into the outer aspect of the humerus from its middle down to a nodule at its lower fourth marking the origin of the long radial extensor of the carpus. The deep layer consists of one short muscle<sup>2</sup> innervated by the circumflex, arising from the portions of the coracoid and scapula and of the ligaments in relation with the shoulder-joint, and inserted into the upper surface of the humerus along a line reaching from the apex of the triangular tuberosity receiving the tendon of the great depressor humeri to the facet receiving the tendon of the great long levator. Overlapped by this muscle, which acts as a levator humeri, and wedged between it and the great pectoral depressor, is a second short levator humeri, innervated as is the coracobrachialis, not as is the deltoid, arising from the coracoid and passing down on the outer side of the tendon of the biceps to be inserted under the upper portion of the tendon of the great pectoral. This muscle therefore should be considered to be a coracobrachialis.

We have thus three muscles—the ‘pectoralis secundus,’ or long levator; and two shorter muscles, the former of which may be called ‘deltoides externus,’ and the latter ‘coracobrachialis brevis’—entrusted with the work of raising the humerus, but each with a distinct innervation. In some birds, e.g. *Anser*, the deltoides externus passes into and takes an enlarged origin from the walls of the *foramen triosseum*, and gains some mechanical advantage by availing itself of its pulley-like outlet.

In relation with the lower portion of the right coracoid may be seen two other coracobrachiales (cut short in this preparation, but shown *in situ* at *v* and *u*, in

<sup>1</sup> The alar extensor muscles and many of the other muscles of the wing in Birds will be found well figured and described in a monograph by Schoepss in Meckel's Archiv, 1829. Those of the Pigeon are similarly figured and described by Macgillivray in his History of British Birds, i. pp. 34-42, Plate iii, a work with which I was not acquainted when the first edition of this book was published. Mr. Macgillivray remarks, p. 38, that the small muscular mass called by him *retractor plicae*, and figured here, Pl. ii. *w'*, *infra*, had not been met with by him in any other birds except Pigeons.

A doubling back of the tendon of the short alar extensor on to the nodule of origin of the long radial extensor of the carpus has been shown by Professor Garrod to be characteristic of the true *Passeres*. See P. Z. S. 1876, p. 509; Prof. Bell's translation of Müller's Vocal Organs of the *Passeres*; Appendix by Garrod, p. 64, Oxford, 1878.

<sup>2</sup> This muscle corresponds with No. 19, the *Deltoides externus* of Schoepss, as given in his monograph on the Muscles of Flight in Birds in Meckel's Archiv for 1829, and is called ‘levator humeri’ by Tiedemann, and ‘le petit releveur de l'humerus’ by Vicq d'Azyr. It appears to have been often confounded with the muscle next to be spoken of and lying close to it, which, though similar in function and size, is differently innervated and quite separate from it. The latter muscle is correctly described by Schoepss, *l.c.* p. 122, and named (No. 20) ‘Deltoides inferior.’

Plate ii, *infra*), the *pectoralis tertius auctorum*, s. *coracobrachialis inferior*, No. 16; Schoepss; and the *coracobrachialis superior*. The 'coracobrachial muscular apparatus' has been shown by Professor Wood, Journal of Anatomy and Physiology, i. 1866, p. 55, to be somewhat similarly multifid in many mammals normally and in man occasionally.

The crop forms a sac with bilateral glandular<sup>1</sup> pouches at the lower end of the distended oesophagus. As in the oesophagus of all Sauropsida, the muscular coat may be seen to consist of two layers, the outer one of which lies transversely<sup>2</sup>, and the inner one parallel to the long axis of the digestive tube, whilst both alike consist of unstriped fibres, and thus contrast in two points with the muscular coat of both Mammals and Fishes. It rests on either side upon the furcula and the muscles arising from it. In the cavity of the thorax a black bristle has been passed between the proventriculus and the aorta as this vessel arches over from the left to the right. The right side of the heart rests upon the right lobe of the liver from which the vena cava inferior is seen to pass up into the right auricle, entering it at a point a little superiorly as well as posteriorly placed to that at which the vena cava superior of the right side opens into it. The left lobe of the liver is, like the right, deeply excavated on its inner aspect for the reception of the heart; and it is still more extensively excavated on its under surface for the reception of the powerful gizzard, so as to be less than one-half the size of the other main lobe of the gland. The veins from the upper extremity and shoulder are cut short at their point of junction with the jugular to form the vena cava superior. The pneumogastric nerve is seen in relation superiorly with the jugular vein; superiorly again, and internally to the nerve, we see the proventriculus; and superiorly again to it, the longi colli muscles arising from the vertebral hypapophyses. Tracing the aorta backwards towards the heart from the point where it arched over the right bronchus, which, together with the pulmonary artery placed before it and the pulmonary vein placed behind it, has been removed in this dissection, we see it pass behind the vena cava superior dextra, and give off the two arteriae innominatee, one for either side of the body, very close to the base of the heart. These two arteries together with the pulmonary artery give a characteristic appearance to the region at the base of the heart in all Birds. Each arteria innominata divides into a common carotid<sup>3</sup> and a subclavian trunk. The subclavian, after giving off a small branch homologous with the internal mammary artery of

<sup>1</sup> This is the usually accepted statement: but see p. 53, *infra*.

<sup>2</sup> Gulliver, P. Z. S. 1842, 1869, 1870; Leydig, Fische und Reptilien, 1853, p. 41; Histologie, 1857, p. 324.

<sup>3</sup> There are two carotids in all *Columbae* and in the majority of non-passerine birds, but in no true Passerines.

anthropotomy, divides into an axillary trunk, which passes into the wing together with the brachial nerves, and into the much larger arteria thoracica externa which supplies the great pectoral muscles. The gizzard is concealed from view by the right lobe of the liver and the posterior or xiphisternal end of the sternum which supports and protects both these viscera. The duodenal loop containing the pancreas, and the segment beyond that portion readily recognisable as belonging to the duodenum by its large calibre, form a rudimentary spiral coil. The distal end of the loop and of the pancreas inside it are bent upon the proximal segment next to the gizzard, and are in relation with the lower lobe of the kidney on the right as the gizzard is with the lower lobe of the kidney on the left side. The distal segment of the duodenum bends up at some distance from its pancreatic loop and comes into relation with the right lobe of the liver which is excavated to receive it. In the interval between these coils of the duodenum portions of the two other convolutions characteristic of *Columbae* show themselves. Of these the distal one is the smaller in calibre; it shows some Peyerian glands, and is connected with the proximal portion of the duodenum by a lamina of mesentery much as is the colon in the Rabbit (see Fig. 2, *supra*). The coil interposed between the duodenal and the distal coil is much the longest and most distinctively spiral of the three, but being placed dorsally to them is not seen in its full extent till they are displaced<sup>1</sup>. The lung, which occupies a much smaller space in the dorso-sternal plane than in mammals, and in an ordinary dissection of a bird's viscera scarcely comes into view until either the ribs are displaced a little outwards or the lobes of the liver a little inwards, reaches backwards so far as to interpose itself for some distance between the anterior lobe of the kidney and the *os ilii*. Anteriorly one of the musculo-tendinous languettes which in the Bird represent the diaphragm of mammals passes inwards from the rib to the covering of the lung and interposes itself between the region of the anterior kidney-lobe and that of the lung. The Bird's differs further from the Mammalian lung in being lodged conformably to the intercostal spaces, and being indented by the six unanchylosed ribs, instead of being freely suspended, as is invariably the case in mammals, and divided into lobes, as is very ordinarily the case in those animals<sup>2</sup>. Another and most important point of

<sup>1</sup> Upon the differences observable in the number and character of these coils Dr. Hans Gadow has based a classification of Birds in two memoirs containing much valuable information, J. Z. xiii. 1879.

<sup>2</sup> That however different at first sight the topographical relations of the lungs, liver, and heart may seem to be in Birds and Mammals respectively, they nevertheless are not essentially dissimilar, may be seen from the fact that the technical works on the physical examination of the heart in man speak of the 'difficulty of separating the adjacent edges of the heart and liver' by percussion, and of the dulness produced by the apex of the heart being indistinguishable from that produced by the convex surface of the liver below it. See e.g. Frerich's *Diseases of the Liver*, New Sydenham Soc. Trans. 1860, p. 30; Walshe, *Diseases of the Heart*, 1862, p. 42.

difference is furnished by the prolongation of the lung, by means of its bronchial stem and branches, into air-cells permeating a very large part of the entire body. The largest of these receptacles are the infra-renally placed 'abdominal air-sacs,' the right one of which extends from the posterior border of the lung above and behind the liver, so as, firstly, to interpose itself between the inferior surface of the kidney and the intestines, and, secondly, to stretch beyond the region of the kidney into that of the rectum. The kidney, like the lung of Birds, is shaped conformably with the bones supporting it; and it is divisible here into three lobes, increasing in size from before backwards in correspondence with the iliac and pelvic surfaces in relation with them.

The division of the kidney into three lobes is better marked when seen as here from the side than from in front. Even from in front however the anterior lobe may be seen to be more or less limited off from the middle lobe by the great vein from the lower extremity which corresponds to the external iliac of mammals; and the middle lobe in its turn to be limited off from the posterior by the chief artery of the lower extremity, which is in most Birds, as here, the sciatic, not the external iliac artery. The sciatic artery gives off branches to the two posterior lobes of the kidney, and an *arteria renalis superior* arising from the aorta mainly supplies the anterior lobe. The veins from the lower limbs are supposed, and with considerable probability, to act as a renal-portal or inferent system, as in the cold-blooded *Sauropsida* (see *infra*, p. 56).

The (*rectrices*) feathers having been removed from the caudal tract, the anal oil-gland (*glandula uropygii*) is brought into view<sup>1</sup>. Its duct projects freely, and is apically biperforate and tongue-shaped. It has no circling of feathers, differing herein from that of the Fowls, the Diurnal *Raptores*, and all Aquatic Birds, and resembling that of the Nocturnal *Raptores* and all Passerines. Its outlines pass gradually into those of the bilobed gland mass, and with them make up a heart-shaped contour, the transverse axis of which is somewhat shorter than its anteroposterior. Though the Pigeon resembles the *Passeres* in the absence of feathers round this duct and upon the skin covering the oil-gland, and herein as in some other particulars comes nearer to that order than do the Gallinaceous Birds, the oil-gland and duct of the *Passeres* are nevertheless sufficiently distinctive to enable us to distinguish a specimen of the order from one of any other, even in the absence, not merely of the head, but also of the feathers of the whole body. These distinctive characters are the predominance of the transverse over the anteroposterior diameter of the gland, the shortness and apical bluntness of its efferent duct, the thinness of its walls, and the distinctness

<sup>1</sup> For a full account of the uropygial gland, see Nitzsch's Pterylography, Ray Soc. Trans. 1867, pp. 38-42. For the correlations of this gland with certain other structural peculiarities, see Garrod, P. Z. S. 1874, p. 118.



of its contour lines from those of the gland itself. The oil-gland of the *Lamellirostres* figured by C. G. Carus, Tab. Anat. Comp. Illust. Pars vii. Tab. 7. fig. 5, furnishes us with a sharp contrast to that of the Pigeon and the *Passeres* in being very deeply bilobed and in having its anteroposterior axis much longer than its transverse. The Ostrich, Emeu, Cassowary, and *Apteryx* agree with the cursorial Bustard in lacking this gland. Its presence is not constant in all the species of either *Columbae* or *Psittacidae*. It is larger in size in Birds of aquatic than in those of other habits.

In all Birds, and in no other class of animals, will the same description as that given here apply to the nerve-system, to the relations of the muscles of the anterior limb, and to the relations of the aorta to the right bronchus. The peculiarities of the pancreas and duodenum are probably nearly equally distinctive. The crop and the uropygial gland are peculiar to, though not universally found in Birds; but the presence or absence of these two latter structures is explicable probably by reference to the special habits or special needs of the species possessing or lacking them, and is therefore of physiological rather than of morphological importance.

The epidermic skeleton consists, as in all birds, of the horny covering of the bill, of claws to the toes, and scales covering the metatarsalia and toes, and of feathers. Of the latter, the Pigeon possesses two kinds, contour feathers or *pennae*, and *filoplumes*—down-feathers or plumulae being absent. Every penna consists of the following parts: a central axis shaft or *scapus* divisible into a proximal hollow tube or *calamus*, and a distal solid white shaft or *rachis*: of barbs borne upon the rachis and bearing in their turn *barbules*. Rachis and barbs together make up the vane or *vexillum*. The calamus is implanted in a follicle of the skin to which small muscular bundles are connected. It has a proximal aperture or *inferior umbilicus*, and a distal, the *superior umbilicus*, at its junction with the rachis. The barbules are implanted on the proximal and distal surfaces of the barb forming two series of process pointing obliquely towards the edge of the vane. The distal series of barbules of one barb overlaps the proximal series of the barb beyond, i. e. nearer the tip of the feather. The distal barbules bear on their under surfaces microscopic hooklets, each one of which catches hold of an underlying proximal barbula. The vane thus acquires great solidity. The filoplumes are closely associated with the pennae from which they differ in having a slender shaft with but a trace of the tube and a rudimentary vane composed of a few barbs bearing simple and disunited barbules. In many birds an after-shaft or *hyporachis* arises close to the superior umbilicus, and resembles when well developed, e. g. in *Ratitae* or gallinaceous birds, a second feather. It varies much in size and in the character of its vane, and is sometimes absent as in the Pigeon. The distal barbules sometimes carry *barbicels*, structures which resemble the hooklets *minus* the terminal hook.

Other varieties of feathers not found in the Pigeon are (1) the down-feathers or *plumulae*, which lie beneath and between the contour-feathers, and have either a simple soft rachis bearing soft barbules or a tube with a crown of soft bar-

bules ; and (2) semiplumes (*penno-plumae*) which have a stiff rachis and soft barbs and lie at the outer margin of the *pterylae* and are covered by the contour feathers. In a few birds down-feathers exist which grow persistently and break off at the apex ; whilst a powder or dust is poured out of the follicle lodging the tube. They are known as powder-down feathers, and either occur scattered all over the body—e. g. in some Parrots, or restricted to limited tracts—e. g. in *Ardea*.

The tuft of feathers springing from the pollex constitutes the *bastard wing*. The row of large wing-feathers is termed *remiges*, and is divisible into a set of *primaries* and of *secondaries* attached, the former along the manus, the latter along the ulna. They are covered above and below by the upper and lower *wing coverts*. The large tail feathers are known as *rectrices*, and they are covered above and below by the *tail coverts*. The feathers are not implanted irregularly into the body but along certain tracts or *pterylae* between which are bare spaces or *apteria*.

The following special points should be noted in the internal anatomy. In the central nervous system the small olfactory lobes ; the cerebral hemispheres pointed in front, broad behind, showing in horizontal section a huge corpus striatum, a lateral ventricle reduced to a narrow chink and thin internal and posterior walls : a small pineal gland, reverted, with walls composed chiefly of fibrous tissue, and its extremity attached to the dura mater : the solid optic lobes widely separate in the middle line where the cerebellum touches the cerebral hemispheres : the cerebellum composed of a large median lobe and two small lateral floccular lobes, the median lobe showing in longitudinal section an *arbor vitae* as in Mammalia : the well-marked angle between the medulla oblongata and spinal cord. The latter has a large lumbar swelling, in which a mass of neuroglia or substantia reticularis lies immediately dorsal to the central canal, the posterior fissure is widely open and the gap filled by a gelatinous tissue derived from the pia mater. This lumbar swelling was of immense size in the extinct *Stegosaurus* (*Deinosauria*). The spinal cord ends with a filum terminale and the posterior nerves form a cauda equina. The sympathetic system is double in the neck : one part accompanies the vertebral artery and vein and is lodged in the vertebrarterial canal : the other accompanies the carotid arteries on the ventral aspect of the neck. The two parts are connected.

The structure of the eye is peculiar in some points. The sclerotic coat has an anterior conical portion containing a ring of bones, and a posterior spheroidal portion. A pigmented vascular fold of membrane—the pecten—runs obliquely forwards from the entrance of the optic nerve and projects into the vitreous humour. The line of attachment marks the position of the embryonic choroidal fissure. Its capillaries are continuous with those of the optic nerve, and not of the choroid, and are contained within lymphatic sheaths. The nictitating membrane is moved by two special muscles—a quadratus or bursalis, and a pyramidalis, which lie at the back of the eye and take origin from the sclerotic. The former is a square muscle ending in a tendinous border, but the tendon is tubular. Through the tube runs the cord-like tendon of the pyramidalis which is inserted into the lower angle or edge of the nictitating membrane. When the pyramidalis contracts, its tendon is prevented from pressing on the optic nerve over which it runs by the simultaneous contraction of the quadratus. There is a well-developed Harderian gland for the third eye-lid lying below the eye-ball.

The tongue is of fair size. It has been discovered by Fraisse (Z. A. iv. 1881, p. 310), that in the embryo Duck there are embryonic feathers developed on the tongue which are arrested in development. The crop in the Pigeon is remarkable for its large size and bilateral symmetry. Gadow has distinguished between a *true* crop with glandular walls and a 'Haut' or 'Schlund' crop with non-glandular walls. The former exercises a chemical action on the food and occurs in the Fowl and Pigeon and in their congeners; whilst the latter exercises no such action and is simply a storehouse for food swallowed, e. g. in many Ducks, Cassowary, &c. But the researches of Hasse (Zeitschrift für Rationelle Medizin, xxiii. 1865) proved long ago that the upper part of the oesophagus and the crop itself are non-glandular in the Pigeon, whereas the portion of the oesophagus below the crop, like the proventriculus, is provided with glands. The crop, and the upper as well as the lower part of the oesophagus, are lined by a many-layered epithelium—the lower cells of which are granular and plump, but as they pass to the surface become flattened out yet not cornified. If the surface of the crop is scraped a small amount of a whitish liquid can be collected at all times. The amount is greatly increased in both sexes for about the first eight days after the hatching of the young, which are fed with the so-called 'pigeon's milk' regurgitated by the parent bird into the mouth of the young. It is a milky liquid containing cheese-like solid morsels. Hasse found that at this time the epithelium of the upper parts of the oesophagus and of the crop, but *especially its side parts* was much thickened, the bloodvessels dilated and full of blood. He also found that the cells of the epithelium undergo rapid division: are granular, and contain abundant fatty granules: that they are set free in masses which break down partially. The remnants form the cheese-like morsels, whilst the fatty cells set free give the liquid a milky look. The cells in the masses retain their nuclei, those set free have either lost them or show them undergoing fatty degeneration. The 'milk' collects within the crop whence it is expelled by the action of two muscles which spring from the upper part of the clavicles and are inserted into the skin ventrally. The physiological properties of the fluid do not appear to have been fully investigated. It is doubtful, perhaps, whether the small amount of it present at times other than the breeding season has any *chemical* effect on the food. The swelling of grain, peas, &c., in the crop may be due only to the action of moisture and warmth, and is therefore a *physical* effect. It is stated by Hasse that a similar milky secretion occurs in some species of Parrots.

The lower oesophagus has an epithelium similar to that of the upper end of the crop, but there are a small number of glands in the mucous membrane with an alkaline or neutral secretion. In the proventriculus the epithelium is reduced to a single layer of columnar cells. The glands of this region secrete the acid gastric juice. In the Pigeon they are small and simple: in the Fowl and Goose they have lateral loculi. But their size and character vary a good deal in different birds. They are largest in *Rhea* and the Ostrich.

The gizzard is well developed in the Pigeon as in the Fowl and the *Lamelirostres* s. *Chenomorphae* (Ducks, &c.). A short tube, which is always pale as compared with the vascular proventriculus, connects that organ to the gizzard. The pylorus is placed on the right side and close to the entrance of the proventriculus. The walls of the gizzard show two tendinous spots which lie one on the

right, the other on the left side in the natural position of the organ. The two tendinous spots are the centres whence radiate the musculi laterales which make up the bulk of the organ. They are composed of smooth muscle fibres which in transverse section appear to lie in columns, the fibres in each column being connected to the fibres in the adjoining columns by short tendinous fibres. Two softer muscular bundles lie one close to the entrance of the proventriculus, the other at the opposite pole. These are the musculi intermedii. The mucous membrane is glandular; and the glands secrete the horny internal lining. This lining is discoloured by the food, and it is continually worn away by the attrition of stones, &c., swallowed with the food; and it is continually formed anew by the action of the glands. If it is stripped off by force, the attached surface appears as if covered by very fine short villi, or processes which have been pulled out of the gland-tubes. In sections of the gizzard these processes can be readily made out dipping into the gland-tubes; they are conical, more transparent, and apparently softer than the superficial layers. Vertical lines, apparently formed either by irregularities of structure or by imbedded cells, are traceable nearly through the thickness of the horny layer. In many birds, e. g. flesh-eating birds, the muscular walls of the gizzard are thin and its secreted lining soft and tenacious. The degree of development of the muscles and the lining is closely connected with the character of the food—as was shown by Hunter's experiment of feeding a Sea-gull with barley. The muscles then became at least double the thickness of those in a Gull which had lived on fish. Cf. Catalogue of Physiological Series, Royal College of Surgeons' Museum, i. p. 49, preps. 522 D, and 523.

For the bile and pancreatic ducts, see description of Plate II.

The two caeca appended to the commencement of the large intestine are very small in the Pigeon—a contrast to the long caeca of the common Fowl, Pheasant, Grouse, &c. The large intestine is short and straight, as in all birds except the Ostrich. The rectal aperture lies at the apex of a cloaca common to it and the urogenital ducts. The rectal region of the cloaca is large and is separated by an annular ridge, which in some birds is but feebly indicated, from a small middle or urogenital chamber into which open the ureters and genital ducts on the dorsal wall, the genital apertures externally to those of the ureters. An annular fold always present separates the urogenital chamber from the third, outer or posterior chamber, the external opening of which is guarded by a strong sphincter muscle. An aperture on the dorsal wall of this outer chamber leads in young Pigeons into the Bursa Fabricii—an ovoid sac with a narrow neck lying dorsally to the cloaca. In the *Ratitae* (? *Apteryx*) the urogenital chamber opens *into* the Bursa owing to the fact that the neck of the latter is not constricted, and its aperture is commensurate with the dorsal aspect of the outer chamber of the cloaca. In *Plotus anhinga* (Darter), a *Carinate*, Garrod found a large aperture to the Bursa, and Forbes has confirmed the fact. The Bursa commences to atrophy in the Pigeon at the sixth, in the Fowl at the eighth, month according to Martin Saint-Ange. There seems to be much variety in this respect among birds, and it is possible that it occasionally persists. As a rule, however, its aperture closes, its cavity is obliterated and its walls atrophied—a more or less fibrous remnant persisting. It is large in the embryo. Its function and homology are unknown: its cavity contains only remnants of faeces or concretions, the origin of which is

not certain. It appears early in development as a solid outgrowth of cells from the dorsal wall of the proctodaeum (= cloaca) *before* the rectal aperture opens into it. The central cells atrophy and thus form the cavity of the organ. In the adult, according to Stieda, the walls consist of a fibrous outer coat with internal prolongations which form the axes of the primary and secondary longitudinal folds which project internally; and an internal epithelium which has several layers of cells, the superficial columnar, the deep angular, separated from the fibrous coat by a *membrana propria*. In addition there are the 'follicles' so-called, which are imbedded in the longitudinal folds. Each follicle consists of a central mass of minute rounded nucleated cells, continuous at the apex of the follicle with the deep layer of the epithelium, and probably never cut off from it; of a *membrana propria* continuous with that of the epithelium; and of a surrounding investment of adenoid or reticular tissue with numerous capillaries developed from the same embryonic cells as the fibrous coat.

The respiratory system has the usual structure seen in birds. The syrinx or lower larynx is simple. The last 3-4 rings of the trachea send towards one another on the ventral surface processes which do not fuse. The two last rings are widely separated dorsally, but they are joined *inter se* by a cartilaginous rod. The bronchial rings are only half-rings, i. e. are incomplete on the inner surface of the bronchus. The free ends of the two first rings meet dorsally and ventrally, and together with the modified tracheal rings form the tympanum. A thin membrane—the *membrana tympaniformis interna*—forms the inner wall of the anterior part of each bronchus where the ends of the half-rings are wide apart. Inside the tympanum the mucous membrane is thickened, and there are two cushion-like projections, one on each side. A fold, the *membrana semilunaris*, projects forwards between the cushions from the point of bifurcation of the trachea. It is supported by the *pellus*, a rod of cartilage, sometimes ossified. The Pigeon has but one pair of syringeal muscles—the *tracheales laterales*. The syrinx is least developed in the *Cathartidae*, or American Vultures. It is a distinctive avian structure, and is present in the *Ratitae*, where it is often said to be absent, and it is best developed in *Rhea*. The trachea is tied to the sternum by a pair of muscles—the *sterno-tracheales*.

The structure of the lungs, bronchi and air-sacs, is very similar in all birds. The main bronchus enters the lung, gives off above the spot where the pulmonary artery crosses it four eparterial bronchi and below that spot nine hyparterial. The ultimate branches of the bronchi are long tubes closely packed. Their inner walls carry projecting circular fibrous septa connected by longitudinal septa. The respiratory capillaries are distributed on these septa. An epithelium lining these tubes has not been detected. Other structures to be carefully noted are the costopleural muscles, small muscular bundles which spring from the junction of the vertebral and sternal ribs and spread out like a fan in an aponeurosis (i. e. tendinous expansion) which lies on the ventral aspect of the lung between the pleura and the air-sacs. The air-sacs appended to certain bronchi are nine in number and are as follows,—an *interclavicular* sac lying in front of the trachea and formed by the fusion of two sub-bronchial sacs, the bronchial apertures of which lie just anterior to the spot where the bronchi enter the lungs; two *prae-bronchial* sacs lying one dorsal to each lobe of the interclavicular sac, with apertures at the anterior border of the lung; two *anterior intermediate* or *thoracic* sacs with apertures

tures close behind the point of exit of the pulmonary veins: two *posterior intermediate* sacs lying one on each side in front of the corresponding *posterior* or *abdominal* sacs, with apertures at the postero-external angles of the lungs. The walls of the sacs are thin, and lined by a pavement epithelium, the ciliated epithelium of the bronchi ending at the spot where they open into the sacs.

The following additional points should be noted in the heart. A thin muscular Eustachian valve protects the entrance of the vena cava inferior. The right auriculo-ventricular valve consists of two muscular flaps, one long and external, the other short, meeting the first at a slight angle and connected to the ventricular wall at the base of the conus of origin of the pulmonary artery, which is long. The left auriculo-ventricular or mitral valve consists of two membranous flaps with chordae tendineae and muscoli papillares as in a Mammal. A transverse section across the ventricles shows a very thick walled left ventricle with a thinner walled right ventricle, the cavity of which is crescentic, embracing the left ventricle. *Ornithorhynchus* alone among Mammals shows a similar section. Three semilunar valves guard the base of the aorta and pulmonary artery. The common carotids run up the demi-canal on the ventral aspect of the cervical vertebrae, hidden by the muscles. The jugulars are connected by an anastomosis across the base of the skull, and there is a remarkable subcutaneous venous plexus in the neck. The connections of the veins of the kidney and of the hind limb are characteristic. The femoral vein coming from the hind limb passes through the kidney between its anterior and middle lobes. Close to the internal border of the kidney it receives on its anterior border the efferent vein of the anterior lobe: on its posterior of the middle and posterior lobes. It then passes on as the common iliac vein, and, joining its fellow, becomes vena cava inferior. Towards the outer border of the kidney the femoral vein gives off an afferent renal vein, which enters and ramifies in the anterior lobe of the kidney; and a second—the renal portal, or hypogastric vein—which traverses the middle and posterior lobes of the kidney, gives off branches in its course, receives the sciatic vein, and then issues from the posterior lobe of the kidney and unites with its fellow. Into the point of union falls the caudal vein: from it issues a large coccygeo-mesenteric vein, which receives veins from the cloaca and large intestine, runs along the mesentery of the large intestine, and joins the portal system. Each lobe of the kidney receives a small artery. As pointed out by Jourdain, the calibre of the veins is out of all proportion to that of the arteries. He states that each renal lobule contains a central vein, or rootlet of the efferent vein, and is surrounded by a number of venules derived from the afferent vein. A capillary network connects the two systems of vessels. As there are no valves in the renal portal veins, with rare exceptions, such as certain *Ratitae*, Bustard, Swan, the blood from the viscera and hind limbs can pass freely either through the iliac veins and thence to the vena cava, or through the coccygeo-mesenteric vein to the hepatic portal system. It can hardly be doubted from these facts that the kidney, as in Reptilia, receives venous blood.

The thyroid is a paired gland, and lies close to the origin of the common carotid arteries. The thymus is also paired, and may be found in young birds as a long gland, one on each side of the neck. The spleen lies on the right side of the proventriculus. The supra-renal capsules are two yellow bodies closely connected to the iliac veins at the anterior end of the kidneys.

The generative system is the same as in all birds. A rudiment of the right ovary is rarely detectable; but there is frequently a rudiment of the oviduct of that side. There is no intromittent organ.

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## 11. THE SKELETON OF THE COMMON PIGEON (*Columba livia*).

A Bird's skeleton has characters both peculiar and well-marked. The bones undergo extensive ankylosis especially in the skull, pelvic region, hand and foot. The bone-substance is dense, and is stated to contain a large proportion of lime phosphate. The cancellated tissue with the marrow is frequently absorbed and its place taken by air derived in the skull from the nasal passages and tympanic cavities: in the rest of the skeleton from extensions of the air-sacs connected with the lungs. All the bones in the Pigeon contain air, i. e. are *pneumatic*, save the caudal vertebrae, the fore-arm and hand and hind-limb.

The skull presents the following general features:—It has, like the Reptilian skull, a single condyle. The cranial surface is smooth, polished, and its sutures obliterated. The orbital cavities are large and separated one from another by a thin vertical inter-orbital septum, formed chiefly by the mesethmoid. The orbit is bounded in front by the lacrymal bone and the homologue of the lateral mass of the ethmoid in man. The beak consists mainly of the praemaxillae, which are continued backwards below the orbit by a slender bony rod. The anterior part of this rod is the maxilla, the posterior which articulates with the quadrate, a jugo-quadrato-jugal bone. A moveable quadrate articulates with the skull on the one hand, and the lower jaw on the other. The two rami of the mandible are ankylosed at the symphysis. A ring of bony plates developed in the sclerotic of the eye is seen suspended in the left orbit. A similar ring is found in many Lacertilia, the Chelonia, and extinct Ichthyosauria.

The vertebral column is divisible into a cervical, dorsal, so called



sacral, and a caudal region. The articular surfaces of the centra are typically procoelous and cylindroidal, i. e. concave from side to side and convex from above downwards anteriorly, curvatures which are reversed posteriorly. The cervical and dorsal vertebrae have synovial joints. A ring of fibres binds together the edges of the opposing surfaces. Between them is interposed a fibro-cartilaginous meniscus thick at its circumference, thin centrally where it is perforated for the passage of the 'suspensory ligament' which unites the vertebral centra. The free caudal vertebrae have usually flattish centra. They articulate as in Mammalia by intervertebral discs (*annuli fibrosi*), which have centrally a 'nucleus pulposus,' the homologue of the suspensory ligament and formed as it is from notochordal cartilage.

The length of the neck in every Bird is at least equal to the height from the ground at which the legs carry the body and to the distance from the root of the neck to the last caudal vertebra. The actual length varies, and depends chiefly on the number of vertebrae present, and not on the length of their centra. In Mammalia while the number of vertebrae is nearly invariable, the length of their centra is very variable. The atlas is ring-like and articulates with the occipital condyle by a deep cup completed as in Reptilia by the odontoid process of the axis. This latter vertebra has a neural spine, and an inferior spine, a structure present also in the two next vertebrae. The odontoid is ankylosed to its centrum. The third vertebra has its neural arch deeply emarginated before and behind, a peculiarity repeated in the seven following vertebrae. It has also, like the next nine vertebrae, cervical ribs ankylosed to the superior and inferior transverse processes, and inclosing a canal which lodges the vertebral artery and vein with the main trunk of the sympathetic. The fourth vertebra has no neural spine, and its centrum has ventrally a pair of downgrowths which form a demi-canal for the protection of the common carotid arteries. These features are repeated in the succeeding vertebrae to the tenth inclusive. The eleventh and twelfth have inferior spines; the two following—the thirteenth and fourteenth—have neural spines; their ribs are free but not connected to the sternum, and the last pair carry recurrent or uncinat processes like the first four pairs of dorsal ribs. By some anatomists the thirteenth and fourteenth vertebrae are counted as dorsal. Five vertebrae make up the dorsal region defined by the presence of free ribs connected to the sternum. They have large neural spines and transverse processes with keel-shaped centra. The three first have their centra ankylosed, and the ligaments connecting their neural spines, inferior spines, and transverse processes ossified. The fourth dorsal is free: the fifth unites with the sacrum. The sacrum contains, as it always does in Birds, vertebrae derived from four regions. The first is a dorsal vertebra with ribs. The six vertebrae succeeding it are lumbar, of which the three

last retain only the upper division of the transverse processes, which are present also in all the remaining sacral vertebrae. The ligaments uniting these processes ossify, and a flat subcutaneous area (absent in Ratite birds) is thus formed. To the lumbar succeed two sacrals, homologues of the vertebrae so named in Lizards, &c. In some specimens of the Pigeon, both of them carry a pair of stout bony rods or ribs visible only from below. These ribs are not free. They swell at their distal ends which fuse to the outer ends of the transverse processes (upper division) of their own vertebrae and coincide with the widest part of the area mentioned above, and lie therefore just internal to the acetabulum. Either the first or the second pair of these ribs may be absent. Behind the sacral vertebrae comes a variable number of caudal vertebrae, termed for distinction's sake 'uro-sacrals.' The free caudal region contains seven to eight vertebrae. They have no articulating processes. The last is thin, compressed, and up-turned. It is known as 'pygostyle' or ploughshare bone (*os en soc de charrue*), and represents four to six fused vertebrae.

The five pairs of ribs consist of ossified vertebral and sternal sections. Each vertebral section articulates only with its own vertebra: the first four bear uncinatè processes united to their posterior borders. These processes, as in *Hatteria*, *Iguana* and the Crocodile, are pre-formed in cartilage. The last sternal section unites with its predecessor, not with the sternum. The sternum covers nearly the whole abdomen and has a deep concave internal surface. There are four borders:—an anterior bearing the rostrum in its centre with a coracoid groove on either side and ending laterally in a costal process; a right and left costal border deeply concave and bearing the ribs; and a posterior or xiphisternal border. This border is convex, of great extent, and interrupted, as in some other Birds, on either side the median line by an outer xiphisternal notch and an inner xiphisternal fontanelle—the inner notch of the Fowl tribe. Notch and fontanelle are in the living bird closed by membrane probably substituted for original cartilage. The border presents accordingly five processes—two outer, two intermediate, and one median. The convex outer surface of the sternum carries the keel or carina, whence comes the name *Carinatae*, applied to the vast majority of living birds as opposed to the Ostrich and its allies, known as *Ratitae* from the raft-like aspect of the keel-less sternum.

The shoulder girdle consists of a scapula, coracoid, and furcula<sup>1</sup>. The scapula is sword-shaped and thin. There is no separate suprascapula. A small conical process internal to the glenoid facet represents the meso-scapula or acromion. The coracoid is firmly united by ligament to the scapula. A prominent *clavicular* process rises in front of its glenoid facet, and there is a thin curved subclavicular, or subscapular process (= praecoracoid),

<sup>1</sup> This word is often, but incorrectly, written *Furculum*. It is written *Furcula* in Bronn's *Klass. und Ordn. des Thierreichs*, vi. Abth. 4 by Selenka, without the mention of any other form.

on the internal, or true anterior, border in contact with the acromion. A rough line runs downwards from it to the broad sternal or epi-coracoidal end of the bone and gives attachment to the coraco-clavicular membrane. The coracoid fits into a groove in the sternum. The furcula, a characteristic Avian bone, is formed by the fusion of the ventral ends of the two clavicles. At its upper end each clavicle expands into a disc or epicleidium, which is tied by ligament to the acromion and to the sub-scapular and clavicular processes of the coracoid. There is thus formed a *foramen triosseum* through which the tendon of the second pectoral muscle, or elevator of the wing, passes to its insertion on the humerus. The spot where the ventral ends of the clavicles fuse is prolonged into a point, the homologue of the large hypocleidium in the Fowl, and united as it is to the keel of the sternum by a ligament which together with the point represents a portion of the interclavicle.

The fore-limb of this specimen is in the position of rest. The humerus lies parallel to the axis of the body, its true ventral surface turned outwards; the fore-arm is flexed on the humerus and the hand is adducted. When the wing is expanded, the hand is abducted: it is incapable of flexion. As to the humerus, its glenoid head is transversely elongated: on its radial or upper margin at the proximal end is a conical process to which the first pectoral, or depressor of the wing, is attached, and dorsally to it is the facet for the insertion of the second pectoral. On the ulnar margin proximally and dorsally is a deep pit, at the bottom of which is a pneumatic foramen. The surface of articulation for the radius is long, oblique and on the ventral surface, as in Lizards. The radius is rod-like; the ulna stout, somewhat curved, and with a short olecranon. Its outer surface is pitted by the sacs of the secondary wing feathers. There are two carpal bones in the proximal row—a scaphoid (= radiale), and a fused lunar and cuneiform (= intermedium and ulnare). The distal carpalia are fused to the heads of the metacarpalia, forming a carpo-metacarpal bone. The first metacarpal is a mere process and carries a single phalanx; the second is stout and long and carries two phalanges; while the third is slight, curved and fused distally to the second, and carries but one phalanx. In no Bird are there more than these three digits.

The pelvis has the three bones ileum, ischium, and pubis peculiarly disposed. The first extends backwards and forwards along the whole extent of the sacrum; the ischium lies parallel to the backward extension of the ileum; the pubes to the ischium, and neither of the two latter have a ventral symphysis. All three unite in the acetabulum. The centre of this cavity is membranous in the living animal. Hence in a prepared skeleton it appears to be perforated. A prominent surface—the antitrochanter—on the posterior-superior margin of the acetabulum, works against the base of the neck which carries the head of the femur. Ileum

and ischium fuse distally, and thus inclose an ileo-sciatic foramen. The obturator foramen between the ischium and pubes is long and narrow, and subdivided partially by the obturator process of the ischium. The femur is remarkably short. The head is prominent, and its neck at right angles to the main axis of the bone. The condyles are large and separated by a deep patellar groove. The external one is typically subdivided, and its outer subdivision plays between the tibio-tarsus and fibula. The former of these two bones is the largest in the limb. It has proximally a cnemial crest on the anterior surface, subdivided into a pro- and ecto-cnemial process; and distally there are two condyles formed from a cartilage in the embryo which represents the proximal tarsalia—astragalus and calcaneum. Anteriorly and above these condyles a narrow bony bar confines the extensor tendons of the toes. The fibula is slender and pointed distally. The third section of the limb is the tarso-metatarsus, a compound bone formed by the union of a bone representing the distal tarsalia to the heads of the second, third, and fourth metatarsalia, of which the third is the longest. Behind the tarsal element lies an ento-calcaneal process, the attachment of the tendo Achillis, pierced and grooved by the flexor tendons of the foot. The first metatarsal is small, incomplete proximally, and united to the second by ligament. There are four digits in all—the first, or hallux, is turned inwards and backwards and carries two phalanges; the three remaining digits carry phalanges increasing successively in number from three to five, the usual succession in Birds. The third is the longest digit; the fourth is so only in a few instances, e. g. Penguin, Gannet, Pelican, &c.

All the bones in the embryo contain marrow. The degree in which it is replaced by air varies much. *Apteryx*, Penguin, small Songsters, have air only in the skull: the Hornbill in every bone of the body. A membranous tube—the siphonium of Nitsche—conveys air from the tympanic cavity to the lower jaw, as in the Crocodile. This tube in the Raven, Thrush, &c. becomes bony. The Cretaceous toothed birds had a pneumatic skeleton, as was probably the case in the Dinosaurian Reptile, *Coelurus*.

The outlines of the cranial bones can only be seen in a young skull. The single condyle is made up, as in some Reptiles, by the basi- and ex-occipitals. The parietals are short but wide. Two membrane bones—the basi-temporals—parts of the parasphenoid, underlie the base of the skull, and the rostrum, or anterior part of the parasphenoid, similarly underlies the mesethmoidal septum. The palatine bones extend forwards to the maxilla and articulate behind with the rostrum. The pterygoids articulate in front with the palatines and the basipterygoid processes of the rostrum, while behind they diverge and articulate with the quadrate. The maxillae have short palatal plates—'maxillo-palatine processes'—which extend inwards above the anterior end of the palatines. The squamosal and jugal are only connected by ligament, not by bone, as in Mammalia.

The Pigeon and Sandgrouse have no vomer, the Fowl has a pointed vomer

at the anterior end of the rostrum. The internal nares open between the rostrum and the palatines, and there is no hard palate. The Pigeon, like many birds, is in a permanent state of cleft palate (schizognathism), owing to the palatal plates of the praemaxilla and maxilla not meeting in the middle line.

The lower jaw of the young Fowl has five bones in each ramus, a dentary, splenial, angular and surangular with one cartilage bone, the articular. Some Birds add a coronoid, thus attaining the standard of the Lacertilian. The symphysis in the Cretaceous toothed birds was ligamentous.

The hyoid is characteristic. There are three median bones, one tongue-shaped, formed by the union of the ceratohyals, followed by the basihyal and a basibranchial. The first branchial arch is well developed, and consists of an upper epi- and a lower cerato-branchial. The joints between the several parts are synovial.

*Archaeopteryx* (Jurassic), *Ichthyornis* and *Apatornis* (Cretaceous) had amphicæulous vertebrae like the Geckoes and *Hatteria* among living Lizards. The third cervical of *Ichthyornis* shows transitional characters to the modern Bird, and closely resembles the corresponding vertebrae in the Tern (Marsh). A transitory amphicæulous stage exists in the chick on the seventh day. Some of the dorsals in the Penguin, Auks, Plovers have spheroidal faces and are opisthocæulous. The cervical ribs remain distinct for a long time in *Ratitæ*. The division between cervical and dorsal vertebrae is somewhat arbitrary. The late Professor Rolleston considered the two vertebrae with ribs not touching the sternum as dorsals, because the ribs indent the lungs, and the last pair carries uncinæ processes. Professor Huxley considers them as cervicals because the ribs do not touch the sternum. But there is embryological evidence in favour of the former view. It has been shown by Miss B. Lindsay that two anterior ribs in the Fowl and one in the Gannet are continuous at an early stage with the sternum, but become separated from it subsequently by atrophy. The identification of two vertebrae as 'sacral' and as homologous with the vertebrae so named in Lizards depends on the following points: (1) their predominant size in the embryo; (2) the presence of free ribs ossifying by separate centres in the embryo while the preceding vertebrae are devoid of them; (3) that these ribs expand and fuse distally, as in the Crocodile; (4) that they are in relation with the acetabulum; and (5) that the nerve passing out between the ribs is the last and weakest factor in the plexus ischiadicus, as in Lizards.

Anchylousis of three dorsal vertebrae is characteristic of the *Peristeromorphae* (Pigeon group), while four are similarly anchyloused in the *Alectoromorphae* (Fowl group), but the first is a cervical.

*Archaeopteryx* has but five anchyloused sacral vertebrae, and the tail contains twenty vertebrae, of which the last fifteen are devoid of transverse processes, and carry each a pair of large feathers. *Hesperornis* has fourteen sacral and twelve caudal vertebrae, of which the last six or seven are anchyloused by their centra only, and are in other respects free.

The sternum is formed from right and left plates of cartilage, constituted by the fusion of the ventral ends of the ribs. The absence of transverse segmentation universal in Mammalia is characteristic of Birds and Reptiles. The carina, according to Götte and Hoffmann, is formed from a single or primitively double

band of tissue continuous with the clavicles. It therefore represents in part the interclavicle of a Reptile. The anterior extremity of the band forms the hypocleidium and the interclavicular or sterno-clavicular ligament. Their view has been recently controverted by Miss B. Lindsay, who contends that the Avian sternum consists (1) of a costal sternum derived from the ribs; (2) of a metasternum, apparently a growth from (1); (3) of anterior lateral processes (costal processes), either outgrowths of (1) e.g. *Struthio*, or formed from anterior ribs, e.g. Chick; (4) of a keel, an outgrowth of (2); and (5) posterior lateral (i.e. xiphisternal) processes derived from (2) also; together with other structures sometimes present. The subject requires re-investigation. The shape, disposition, &c. of the several parts of the sternum vary much in Birds.

The scapula and coracoid are fused in *Ratitae* and connected by ligament in *Carinatae*. Each ossifies from a single centre. With rare exceptions (*Psophia* among *Carinatae*, *Apteryx* among *Ratitae*), the inner or anterior border of the coracoid becomes partially ligamentous. The sub-scapular process when large, e.g. Gull, Eagle, is pierced by a foramen; when small, this foramen lies in the ligament. A foramen similarly placed exists in the complete coracoid of *Psophia* and *Apteryx*, and in the Crocodile and most Lizards. It transmits a nerve for a muscle, the second pectoral in the Bird. These facts point to a homology, as maintained by Sabatier, of the sub-scapular process of the coracoid with the praecoracoid of the Reptile, i.e. with its proximal extremity. In the embryo, as figured by Miss Lindsay, there appears to be a large praecoracoid rudiment. The ligamentous portion of the coracoid is well characterized by its tough nature and parallel fibrillation. It is invaded more or less by ossification in *Ratitae*, and in an old Ostrich its anterior margin ossifies, inclosing a coracoid fontanelle. In a Carinate it forms part of the coraco-clavicular ligament. The clavicular process of the coracoid gives attachment in *Carinatae* to the deltoideus minor muscle and principal ligament of the shoulder-joint. In *Ratitae* it is represented by a mere roughness or slight tuberosity. It must be considered as a process developed for the same reason and for the same purpose as the deltoid tubercle or supinator ridge in the humerus of some Mammalia, e.g. Armadillo. The structures attached to it are of prime importance in flight. The two clavicles ossify parosteally. They may be absent, as in all *Ratitae* save the Emu, and in some Parrots; or fail to meet ventrally—Emu, Toucan, some Parrots and Owls. The upper end (epicleidium), small in the Pigeon, may be large, e.g. Goose, and is stated to be in this case cartilaginous in the embryo. The hypocleidium is small in the Pigeon; it is large and directed downwards, e.g. Fowl, or backwards, e.g. Rook. A coraco-clavicular ligament unites each clavicle to the inner border of the coracoid, and a sterno-clavicular ligament unites the hypocleidium to the carina. Irregular ossifications may appear in these membranes.

The proportions of the segments of the fore-limb one to the other vary much. In *Ratitae* they show scarcely a trace of the characteristic Avian position when at rest. The Cretaceous *Hesperornis* has only the humerus, and the limb is either absent or reduced in the extinct *Dinornithidae*. In *Archaeopteryx* the parts of the hand are free, and each digit appears to have borne a claw. A carpo-metacarpus exists in all other birds. In the embryo fowl a mass of cartilage (=carpalia i + ii) corresponds to the two first metacarpals, and a second (=carpalia iii + iv) to the third and embryonic fourth metacarpals. *Uria grylle* has, according to Morse, embryonic claws to the first and third digits.

The bones of the pelvis are separate *inter se* in *Archaeopteryx*. In all other birds they fuse, at least in the acetabulum. The *real length* of the ilium is to be measured from the outer ends of the sacral ribs to the acetabulum. The great extension of the bone along the sacrum represents *breadth*, and is an exaggeration of a Crocodylian and Deinosaurean feature. The praeacetabular section, with few exceptions, ossifies parosteally, and it is rarely shorter than the postacetabular section, as in the Ostrich, Divers, and *Ichthyornis*. The *length* corresponds with the iliac axis of Professor Huxley. As in all Sauropsida this axis makes an acute angle forwards, not backwards as in Mammalia, with the sacral axis, i. e. a line drawn antero-posteriorly through the centra of the sacral vertebrae. The dorsal iliac area is little developed in some birds, e. g. Ostrich, Divers.

The backward inclination of the pubes and ischia, and the loss of the ventral symphysis is characteristic of birds among living Vertebrata. So far as the pubes are concerned, there was no symphysis in many of the extinct *Deinosauria*, and the same is true in some instances of the ischia also; and this is especially the case in the two groups *Stegosauria* and *Ornithopoda*, in which the conformation of the pelvis is Avian and the ischia with the main part of the pubes (post-pubes) are inclined backwards. The Ostrich is the sole example of a bird with a pubic symphysis, and in *Rhea* the ischia meet not ventrally, however, but dorsally immediately under the backbone. The union between the distal ends of the pubis and ischium of the same side, and of the latter with the ileum, does not always occur, e. g. Cassowary, Emu, *Apteryx* among *Ratitae*; the Tinnamou among *Carinatae*. There is a well-developed pectineal process in front of the acetabulum in the Ostrich. An examination of a young specimen shows that both ileum and pubis enter into its formation. A similar process is found in some *Carinatae*; but it appears to be formed entirely by the ileum in the Fowl. The chick, however, as proved by Miss A. Johnson, has at an early period a large forward extension of the pubis which gradually dwindles away. This process appears to be the homologue of the prae-pubis (so-called) in the *Stegosauria* and *Ornithopoda* among *Deinosauria*, whilst the main portion of the bird's pubis is the homologue of the post-pubis (so-called) in the same groups. There does not appear to be much ground for supposing, (as has been done) that the prae- and post-pubis represent separate bones. They are continuous one with the other in *Stegosaurus* (cf. Marsh, American Journal of Science and Arts, xxi. p. 169, Pl. viii.), in *Camptonotus* (op. cit. xviii. p. 502), *Laosaurus* (op. cit. xvi. p. 415, Pl. x.), and in *Iguanodon* (Dollo, Bull. Mus. Roy. d'histoire Naturelle de Belgique, ii. 1883, Pl. iii.). And the solitary instance of *Allosaurus*, which was supposed by Marsh to have had a *separate* post-pubis (American Journal cited, xvii. p. 90, Pl. vii. 2), is now included by that author in a group of Carnivorous *Deinosauria*, the *Theropoda*, in which the post-pubis is absent. See Marsh on *Theropoda*, American Journal of Science, xxvii. 1884. Baur has recently suggested that the pectineal process (in part) of Birds and of *Deinosauria*, or the prae-pubis in some of the latter group, is the homologue of the Os acetabuli of Mammalia (see note, p. 107, Z. A. ix. 1886). For the Os acetabuli, see Gegenbaur, Ausschluss des Schambeins von der Pfanne, &c., M. J. ii. 1876; Krause, Centralblatt für Medicin. Wissenschaften, 1876, p. 817; Leche, Bronn's Klass. und Ordnungen des Thierreichs, vi. pt. 5, Mammalia, p. 576; Id. Monthly Internat. Journal of Anat.

and Histology, i. p. 363. For a figure of *Iguanodon*, see Moseley, Nature, xxviii. 1883, p. 441; or Dollo, op. cit. *supra*, Pl. v. Cf. Hulke, Journal Géol. Soc. xl. 1884, p. 53; and Huxley, Anatomy of Vertebrated Animals, 1871, pp. 223-228.

The process of the ischium which divides the obturator foramen into two portions is very large in the Deinosaur *Laosaurus*. The upper division of the foramen transmits in birds the tendon of the obturator internus muscle, a rather curious point.

Of the segments of the hind-limb, the femur is remarkably short and very broad in *Hesperornis* and the Divers; while the tibio-tarsus is of great length in *Ratitae* and *Waders*. The fibula is as long as the tibia in *Archaeopteryx*. It is so at one time in developing birds but shortens subsequently. The tarsal element of the tibio-tarsus has been found by Baur to appear in the embryo chick as two bones, a tibiale and a fibulare, corresponding to the tibia and fibula respectively. The tibiale develops an ascending anterior spur, while the tibia broadens out so as to cover the fibulare, and the fibula itself shortens. The two tarsal bones subsequently unite. According to Morse the ascending process corresponds in the embryos of certain birds representing various groups (*Alcidae*, *Laridae*, &c.) to a separate intermedium. If this is so, there are three proximal tarsalia in some birds, each with its own ossific centre. The ascending spur of the tibiale (? = astragalus) is present in *Deinosauria*. The bony arch confining the extensor tendons in the Pigeon as they pass over the tarsal region of the tibio-tarsus is ligamentous in *Ratitae*. This ligament is united at one end to the tibia, at the other to a bony projection apparently developed on the fibulare (= calcaneum) both in the Ratite and the young Carinate. It probably corresponds to the anterior annular ligament of the human foot. The distal tarsal elements are represented by a single cartilage which corresponds eventually to the second, third, and fourth metatarsalia. The rudimentary fifth metatarsal fuses with it (Baur).

The metatarsalia in *Archaeopteryx* are apparently free, or but slightly ankylosed. In Penguins the three metatarsalia (ii., iii., iv.) are short and lie parallel to one another. They are not raised from the ground in them nor in Auks and Divers. Mt. iii. is the largest as a rule, but Mt. iv. is as large in some birds and much larger in *Hesperornis*. The calcar of the Fowl ossifies independently, but fuses with Mt. iii. Mt. i. is only ankylosed to Mt. ii. in *Phaethon*. All the toes are united by a common web in the embryo—a condition which persists in the Pelican, Cormorant, Solan Goose, and Divers. They rarely all retain their primitive forward position, e. g. in the Penguin, Swift, &c. The hallux is sometimes absent.

*Aves*, Selenka and Gadow, Bronn's Klass. und Ordn. des Thierreichs, vi. Abth. iv. *Birds*, W. K. Parker and A. Newton, Encyclopaedia Britannica, (ed. ix.) iii. *Oiseaux fossiles de la France*, &c., Milne-Edwards, 2 vols. and Atlas, Paris, 1867-71. *L'appareil locomoteur des oiseaux*, Alix, Paris, 1874. *Palatal and other characters*. Huxley, P. Z. S. 1867, 1868.

*Pigeon*. T. J. Parker, Zootomy, London, 1884, p. 182.

*Fossil Birds*. *Archaeopteryx*. Damès, Palaeont. Abhandl., Berlin, ii. part 3, 1884. Marsh, Nature xxv. 1881-82. Vogt, The Ibis, 1880. Owen, Ph. Tr. 153, 1863. Cf. Baur, Z. A. ix. 1886, for complete lit. *Odontornithes* (*Hesperornis*, *Ichthyornis*). Marsh, Memoir, United States Geological Exploration, 40th parallel,



1880. *Odontopteryx*. Owen, Journal Geol. Soc. xxix. 1873. *Dinornis*, &c. Id. Extinct Birds of New Zealand, 2 vols. 1879. *Dodo*, Strickland and Melville, London, 1848. *Solitaire*, Newton and Clark, Ph. Tr. 168, 1878.

*Skull*. Development and Structure, W. K. Parker, 'Fowl,' Ph. Tr. 159, 1869. Cf. Id. Morphology of Skull, London, 1877, p. 219. Of other Birds and groups, Monthly Microscopical Journal, 1872, 1873; Tr. L. S. (2) i. 1879; Tr. Z. S. ix. 1877; x. 1879.

*Structure of Pneumatic bones*. Wildermuth, J. Z. xi. 1877.

*Vertebral column*, &c. *Articulations*, Jäger, SB. Wien. Akad. xxxiii. 1858. *Axial skeleton*. Mivart, Tr. Z. S. viii. 1874; x. 1879. *Pygostyle*. W. Marshall, Niederländ. Archiv f. Zool. i. 1871-73, p. 194. *Birds vertebrae*. Marsh, American Journal of Science and Arts, xvii. 1879.

*Processus uncinatus*. Behrens, Inaugural Dissertation, Göttingen, 1880.

*Shoulder-girdle*. Hoffman, Niederländ. Archiv f. Zool. v. 1879-82. Bunge, Inaugural Dissertation, Dorpat, 1880. Gegenbaur, Untersuch. zur Vergleich. Anat. der Wirbelthiere, ii. Leipzig, 1865. Sabatier, Comparaison des ceintures, Paris, 1880. Harting, L'appareil episternale des oiseaux, Naturkundigen Verhandlungen, Utrecht, 1864. *Shoulder and Elbow joint*. Fürbringer, M. J. xi. 1885.

*Shoulder girdle and Sternum*. Götte, A. M. A. xiv. 1877, p. 549. W. K. Parker, Ray Society, 1868. Miss Lindsay, P. Z. S. 1885.

*Sacrum and Pelvis*. Gegenbaur, J. Z. vi. 1871; cf. Huxley, P. R. S. xxviii. 1879, p. 399. Pelvis of Birds and Deinosauria, Baur, M. J. x. 1885. *Prae-pubis*, Miss Johnson, Q. J. M. xxiii. 1883.

*Carpus and carpo-metacarpus*. Rosenberg, Z. W. Z. xxiii. 1883

*Tarsus*. Morse, Memoirs, Boston Soc. Nat. Hist. 1880. Baur, M. J. viii. 1882. Cf. Id. op. cit. x. 1885, p. 446, and Z. A. viii. 1885. *Foot in Birds*. Forbes, Ibis, 1882. *Rudimentary Hallux*. Id. P. Z. S. 1882.

*Teeth in living Birds*. Fraisse, Verhandl. Phys. Med. Gesellschaft, Wurzburg, xv. 1881, SB. p. iii.

*Effects of artificial selection*. Darwin, Animals and Plants under Domestication, i. caps. v. vi. (ed. ii.) 1875. See also his Index.

## 12. COMMON RINGED SNAKE (*Tropidonotus Natrix*),

Injected and dissected so as to show the manner in which the viscera are arranged *in situ*.

THE following external characters, for the most part discernible in this specimen, should be noted:—the absence of limbs: the transparent cornea-like structure covering the eye formed by the union of the eyelids: no external mark indicating the position of the ear: the slight furrow between the two rami of the lower jaw permitting the free extrusion of the tongue when the mouth is closed. In these points as well as in the total loss of the shoulder-girdle Ophidians differ from Lizards, but they agree with them in having the cloacal aperture transverse and a complete investment of scales. These scales, with the exception of those upon the head

overlap one another. They are processes of the dermis with an epidermis, the outer layers of which are thick and horny. These layers, together with the outer coat of the fused eyelids and the labial organs of sense, are moulted periodically, apparently at intervals of one month, during the active summer life of the animal. There are three types of scales: the flat plates of the head with apposed edges: the series of broad ambulatory ventral scales extending from the throat to the divided scale which protects the cloaca: and the triangular scales of the body, smallest, and strongly keeled near the median dorsal line.

The Harderian gland of the eye and the labial glands of the mouth have been exposed by the removal of the skin. The lobed extremity of the former appears behind the eye: it extends *below* that organ and opens by a single duct at the inner angle. The true lacrymal gland which lies *above* the eye is absent in Serpents but present in Lizards, e.g. the Blind-worm. The labial glands of the upper jaw are divisible into two kinds, readily distinguishable in the freshly killed animal. The first kind is grey in colour and forms (1) the *azygos rostral* gland lying upon the praemaxillae and not exposed here, and (2) a series of composite glands, each with its own duct extending back to the angle of the gape. The second kind is naturally white, but assumes a yellow colour in spirit preparations. It is large, and opens by a single duct between the maxillary teeth, and is the homologue of the poison gland in the Viper. The glands of each ramus of the lower jaw form an unbroken series and are grey in colour.

The integument has been divided in the median ventral line as far as the prae-cloacal scale, and then reflected to the right and left. The dark-coloured tongue formed by the hyoglossi muscles extends backwards from the chin. On either side of it is a white rod, generally considered to be the larger cornu of the hyoid bone. The common jugular veins lie to the outer side of these rods. They rise into view at the angle of the mandible, and the right vein is well displayed in its whole course, the left only close to the heart. The trachea is seen externally to the right jugular close to the heart. This portion of it is dilated and marked by irregular ridges: the first portion lies dorsally to the tongue and has complete rings. The oesophagus, at first dorsal to the trachea, passes to the left side of the body where it becomes visible close to the heart. It dilates gradually into the stomach. Between the two jugular veins, and close to the heart, is the thymus gland, and between the latter and the heart three vessels are visible, one in front, the left aorta, one difficult to see in the middle, the carotid, and a third passing to the right, the right aorta. The left aorta reappears at the outer side of the left jugular vein, embracing the oesophagus. This organ is twisted to show the dorsal junction of the two aortae, beneath which a black bristle has been passed. The dorsal aorta in Snakes is not closely tied to the backbone as it is in other Vertebrata.

The pericardium has been cut away. The right auricle is large and has its wall removed to show the right auriculo-ventricular aperture. The left auricle is small and is crossed by the left jugular vein. The ventricle touches the small and rudimentary left lung, and rests upon the large and long right lung which lies behind the liver. Crossing the ventral surface of the right lung is the vena cava inferior, accompanied by the pulmonary artery which lies to its outer side. The liver is long and unilobar. A furrow on its outer surface lodges the vena cava inferior. The gall-bladder is large, and lies about a half inch from the posterior end of the liver. It is bent sharply upon its duct, beneath which a piece of blue paper has been passed. This duct and the bile duct unite *inter se*, and with the pancreatic duct in the substance of the pancreas, a globular gland lying on the intestine close behind the gall-bladder. The first portion of the intestine is straight, but from the pancreas onwards it is disposed in short abrupt coils. These are supported by a mesentery, but the peritoneal coat does not follow every turn of their course as is usual, but passes from the end of one coil to the end of the next succeeding. The coils are closely united by connective tissue.

The lobed fat body commences about the level of the pancreas. It is fastened out on the animal's right side; the branches of a vessel, the remnant of the epigastric vein, may be seen here and there among its lobes. The vessel in question joins the portal vein. About four inches from the liver is the right ovary with a single row of ova, and between it and the fat body is the vascular oviduct. The left ovary and oviduct have similar relations on the left side, but are placed more posteriorly. The same asymmetry is visible in the position of the two kidneys, organs consisting of a number of leaf-like lobes placed one behind the other. Close to the cloaca, the large intestine is seen lying between the two oviducts. It has been opened and a black bristle passed through it into the cloaca. The left oviduct has a white bristle similarly inserted into it. The skin and muscles behind the cloaca have been removed to show the two sacs, homologues of the two eversible sacs or intromittent organs of the male.

The following points of anatomy may be noted, not visible in the specimen. The subcutaneous connective tissue is very scanty in amount and absent altogether on the abdominal surface.

Nervous system. The olfactory lobes of the brain are swollen terminally and are long; the prosencephala broad; the cerebellum somewhat tongue-shaped and projecting over the fourth ventricle. The pituitary body is broad. The parts of the brain lie nearly all in one plane. There is no spinal accessory nerve.

Special sense organs. There is no tympanic cavity. Among Lizards, the Geckoes (*Ascalabota*) *Amphisbaenae* and some others resemble the Ophidia in the fusion of the eye-lids. There is thus formed a lacrymal sinus.

Circulatory organs. There is a sinus venosus formed by the union of the vena cava inferior and the right jugular vein. It opens into the right auricle by an aperture guarded by two valves. The left jugular opens into the auricle separately. A single pulmonary vein opens into the left auricle. The two auricles are separated by a septum, the free edge of which is produced into a right and left auriculo-ventricular valve. The ventricle has a single cavity partially subdivided by a muscular band or septum on its anterior wall. To the right of this septum is the cavum pulmonale from which the pulmonary artery arises. The left side of the ventricular cavity is divisible in turn into a left cavum arteriosum into which the left auricle opens and a right cavum venosum from which arise to the right the left aorta, to the left the right aorta. Hence these two vessels cross at their origins. In contraction of the heart the septum isolates the cavum pulmonale completely. The three great vessels, i. e. two aortae and pulmonary artery have, as in all Reptilia, two semilunar valves at their origin.

In the arterial system the right aorta gives off, first, two coronary arteries; secondly, an arteria cephalica, the common origin of the two carotids; thirdly, an arteria collaris, which runs beneath the back-bone and ends close to the head. The left aorta gives off no branches. The subvertebral aorta has no caeliac axis; there are several hepatic and renal arteries, and the right and left intercostal arteries arise by a common stem. The aorta is continued into the tail as the caudal artery. The pulmonary vein lies hidden by the vena cava.

In the venous system, the right inferior jugular close to the heart receives two veins, a short anterior and a long posterior azygos. The vena cava inferior is formed by the union of the two efferent renal veins; it receives the ovarian (or testicular) veins, and the hepatic veins in its course along the liver. The portal vein rises on the dorsal wall of the cloaca and receives the veins of the intestines, stomach, spleen, pancreas, the epigastric vein and the intercostal veins. It runs on the visceral surface of the liver to which it is distributed. The reni-portal veins of the kidneys are formed by the bifurcation of the caudal vein. There are anastomoses between them, the portal, and the epigastric veins.

Digestive system. The tongue is partially contained in a sheath which opens anteriorly on the floor of the mouth. Leydig describes a paired and an azygos gland in connection with this sheath. The stomach gradually contracts to the pylorus, which is well developed. The last six inches of the small intestine are nearly straight; it opens laterally into the large intestine, and there is in some specimens a short caecum (as in the Pythons) at this spot. The large intestine is about three and a half inches long; it gradually increases in calibre to the cloaca, from which it is marked off by a constriction.

Respiratory system. The posterior portion of the lung is thin and not alveolated, and receives blood from the hepatic arteries. In Pythons the left lung is functional, though smaller than the right. In *Hydrophis cyanocincta*—a marine serpent—the lung extends to the cloaca, beneath the back-bone.

Urinary system. The ureter runs centrally between the reni-portal vein on the outer and the efferent renal vein on the inner side. There is no urinary bladder.

Generative organs. The testes are elongate, rounded organs with a small epididymis, and placed asymmetrically like the ovaries. The vas deferens is thrown into short coils and accompanies the ureter of its own side, and opens

finally into the terminal dilatation of the ureter, in which spermatozoa are found at the breeding season. Each ureter opens on a dorsal papilla in the cloaca; and a groove leads from it to the apertures of the intromittent sacs. These are eversible, and their inner surfaces are clothed with epidermic spines. They are retracted by muscles.

The right is often larger than the left ovary. The oviduct has a large ostium with an entire margin as in all Vertebrata, save Mammalia. The two oviducts fuse into a short vagina, which opens dorsally into the cloaca near its outlet. The two ureters open on a dorsal papilla quite close to the same outlet. The post-cloacal sacs of the female are smooth and non-eversible.

*Note on the poison glands.* The white gland mentioned above in the English Grass-snake becomes much enlarged in those colubriiform snakes in which one or more of the posterior maxillary teeth are grooved. Such serpents were termed *Opisthoglypha* by Bibron and Dumèril, *Ophidia suspecta* by Schlegel. But a serpent with furrowed teeth may be found in the same family as a serpent with none but solid teeth, e.g. *Homalocranion* with grooved and *Calamaria* with solid teeth in the family *Calamaridae*. Hence the terms have been abandoned as of no classificatory value. The members of certain families, however, among the colubriiform snakes are always opisthoglyph, e.g. *Psammophidae*, *Dipsadidae*, and some of them appear to be undoubtedly poisonous.

The serpents belonging to the suborders, *Proteroglypha* and *Solenoglypha*, are all venomous in the highest degree. In the former there is a large furrowed tooth at the anterior end of the maxilla, and behind it a series of small solid teeth: in the latter the maxilla is much reduced, very moveable, and provided with but a single large furrowed tooth and the germs of its successors. The *Proteroglypha* include the *Elapidae*, e.g. the Cobra di Capello (*Naja tripudians*) and the marine *Hydrophidae*; the *Solenoglypha*, the *Viperidae*, e.g. the English Viper (*Pelias*), and the *Crotalidae*, e.g. the Rattlesnake (*Crotalus horridus*). In both these sub-orders the white gland (*supra*) reaches its maximum of development. The ligamentum zygomaticum (= an unossified jugal) which stretches internally to the gland between the maxilla and the quadrate, develops a silvery fascia-like pouch enclosing the gland. One of the three divisions of the temporal muscle is attached to the internal aspect of this pouch: and from its posterior end the masseter takes its origin and passes down to the mandible. The gland is also enclosed in a tough fibrous investment of its own. Within this investment there is in *Pelias berus* loose connective tissue with large lymphatic spaces said to be absent in *Naja haje* (Emery). The gland tubes are united together by a fibrous coat with which the loose investment is continuous. The tubes are collected into bundles, and open into a single duct. This duct opens above the base of the furrowed tooth, and a fold of the mucous membrane surrounds both the base of the tooth and the aperture of the duct. Hence the poison flows down the channel of the tooth, when the contraction of the muscles attached to the outermost capsule forcibly ejects it in the act of closing the jaw. The poison is not only secreted in the gland tubes, but is likewise stored within them. The quantity ejected is large at the first bite, but becomes less and less with successive bites. In *Elaps* (? all species) the poison glands are much elongated, and reach far down the body. As a rule they do not extend beyond the angle of the jaw.

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*Natrix*. Bell, British Reptiles. London, 1839, p. 47.

*Integument with sense organs*. Leydig, A. M. A. viii. 1872; ix. 1873. Todaro, Atti dell' Accademia dei Lincei (3), ii. part 2, 1878 (Math. Nat. Class). Merkel, Endigungen der sensibeln Nerven, Rostock, 1880. Cf. Knauer, Z. A. ii. 1879.

*Organs of circulation*. Jacquart, A. Sc. N. (4) iv. 1855. Brücke, Dk. Akad. Wien, iii. 1852. Rathke, *ibid.* xi. part 2, 1856. *Heart*. Sabatier, Études sur le Cœur, Paris, 1873. *Renal-portal System*. Jourdain, A. Sc. N. (4) xii. 1859.

*Organs of respiration*. Milne-Edwards, Leçons sur la Physiologie, &c. ii. 1857; Schulze, Stricker's Histology, (Sydenham Soc.) ii. 1872.

*Organs of digestion*. *Teeth*. Tomes, Ph. Tr. 165, 1875; Leydig, A. M. A. ix. 1873; Gervais, Journal de Zoologie, ii. 1873. *Glands*, Leydig, A. M. A. ix. 1873; Meyer, Monatsberichte, Akad. Berlin, 1869; Emery, A. M. A. xi. 1875; Reichel, M. J. viii. 1882; *Digestive tract, spleen, &c.*, Duvernoy, A. Sc. N. 26, 1832; 30, 1833. *Stomach*, Edinger, A. M. A. xvii. 1880.

*Excretory organs and genitalia*. Braun, Arb. Zool. Zoot. Inst. Wurzburg, iv. 1877-78. *Supra-renals*. *Id. op. cit.* v. 1882.

*Reproductive organs*. Martin Saint-Ange, Études de l'appareil Reproducteur des Animaux Vertébrés, Paris, 1854 (Mém. par divers savants, Académie des Sciences, xiv. 1856).

### 13. VERTEBRA OF CONSTRICTING SERPENT (*Python* sp. ?).

THE vertebral column of Ophidians is, according to most authorities, divisible into three sections.—A cervical region containing only an atlas and axis: a second region containing vertebrae very numerous and corresponding to the posterior cervical, the dorsal lumbar and sacral regions in other Reptiles, and bearing freely moveable ribs, important organs of locomotion in these animals: and a third or caudal region. The last named is characterized by the ankylosis of the ribs to the centra, and the presence of bifid descending processes, which protect the caudal artery and replace the chevron bones found in all other Reptilia. The number of caudal vertebrae varies very much.

These vertebrae of a constricting Serpent are selected from the second section of the column. Each one has the following characters. The centrum is short and prismatic. Its anterior surface forms a deep cup with thin prominent edges and the vertebrae is therefore pro-coelous; its posterior surface has a ball *peculiarly* prominent. Both ball and cup are placed obliquely to the axis of the centrum. The inferior surface has a low ridge terminating in a knob posteriorly and representing the inferior spine (hypapophysis) seen in the anterior trunk vertebrae of the *Python* itself and in all the vertebrae of the common Ringed Snake and of venomous

serpents. The neural canal is surrounded by a neural arch which is ankylosed to the centrum as it is in *Lacertilia* and in *Chelonia* with few exceptions. The neural spine is low. At its base anteriorly, there stands above the neural canal a bony wedge, the zygosphene, with articular surfaces looking obliquely outwards and downwards. In a similar position but posterior to the spine is a deep cavity, the zygantrum, with articular surfaces looking obliquely inwards and upwards. The wedge and cavity fit the one into the other in contiguous vertebrae. Similar structures are found in the *Iguana* among Lizards, and the *Edentata* with the exception of the Sloths among Mammalia. The articulating processes are remarkably large and flat. The anterior pair (prae-zygapophyses), placed externally to the zygosphene, have their surfaces disposed typically, i.e. looking obliquely inwards and upwards, relations reversed in the posterior pair (post-zygapophyses). A low ridge connects the prae- to the post-zygapophysis of the same side.

The size of the articular surfaces, their disposition, the depth of the cup and of the zygantrum, and prominence of the ball and zygosphene permit great freedom of motion and at the same time prevent dislocation. The fact that the cup and zygosphene are both anterior, and the ball and zygantrum posterior, constitutes a further safeguard in the same direction.

Below the prae-zygapophysis lies the diapophysis or articulating surface for the rib. Its upper portion is convex in every direction, while the lower portion is concave from above downwards but convex from before backwards. This lower portion in some Snakes, e.g. Rattlesnake, is much prolonged ventrally.

The atlas resembles the corresponding vertebra in *Lacertilia* and *Chelonia*. It consists of three pieces: one inferior, prolonged ventrally into a spine; and two, one on either side, forming the neural arches. There is no neural spine. The odontoid process is united by ankylosis to the centrum of the axis. It carries an inferior spine united to it, at least in young specimens, by a suture and representing perhaps a sub-vertebral wedge-bone such as exists in many Lizards between the centra of two adjoining vertebrae. There are no ribs to the atlas and axis, but in a specimen of *Python* (*sp.?*) in the Oxford Museum cartilaginous representatives of these structures exist. The anterior caudal vertebrae, to the number sometimes of ten but never more, have ribs apparently forked at their vertebral end. The ventral division of the fork is perhaps an outgrowth from the centrum; i.e. represents the lower transverse process (= parapophysis). The lymphatic heart is lodged in the space enclosed by the fork.

*Vertebral column.* Owen and Bell, Reptilia of the London Clay, Part iii. Palaeontographical Society, 1850; De Rochebrune, Journal de l'Anatomie, &c. (Robin), 17, 1881.

*Skull of Common Snake.* W. K. Parker, Ph. Tr. 169, 1878.

14. COMMON FROG (*Rana temporaria*),

Injected and dissected so as to show its nervous, circulatory, and respiratory systems, together with some of its reproductive and digestive organs.

THE following external points may first be noted: the two slit-like external nostrils at the end of the snout, placed dorsally and widely separated: the large eyes partially covered by the thin moveable lower lid, the homologue of the third lid or nictitating membrane of higher Vertebrata, the upper lid being immovable: the dark round smooth spot behind each eye where the outer skin adheres to the tympanic membrane: the pigmented skin with its innumerable minute vessels, injected in this specimen and correlated with the presence of the numerous glands characteristic of the soft moist transpirable skin of the Amphibia: the projections of the epidermis visible to the eye only when the specimen is held in certain positions, and best developed on the dorsum proper and the dorsal surface of the hind limbs: the cloacal aperture placed somewhat dorsally between the hind limbs: the short fore-limb: the base of the second finger (= index), dilated as it always is in the male at the breeding season: and the long hind limb with its webbed foot.

The brain and abdominal viscera have been exposed by the removal of the skin, muscles, cranial roof, and left fore-limb. A space separates the skin from the underlying structures. It is divided into lymph sacs, fifteen in number, by vertical septa or by the union of the skin to the parts beneath. The two cerebral hemispheres of the brain are visible anteriorly: narrow in front where they pass into the olfactory lobes which are not exposed in this preparation, and broad behind where there is a diamond-shaped interval occupied in the centre by the base of the pineal gland and to either side by the optic thalami. Next come the large oval and obliquely placed optic lobes or corpora bigemina. A narrow transverse band behind the optic lobes represents the cerebellum. It leaves the large fourth ventricle or sinus rhomboidalis completely exposed.

The following structures in the body are visible from the ventral surface. Close to the angle of the lower jaw on the left side is an aperture, the passage to the croaking sac present only in the male. The heart lies medianly. It has been turned out of the pericardium, the thin membrane seen lying immediately below it. It consists of a conical yellowish opaque ventricle, separated by a well-marked auriculo-ventricular furrow from the thin transparent right and left auricles. The conus arteriosus lies ventrally between the auricles and is continued on into the truncus aortae which is extremely short in the Anura, the division of the Amphibia to which the Frog belongs. It appears to divide into a right and left half, each of which really consists of three vessels, carotid in front, aorta in the middle, pulmonary artery behind, none of them readily visible here. But the left



vena cava superior may be seen between the root of the left lung and the left auricle where it dips down on its way to the sinus venosus. The liver with its right, central, and left lobes lies inferiorly to the heart. Some coils of the intestine are to be seen below the right lobe and leading downwards in the middle line from the median lobe is the epigastric vein. At the lower end of this vein the left division of the bifid allantoid bladder projects sideways: the right division lies behind the vein with a small portion of the rectum visible just behind it. Turning the preparation so as to show the left side, the deeply injected left lung is observed to occupy the space between the left lobe of the liver and the cut edges of the dorsal skin and muscles. The oval yellow testis with black pigment speckled on its surface is placed dorsally, and posteriorly to the lung. At its lower end the vesicula seminalis projects touching the pylorus. The stomach and duodenum lie between the left and median lobes of the liver, and the lung and testis. The stomach tapers to the pylorus.

A remarkable hermaphrodite Nematode worm, *Angiostomum nigrovenosum* (= *Ascaris* or *Leptodera nigrovenosa*), is commonly found in the lungs. Its young pass through the intestine and become sexually mature in earth saturated with decaying animal matter. They are minute compared to their parent and their progeny wander back into the lung. A Trematode parasite, *Polystomum integerrimum*, with six posterior suckers and two large hooks, frequently occurs in the allantoid bladder: and the multi-nucleate Holotrichous Infusorian, *Opalina Ranarum*, inhabits the rectum.

The outer layers of the epidermis are shed periodically—a process which does not extend to the cornea of the eye. The skin-glands are of two kinds: (1) mucous glands with clear contents; (2) glands with granular contents, and probably poisonous like the similar glands in the Toad and Salamander. Chromatoblasts connected to nerves occur in the epidermis, but are most numerous in the outer layers of the corium. The concentration and diffusion of the black pigment within the cells depends on a reflex action of the nervous system set up through the eyes. In this manner the colour of the animal becomes adaptable more or less to its surroundings. The adult frog retains no trace of the organs of the lateral lines present in the tadpole. Besides free nerve-endings, the skin contains special 'touch spots'—flat cells lying near one another, each supplied by a nerve-filament.

The two olfactory lobes of the brain, generally so-called, are connected anteriorly by a transverse commissure: each lobe has a second root. They are solid, and it is probable that 'small papillae, situated at their base from which the olfactory nerves spring, and which contain a process of the lateral ventricle, should properly be regarded as the olfactory lobes. These papillae arise prior to the solid anterior prolongations of the hemispheres' (Balfour). The pineal gland is long and filamentous, pierces the cranial roof, and is attached to the skin at the level of a line drawn through the anterior angles of the two eyes. With the exception of the tips of the olfactory lobes, the several parts of the brain contain ventricles. The facial

and auditory nerves have a common origin, and the ganglion of the former unites with the Gasserian ganglion. The ganglion of the glossopharyngeal is fused with that of the vagus, and the hypoglossus is the first spinal nerve. Of the latter there are ten in all. The anterior and posterior nerve-roots unite outside the neural canal. Round the ganglia, formed at the place of union, there lie sacs containing crystals of calcium carbonate—the so-called glands of Swammerdam. The Gasserian ganglion is similarly surrounded. The sympathetic trunk commences at the Gasserian ganglion, is connected with the vagal ganglion, and passes out with the vagus through a foramen in the exoccipital. A ramus communicans connects it with each of the spinal nerves from the first to the sixth inclusive, and a single ganglion, corresponds to each ramus. But the posterior spinal nerves, especially the tenth, give off a variable number of rami communicantes, and the ganglia vary correspondingly. The first and second sympathetic ganglia send important (accelerator) twigs to the heart: the fifth sends a twig to the caeliac plexus, which is in connection with the root of the mesenteric artery.

The sinus venosus of the heart is divided into a large right moiety receiving the two venae cavae superiores and the vena cava inferior, and a small left moiety receiving the pulmonary veins. Two valves guard the aperture into the right auricle. A thin non-muscular septum separates the two auricles: its lower free edge is adherent to the two auriculo-ventricular valves, one anterior, the other posterior. Their free edges and under surfaces are tied by chordae tendineae to the walls of the ventricles. These walls are produced into trabeculae which have a fixed direction and therefore influence the course of the arterial and venous blood-currents respectively. A conus arteriosus leads from the ventricle: its walls are yellowish, semi-transparent, and contain striated muscular fibre. From it springs the truncus aortae which is extremely short and gives origin at once to a right and left branch; its walls are whitish, somewhat opaque, and contain only smooth muscle fibres. The conus is separated from the ventricle by three valves, and from the truncus also by three valves. Of these latter, one is a large right valve prolonged as a spiral fold down the dorsal wall of the conus; the other two are small valves lying a little to the left, one dorsally, the other ventrally. A vertical septum, placed transversely, divides the origin of the pulmonary arteries from the origins of the aortae and carotids. It is continued into the sinus of the large valve, is fixed to its free edge and to the wall of the conus between the two small valves. The cavity of the conus is consequently divisible physiologically into a dorsal portion which leads to the pulmonary arteries and a ventral from which arise carotids and aortae. Each half of the truncus contains three vessels, carotid anteriorly, aorta in the middle, and pulmonary artery posteriorly. A fibrous band replaces a vessel, the ductus Botalli or primitive union between the carotid and aorta of each side. At the spot where the carotid splits into the lingual artery, which corresponds as in *Reptilia* to the external carotid of *Aves* and *Mammalia*, and into the carotid so-called in *Amphibia*, or internal carotid of higher *Vertebrata*, there is a rete mirabile, the carotid gland, formed by the development of anastomoses between the lingual or external carotid, and the first branchial artery of the Tadpole (the common stem of the lingual and carotid of the adult) where they are contiguous to one another. The two aortae unite into a sub-vertebral aorta under the backbone, and the left arch gives off a

large caeliaco-mesenteric artery before it unites with the right. The pulmonary artery divides into the pulmonary vessel proper and the cutaneous artery. It represents the fourth aortic arch of the Tadpole, the third disappearing.

Each cava superior traced upwards breaks up successively into the external jugular, the vena anonyma, and the cutanea magna, which receives the subclavian vein. The cava inferior is formed by the union of the efferent renal veins and receives the veins of the genital glands, the fat bodies, and near the heart the hepatic veins. The epigastric vein divides proximally into three branches, one for each lobe of the liver, and a third which takes up the portal and splenic veins and then enters the left liver lobe. Traced downwards, this vein receives first a cardiac vein from the conus, secondly veins from the right and left abdominal parietes, finally the veins of the allantoid bladder. It then divides into a right and left branch traceable respectively to the right and left femoral veins. Each femoral vein gives off also the reni-portal vein which passes to the outer side of the kidneys. Into each reni-portal falls a dorso-lumbar vein, and in the female the oviducal veins. Anastomoses exist between the allantoid, rectal and oviducal veins.

The spleen is a reddish-brown body attached to the mesentery at the level of the commencing rectum. A pair of lymphatic hearts opening into the subscapular veins lie posteriorly to the outer ends of the transverse processes of the third vertebra. A second pair lie one on either side the urostyle posteriorly, and opens into a vein which falls into the communicating vein between the femoral and ischiadic veins. A large lymphatic sac, *cisterna lymphatica magna*, lies at the back of the abdomen. Its ventral wall, formed by the peritoneum, is pierced by microscopic apertures or stomata.

There is an upper but no lower lip. On the roof of the mouth are (1) the minute apertures of the intermaxillary glands, the homologues of the internasal glands of the Urodela, immediately behind the fold of mucous membrane which protects the praemaxillary teeth; (2) the internal nares to the outer side of the vomers; (3) the Eustachian tubes close to the articulation of the lower jaw. The broad flat tongue is affixed to the symphysis of the mandible: its free end is bifid. In the male an aperture on either side, close to the ramus of the lower jaw, leads to the croaking sac. The teeth are conical, and restricted to the upper jaw and vomers. They consist of enamel, dentine, and a bony base or pillar. New teeth are continually formed during life to replace those that are worn or broken away. A short oesophagus leads into a stomach which is at first dilated, then narrows to the pylorus, and lies on the left side of the body. It is surrounded to a great extent by a lymph sac. The duodenum is bent at a sharp angle with the stomach. The coils of the intestine lie on the right side, and end in a short median dilated rectum which opens into the cloaca dorsally to the aperture of the bifid allantoid bladder. The gall-bladder lies in the notch between the median and right liver lobes. The pancreas is a thin lobed gland lying between the stomach and duodenum; its duct enters the bile duct which opens on the dorsal wall of the duodenum. The aperture of the larynx opens on the ventral wall of the oesophagus; it is protected by the two arytenoid cartilages and a ring-like cricoid and leads to the two large oval lungs. The lungs have much reticulated walls and are covered externally by peritoneum. The thymus is a small gland lying close behind the angle of each jaw. The thyroid is paired, and each body lies in the angle between the two, i. e. the large and small posterior horns of the hyoid, and adheres to the vena jugularis of its side.

The kidneys are concealed by the fat bodies and genitalia. The former are golden yellow in the fresh state, vascular, and of unknown use. The testes vary in size according to the time of the year. The vasa efferentia run towards the inner border of the kidney: the majority fall into a longitudinal vessel close to that border, while a few may end blindly. From this vessel transverse canals, *dilated* at their origin, pass outwards, receive tubuli uriniferi, anastomose, and fall into the ureter or Wolffian duct, which runs on the outer margin of the kidney. In the Toads the efferent vessels unite with functional Malpighian corpuscles, represented perhaps by the dilatations (*supra*) in the Frog. A solid remnant of Müller's duct may be found running forwards on the outer margin of the kidney. It ends blindly. In the Toads this remnant is large, hollow, and uniting with its fellow, opens on the dorsal wall of the cloaca. Each ovary is divided by internal septa into fifteen sacs: the outer surface is lobed. The two oviducts commence by slit-like openings close to the roots of the lungs. At first narrow and straight they become convoluted and glandular, and finally, near their termination, thin-walled and dilated. Narrowing again, they open on papillae situated anteriorly to the openings of the ureters on the dorsal wall of the cloaca. The kidneys are semi-lunar glands covered by peritoneum only on their ventral faces. Whitish spots, especially numerous near the efferent veins, mark the position of the nephro-stomata or ciliated funnel-shaped apertures which open into the abdominal cavity and are connected by ciliated tubes with the tubuli uriniferi in the Tadpole (as in *Urodeles* throughout life); but in the adult, according to Nussbaum, with the reni-portal capillaries. The ureter (Wolffian duct) begins at the anterior end of the kidney, runs along the outer margin, and, in the male, is dilated and glandular just where it quits the kidney, forming the receptaculum seminis. Both ureters open on the dorsal wall of the cloaca separately. The supra-renal capsules are yellow when fresh and e in the median line on the ventral face of the kidneys.

*Amphibia*, Hoffmann, Bronn's Klass. und Ordnungen des Thierreichs, vi. Abth. 2. 1873-1878; Huxley, Encyclopaedia Brit. (ed. ix.), i. *Anura Batrachia d. Deutschen Fauna*, Leydig, Bonn, 1877.

*Rana temporaria*. Bell, British Reptiles, London, 1839, p. 84.

*The Frog*. Ecker and Wiedersheim, Anatomie des Frosches, Brunswick, 3 parts, 1864, 1881, 1882 (with references to literature), in process of translation. A. M. Marshall, Owen's College Course of Elementary Biology i. (ed. 2), 1885. *Figures*. Atlas of Practical Elementary Biology, Howes, 1885.

*Integument*. Leydig, Allgemeine Bedeckungen, &c. A. M. A. xii. 1876. *Chromatoblasts and change of colour*, Lister, Ph. Tr. 1858, p. 627. *Connection of chromatoblasts with nerves*, Ehrmann, SB. Akad. Wien. lxxxiv. Abth. 3. 1882. *Nerve-endings*. Merkel, Endigungen der sensibeln Nerven in der Haut, Rostock, 1880. Cf. *On the Epidermis of Salamander*, Pfützer, M. J. vi. 1880. *The periodical moult of cuticle*, Knauer, Z. A. ii. 1879.

*Digestive tract. Teeth*. Tomes, Ph. Tr. 1875; Hertwig A. M. A. xi. (Suppl.), 1874. *Intermaxillary gland*, Wiedersheim, Z. W. Z. xxvii. 1876. *Tongue, organs of Taste*. Engelmann, Stricker's Histology (Sydenham Soc.), iii. 1873, p. 14. Cf. Z. W. Z. xviii. 1867-69. *Glands of Stomach*. Partsch, A. M. A. xiv. 1877. Cf. Swiecicki, Arch. f. Physiol. (Pfüger's), xiii. 1876.

*Lungs*. Schulze, Stricker's Histology (Sydenham Soc.), ii. 1872, p. 72.

*Heart, vessels, carotid gland.* Boas, M. J. vii. 1881, p. 488; cf. especially pp. 502 and 540; M. J. viii. 1882. Sabatier, Études sur le Cœur, &c., Paris, 1873; Fritsch, Archiv. f. Anat. und Physiol. 1869.

*Spleen.* Phisalix, A. Z. Expt. (2) iii. 1885.

*Lymphatic system.* Langer, SB. Akad. Wien. viii. Abth. i. 1866; iv. Abth. i. 1867.

*Urogenital system.* Spengel, Arb. Zool. Zoot. Inst., Würzburg, iii. 1876. *Connections of nephrostomata.* Nussbaum, Z. A. iii. 1880.

*Spermatogenesis.* Blomfield, Q. J. M. xxi. 1881. *Albumen glands of Oviduct.* Loos, Z. W. Z. xxxv. 1881.

15. SKELETON OF COMMON FROG (*Rana temporaria*),

With Figures 6 and 7.

THE skeleton, as is commonly the case in Amphibia, retains a large amount of cartilage, in the deeper portions of which much calcareous matter is deposited, but not in the form of bone.

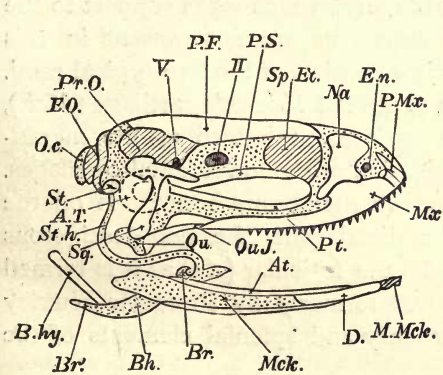


FIG. 6.

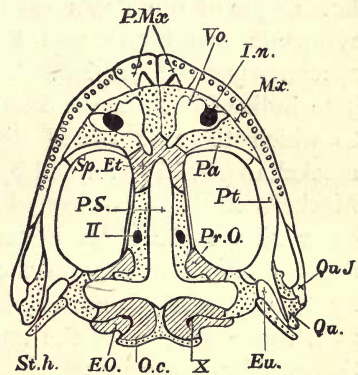


FIG. 7.

After Professor W. Kitchen Parker. The cartilage is dotted; the cartilage bones are shaded with oblique lines, and the membrane bones left white. The lettering is explained in the text.

The skull is remarkably flat, and the cranium proper of small size, though the total breadth is great owing to the large size of the orbital fossae. Its parts may be readily identified with the help of Figs. 6 and 7. There are two condyles (*O.c.*) formed by the two exoccipitals (*E.O.*) which are pierced each by a foramen for the vagus nerve (*X*). The otic capsules project laterally but contain only one ossification, the pro-otic (*Pr.O.*) which is pierced by the fifth nerve (*V*). The cranium in front of the otic capsules is cartilaginous and the cartilage is pierced by the optic nerve (*II*), but most anteriorly of all it contains a bone, the girdle bone, *os en ceinture*, or sphen-ethmoid (*Sp.Et.*). This bone has an internal vertical septum. On the upper surface of the cranium lie the fronto-parietals (*P.F.*): on its

under surface the large para-sphenoid (*P. S.*), both developed in membrane. Other membrane bones are the two nasals (*Na.*): the two praemaxillae (*P. Mx.*) and the two maxillae (*Mx.*) which carry teeth in a simple series: and the quadrato-jugals (*Qu. J.*) which continue the line of the maxillae back to the distal ends of the quadrate cartilage (*Qu.*). The apertures of the external nares (*E. n.*) lie just in front of the nasals. On the roof of the mouth, in front of the sphen-ethmoid, are the two dentigerous vomers (*Vo.*), and at their anterior ends are the internal nares (*I. n.*). The palatine bone (*Pa.*), an investing membrane bone, is here placed transversely—a rare position seen again in *Ichthyosaurus*: while the pterygoid (*Pt.*) lies parallel with the cranial axis. The latter is deeply forked behind: the outer process underlies the quadrate cartilage: the inner or pedicle is continuous with the quadrate and articulates with the ear-capsule. The squamosal (*Sq.*) is seen in the lateral view. It is the homologue probably of the squamosal + the praeopercular of bony Ganoids, two bones actually fused in *Polypterus*. The complex stapes (*St.*) or columella auris, the homologue of the Perch's hyomandibular; the cartilage ring or annulus tympanicus (*A. T.*), the homologue of the Ray's spiracular cartilage (?), which gives support to the tympanic membrane, and the hyoid apparatus are not present in this specimen (see p. 81, *infra*). The lower jaw consists of the two typical rami. The bulk of each ramus consists of an unaltered Meckel's cartilage (*Mck.*), to which there is added distally an ossification known as the mento-meckelian (*M. Mck.*) formed by the ossification of the lower labial cartilages. Meckel's cartilage is covered in part by two membrane bones, one on the outer side for a short distance of its distal part, the non-dentigerous dentary (*D.*): the other on the inner side, the articular (*At.*) as it is termed by Professor W. K. Parker, but identified formerly by Professor Huxley as a representative of the angular, coronary and splenial elements of the Sauropsidan lower jaw.

The vertebral column numbers nine vertebrae and a urostyle. The first vertebra is the only cervical vertebra: it is ring-like with a shallow centrum, two concave facets for the occipital condyles and two post-zygapophyses. The centra of the second to the seventh vertebra inclusive are pro-coelous. The centrum of the eighth is amphi-coelous, and of the ninth or sacral vertebrae biconvex anteriorly, the posterior surface being divided into two facets for the articulation of the urostyle. The neural arches are thin and narrow centrally, leaving in this region interspaces, one between the other. The articulating processes or zygapophyses are flat, and disposed normally. All the vertebrae except the first have lateral processes tipped with cartilage and varying in length, size, and direction. These appear to represent ribs fused to transverse processes. The urostyle is long and curved. Its posterior end lies just above the cloacal aperture. It is pierced laterally at its anterior end by the tenth pair of spinal nerves,

and lodges the posterior part of the spinal cord. The neural canal is often open terminally.

The shoulder-girdle is complete: and the glenoid cavity divides it into a dorsal scapular, and a ventral coraco-clavicular, moiety. The former consists of a broad semicartilaginous supra-scapula and an ossified scapula, the latter of an anterior clavicular bar separated by a fenestra from a posterior coracoid. Both clavicle and coracoid are connected by cartilage medianly to one another and to the corresponding parts on the opposite side. In the middle line project (1) anteriorly a conical bone ending in a cartilage plate—the episternum or anterior part of the interclavicle: (2) posteriorly a flattish bone with a cartilage disc, the hypo-sternum.

The pelvis has the V-shape characteristic of *Anura* or tail-less Amphibia. The long ilium trends backwards to a disc-like symphysis into which it enters, and which is partly cartilaginous and partly formed by the two ischia. The acetabulum is a deep cup.

The fore-limb consists of a humerus, and of a radius and ulna fused together, a furrow indicating externally the line of union. The elements of the carpus are small and consist in the proximal row of a scaphoid (=radiale) and a cuneiform (=ulnare): of a centrale displaced to the radial side: and in the distal row of a trapezium (=carpale 1) carrying the thumb, represented by a single bone: a trapezoid (=cp. 2) carrying the second digit, which in the male enlarges at the breeding season, and a single element (=cp. 3, 4, and 5?) carrying the remaining three digits. The long hind-limb consists of a femur, and of a fused tibia and fibula. A long astragalus (=tibiale) and calcaneum (=fibulare) united at each end form the proximal row of the tarsus. The distal row consists of a tarsal element which carries a single bone, the extra digit or sixth toe; of a fused meso- and ecto-cuneiform (=tarsalia, 2 and 3), while the ento-cuneiform (tarsale 1) and the cuboid (t. 4 and 5) are represented by ligament. The five ordinary toes are present, the number usual in the hind foot of both *Anura* and *Urodela*.

As in the majority of Amphibians, the skull of the Frog has no basi- or supra-occipital; no basi- or ali-sphenoid; and no epi- or opisth-otics. The palatine and pterygoid bones are here membrane bones, at first lying on the surface of a cartilage rod, not as in Teleostean fishes ossifications in the cartilage. The pterygoid however invades the subjacent cartilage. The hyoid apparatus (Fig. 6) consists of a median basi-hyo-branchial plate (Bh.) suspended to the skull by a slender hyoid arch (St. h.). Behind the lower end of this arch a process represents the remains of the two first branchial arches, or cerato-branchials (Br.); another process on the posterior edge of the median plate represents the third branchial arch, or cerato-branchial (Br<sup>1</sup>); while ossifications represent the fourth arch, the so-called thyrohyal (B. hy.). The Eustachian tube (Eu.) passes between the ear-capsule and the outer process of the pterygoid.

There is a remnant of the notochord in the middle of the centrum of each vertebra. A small tubercle, very rudimentary in the Frog, projects in some Amphibia, most of all in *Urodela*, from the centrum of the first vertebra, and fits into a pit in the basi-occipital condyle. It has been supposed in consequence that the first vertebra represents an axis, and that an atlas is fused with the skull, or rather has disappeared, leaving a slight trace behind. The urostyle in *Bombinator igneus* appears from Götte's researches, to be derived from (1) three vertebrae, the x<sup>th</sup>, xi<sup>th</sup>, xii<sup>th</sup>, and (2) a rod of cartilage which lies below the notochord. In the animal when  $\frac{1}{2}$  of adult size, the x<sup>th</sup> vertebra has a pair of nerve foramina behind it; the xi<sup>th</sup> has a similar pair, not found in the Frog, and the xii<sup>th</sup> has the neural canal opening behind its arch. The notochord behind the vertebrae atrophies.

The part of the shoulder-girdle termed clavicle by Götte, consists of a cartilage bar with a membrane bone overlying it. Bar and membrane bone constitute the praecoracoid of W. K. Parker. The bone is the clavicle, the cartilage the praecoracoid of Gegenbaur. The bar is at first, as in the *Chelonia*, according to Götte, a process of the scapula which grows ventrally, fuses medianly with the coracoid, and gives rise to a little mass of tissue which fuses with its fellow and forms the episternum as well as the connecting cartilage which unites the two halves of the shoulder-girdle ventrally. This connecting cartilage represents the posterior prolongation of the Lacertilian interclavicle. The hyposternum, according to Götte, is *not* formed, like the sternum of higher Vertebrata, from the ventral ends of ribs, but by a chondrification of the membrane uniting the epicoracoids (median cartilage borders of the coracoids). In *Bombinator* and *Urodela* other structures are added, viz. in the former a pair, in the latter sometimes more, e. g. in *Menopoma* three pairs, of cartilage bands lying in the linea alba and intersections of the recti abdominalis muscles. Götte compares them to the false ribs of the Crocodile and *Hatteria*, but Ruge (M. J. vi. 1880, p. 369) suggests that they are rudiments of the ventral ends of true ribs.

The ileum, according to Hoffmann, is an ileo-pubis. In a young *Dactylethra capensis* he found the symphyseal portion to contain a pubic ossification fused in the adult to the ileum. In the middle line there was a projecting rod-like epipubis, a structure generally present in *Urodela*. In the Frog a pubic ossification appears to be absent, but Hoffmann mentions in *Rana* and *Bufo* 'a flat, thin, fairly strong tendon,' with the same attachment as the epipubis. The obturator nerve which perforates the cartilage in *Urodela* and marks off the pubis, passes *over*, i. e. outside the pubic region in the *Anura*.

It is not certain whether or no the cuneiform in the carpus represents the ulnare and intermedium as it does in some *Urodela*. The carpalia 3, 4, 5, do not always fuse in *Anura*. The astragalus and calcaneum are in some genera separate. The sixth toe is very commonly present. In a young *R. temporaria* it consists of a tarsale, and of a metatarsal with two phalanges which ultimately fuse, but remain separate in *R. esculenta*. The sixth and first toe bear nails in *Rhinophrynus dorsalis*, as they do with the addition of the second and third toes in *Xenopus laevis*.

*Skeleton in general*, see Hoffmann, Huxley, Ecker and Wiedersheim, p. 78, ante.

*Skull of Anura*. W. K. Parker, Ph. Tr. 166, 1876; 172, 1881.



*Skull of Frog.* Id. Ph. Tr. 161, 1871; cf. Parker and Bettany, The Morphology of the Skull, London, 1877. *Basioccipital.* Albrecht, Bull. Mus. Hist. Nat. Belg. ii. 1882-83.

*Vertebral column.* Gegenbaur, Untersuchungen zur Vergleich. Anat. der Wirbelsäule bei Amphibien und Reptilien, Leipzig, 1862. *Urostyle.* Götte, Entwicklungsgeschichte der Unke (*Bombinator igneus*), Leipzig, 1875, with Atlas, p. 391. *Ribs.* Götte, op. cit. p. 381.

*Sternum and shoulder-girdle.* Götte, A. M. A. xiv. 1877.

*Pelvis.* Hoffmann, Niederländ. Archiv. für Zool. iii. 1876-77.

*Carpus and Tarsus.* Gegenbaur, Untersuchungen zur Vergleich. Anat. der Wirbelthiere i., Leipzig, 1864.

*Sixth Toe.* Born, M. J. i. 1876; vi. 1880, p. 49. *Structure of toes, &c.* Leydig, M. J. ii. 1876.

## 16. THE COMMON PERCH (*Perca fluviatilis*),

Dissected so as to show its nervous, respiratory, circulatory, digestive, and reproductive systems *in situ*.

THE following external characters are to be noted:—the laterally flattened body and pointed head: the general investment of cycloid scales: the conformation of the mouth: the large eye devoid of eyelids; and the two dorsally placed apertures, anterior and posterior, of the nose, neither of them communicating with the mouth: the *lateral line* of sensory organs extending down each side of the body to the tail, and the four depressions on the under surface of each lower jaw indicating the position of the sense organs contained within one of the so-called mucous canals of the head: the opercular apparatus, composed of the operculum and the branchiostegal membrane with its supporting rays which cover the branchial arches laterally and meet on the ventral surface under the chin: and the two sets of fins, azygos and paired. The former consist of the two dorsal, the caudal and the anal fins, imperfectly seen in this specimen, because the caudal region has been removed and the body cut through about the middle of the second dorsal and the anal fins. The paired fins are to be seen on the left side—the pectoral above, i.e. dorsally, and the ventral below. A line drawn through the attachment of the pectoral fin, and at right angles to the long axis of the body, passes just in front of the ventral fin; the latter is therefore said to be *thoracic* in position. When such a line passes behind the ventral fin, the latter is said to be *jugular* in position. In a certain group of *Teleostei* which preserves the duct to the air-bladder and is hence termed *Physostomi*, the ventral fins are placed somewhat in front of the anus, but remote from the pectoral, and are then said to be *abdominal*, e.g. Pike, Salmon.

The brain and viscera have been exposed *in situ* by the removal of the

roof of the cranium, the right opercular apparatus and right side of the body walls.

There are four divisions of the brain visible. They do not overlap one the other, nor do they fill the cranial cavity as in the young frog. The first division forms the olfactory lobes or rhinencephala from which the olfactory nerves may be seen passing forward: the second division the cerebral hemispheres or prosencephala: the third the optic lobes, corpora bigemina or mesencephalon, the largest of all the divisions in *Teleostei*: and the fourth the cerebellum which is subglobular and, unlike the preceding parts of the brain, unpaired.

The removal of the operculum on the right side displays the four gill-arches with their *double* series of gill-filaments, arranged like the teeth of a comb. Each arch is hence said to be bi-pectinate. Internally to the last or fourth gill-arch, and anteriorly to the liver from which in the natural state it is separated by a fibrous septum, lie the heart and ventral aorta. The aorta has a distinct bulb or swelling where it springs from the ventricle: this, the most muscular part of the heart, is in contact with the body walls ventrally while the thin auricle is placed dorsally to it. The liver is large and imperfectly divided into three lobes of which the left is not exposed to view. The single ovary lies posteriorly to the liver and being ripe occupies the greater portion of the abdominal cavity, having displaced the remaining viscera. The anterior three-quarters of its right side have been removed, but owing to the extreme state of distension of the organ, it is not possible to make out the transverse ovigerous lamellae which cross its interior. The commencement of the duodenum with one—the shortest of the three pyloric appendages, may be seen between the liver and ovary. The two other appendages, the stomach, and the loop of intestine containing the spleen in its concavity, are all alike hidden on the left side of the body. The gall-bladder has been displaced upwards and to the right. It is lying on the under surface of the liver in a depression, the homologue of the fossa cystis felleae of man, with which it does not in this fish usually come into relation save when the ovary is in a state of turgescence.

The terminal portion of the intestine and the rectum pass with a straight course down the middle line of the body to the anus. This aperture, into which a black bristle is inserted, is superficial in *Cyclostomi*, in *Teleostei* and *Ganoidei*, and it is placed in front of the genito-urinary depression, clearly visible here behind it. The air-bladder lies dorsally to the ovary, and between its upper end and the liver posteriorly, and the fourth gill arch anteriorly is a gland (really paired) the homologue of the thymus. Bands of yellow-coloured fat in a state of atrophy correlated with the hypertrophy of the ovary, are to be seen contained in the peritoneal lamellae which unite the intestine to the ventral surface of the ovary as well as along the outer or attached edge of the air-bladder.

An Acanthocephalous parasite, *Echinorhynchus Proteus*, is not uncommon in the intestines. *E. angustatus* is also found in the same place as well as the Nematode *Cucullanus elegans* and the remarkable Cestode *Triænoporus nodulosus*. A variety of other parasitic worms may be met with, a list of which is given in Zschokke's work cited below (p. 90) or in von Linstow, Compendium der Helminthologie, Hannover, 1878, p. 206, an invaluable work for all students in this difficult branch of Zoology.

The epidermis consists of several layers of cells, which are united by protoplasmic processes. The external cells generally bear a striated cuticle. Glandular cells are present and open on the surface. There are also 'Retort-cells,' or 'Kolbenzellen,' with clear contents, which rise to the surface and burst. The scales are dermal ossifications, and doubly refractile. They are covered by the epidermis, and contained within pouches of the dermis. When the free border is evenly, or nearly evenly round as in the Perch, they are said to be cycloid; when it is produced into more or less prominent teeth, they are said to be ctenoid, as in many other *Acanthopteri*. The scales of the lateral line are modified. They are perforated for the passage of a nerve, and channelled on the outer surface near the free edge. The channel towards the base of the scale is converted into a canal for the protection of the sense-organs of the lateral line.

These organs are composed of two sets of elements: (1) short pyriform sense-cells terminating in a sensory hair at their outer free extremity, and a nerve-fibril at their inner; (2) supporting cells which are long, and reach the cutis, and secrete a limitans externa on their outer surface, which is pierced by the sensory hairs. These elements are grouped into eminences or ridges, which are connected in the lateral line in many instances by either modified epidermis, or by non-medullated nerve fibres. The eminences may occur on every scale of the body, e. g. in the Grey Mullet; or they may be grouped along the lateral line, while isolated eminences occur here and there on the body, e. g. in the Pike, where they are found in numbers towards the tail. In the Perch they are found only in the lateral line of the body, and in its continuation, the mucous canal system of the head. A single canal runs along the post-temporal scale. It divides, and one branch traverses the upper fork of the scale, and crosses the parietal to the opposite side of the body. A second branch runs along the edge of the pterotic bone, and divides into a *supra-orbital* branch which pierces the frontal bone, and runs above the nostril along the nasal bone, and an *infra-orbital* branch which runs along the chain of sub-orbital bones, and forward through the homologue of the lacrymal (?), and as a rule unites with the supra-orbital branch in front of the anterior nostril. The third main branch, the *infra-maxillary*, runs down the praeoperculum externally, crosses the articular, and perforates the dentary bone. The position of the sense bodies on these branches is not very evident in the Perch. There appears to be none on the connecting branch, two only on the supra-orbital, one just behind the posterior narial opening, and a second between the two apertures; four may be discovered near the free edge of the lacrymal (?), three or four on the praeoperculum, and four very evident in the dentary region. There are as a rule in the Perch no perforations corresponding to these bodies. They exist however in the Pike, and

the course of the canals is therefore more easy to trace. There is much variety in fish in the arrangement, &c., of these bodies. The canals are filled with a soft mucus, secreted by goblet-cells in the lining epithelium.

Other sense-organs—terminal or end-buds—occur on the general surface of the body, on the fins, barbules when present, lips, as well as in the mouth, and on the branchial arches. They generally project above the surface; the sensory and supporting cells are of the same length, and both alike are terminated at their free extremities by short fine points

The brain fills the brain-case only in the young fish. The space developed in the adult between the brain and the cranium is filled by a fatty arachnoid tissue. There is some doubt how far the olfactory lobes do really correspond to the structures called by the same name in higher animals. The apparently homologous parts in *Lepidosteus* are parts of the cerebral hemispheres, and the true olfactory lobes are very small. In some *Teleostei*, e. g. the Tench, the lobes are as in many *Elasmobranchii* connected by a long peduncle to the brain. The cerebral hemispheres are solid. They touch the optic lobes behind, and the thalami optici are hidden from view. The pineal gland varies much in form, &c., in fish. In the Perch its basal part is conical; its middle region filamentous; its terminal part enlarged and fixed to the skull in the frontal region. The optic lobes contain large ventricles. A peculiar fold—the fornix of Gottsche—projects from the region corresponding to the valve of Vieussens in Mammalia, and divides the ventricles almost completely from the iter a 3<sup>tio</sup> ad iv<sup>tum</sup> ventriculum. The cerebellum varies much in size and shape in *Teleostei*, but it generally leaves the fourth ventricle more or less uncovered. The sides of this ventricle are often enlarged at the roots of the fifth nerve forming trigeminal lobes, = lobi posteriores, e. g. in the Loach, Herring, and to a certain extent the Perch. Similar enlargements often occur in relation with the roots of the vagus, forming vagal lobes, e. g. in Cyprinoids. The pituitary body is composed of two parts, an anterior downward prolongation of the infundibulum, and an appended saccus vasculosus. Close to this structure, on either side, are the lobi inferiores or hypoaria, which are remarkably developed in *Teleostei*, and contain ventricles communicating with the infundibulum. The optic nerves, as in all *Teleostei*, cross or perforate one the other. The fifth and seventh nerves are closely united at their roots. The glossopharyngeal quits the skull by a special foramen as in Elasmobranchs, Ganoids, *Dipnoi*, and perenni-branchiate Amphibia. The sense-organs of the mucous canals of the head are supplied by the fifth nerve; those of the lateral line by a branch of the vagus.

The anterior narial aperture is very prominent in the Perch; it is in some fish prolonged into a tube. The posterior aperture rarely perforates the lip in *Teleostei*, e. g. in some Muraenoids. The folds of the mucous membrane in the Perch are, as is commonly the case, arranged in a rosette: in some instances they are parallel to one another. In the eye, the cornea is flat, the lens spherical, the retina non-vascular. There is a pecten or falciform process, highly vascular, and pigmented, which projects into the vitreous humour, and terminates in a Campanula Halleri, connected to the equator of the lens. The ear has the three typical semi-circular canals. A sacculus and recessus cochleae are differentiated, and each possess a crista acustica. The aquaeductus vestibuli is closed terminally, not open as in Elasmobranchs on the surface of the head. There are generally two large otoliths, a sagitta in the sacculus, an asteriscus in the recessus cochleae.

The teeth of the Perch are fine, long, close-set, and they are ankylosed to the bone that supports them. There is much variety in the dental structures of the *Teleostei*. An external cap or tip of enamel is commonly present, but the main body of the tooth is made up of dentine in one of its three chief modifications, tubular, vaso- or osteo-dentine. Ankylosis takes place by bone developed specially in connection with each tooth. The oesophagus passes without clear distinction into the stomach, which in the Perch is of the type known as *caecal*, i. e. prolonged backwards beyond the pylorus. It is siphonal, i. e. bent on itself, in the Pike. There is a well-marked pylorus, and the first (duodenal) portion of the intestine is dilated. It carries three appendices pyloricae, structures which may be absent, e. g. Pike, or present in large numbers, e. g. Salmon, where they have a linear arrangement. They are rarely united in *Teleostei* into a mass by connective tissue, e. g. Tunny. In the Perch, according to Krukenberg, they secrete merely mucus; in some other fish they have a pancreatic function. The loop of intestine containing the spleen is short, and there is no external mark of separation between the intestine and rectum. There is however an internal valve, a remnant perhaps of a spiral valve, which is stated to exist only in *Chirocentrus* (*Clupeidae*) among *Teleostei*. The folds of the mucous membrane vary much in character, and villi are rare. Peptic glands are well marked in the stomach of the Perch; they are sometimes absent. Ciliated epithelium occurs in the pyloric appendages. The epithelium of the intestine is columnar, and contains goblet-cells; and it throws out pseudopodial processes. The gall-bladder is never absent; its duct in the Perch opens near the base of the pyloric appendage, which crosses the oesophagus. The true pancreas is present in the Perch as a diffuse gland. The lobules are chiefly found along the veins of the pyloric appendages, and the left branch of the portal vein. The air-bladder is simple in shape, occupies the whole of the dorsal portion of the abdominal cavity, is firmly fixed laterally to the body-walls, and its ventral surface is covered by peritoneum. Its walls are thin, and there are many vaso-ganglia or retia mirabilia developed on its ventral surface anteriorly and internally. There is no trace of the air-duct which connects the bladder with the digestive tract in the *Teleostei Physostomi*.

The inner surface of the operculum, or more strictly speaking, the posterior edge of the hyomandibular bone, carries a filamentous pseudo-branchia or opercular gill. In the adult Pike and many other *Teleostei* this structure is hidden under the mucous membrane. It is a functional hyoidean gill in the young, but in the adult it receives arterial blood from the hyoidean artery, and transmits it to the choroid gland of the eye. Each of the first four branchial arches carries gill-filaments arranged in two rows, i. e. they are biserial. These filaments are separated to their base as in all *Teleostei*. The artery and vein run on the convex side of the arch, the vein at a deeper level than the artery.

In the heart there is a sinus venosus constituted by the fusion of the right and left ductus Cuvieri. It receives the hepatic veins, and its aperture into the auricle has two thin valve-like folds. The walls of the auricle are thin, and muscles arranged more or less in a network. An anterior and posterior valve guard its entrance into the ventricle. This structure has a thick wall, which in most *Teleostei* and *Ganodei* is divisible into two muscular layers, an outer and an inner, separated by a space. This space is lymphatic, and its surfaces are covered by an endothelium. Two valves, a right and a left, guard the passage from the ventricle to the bulb

aortae. The conus arteriosus of the Elasmobranch and Ganoid has been absorbed into the ventricle of the Teleostean. A slight trace of it is found in some *Teleostei*, but in *Butirinus* (*Clupeidae*) alone are there two sets of valves. The persistent valves appear to be those of the distal row of the Ganoid and Elasmobranch. The ventral aorta gives off (1) the fourth and third branchial arteries, which have a common origin, and (2) the second and first arteries separately. The veins unite dorsally on each side into an epibranchial artery, and in the same manner as the arteries rise from the ventral aorta. Each epibranchial gives off the common carotid anteriorly, and the two carotids unite by a cross vessel which passes above the parasphenoid. Posteriorly, the two epibranchials fuse to form the subvertebral aorta. By these unions a circulus cephalicus is formed from which the external and internal carotids arise anteriorly, and into which the hyoidean artery falls dorsally. This artery rises from the ventral end of the first branchial vein, and in its course it supplies the pseudobranchia. In the Perch a caeliaco-mesenteric artery, which supplies most of the abdominal viscera, springs from the right epibranchial before it fuses with its fellow. The blood from the abdominal viscera (stomach, pyloric appendages, spleen, intestine, air-bladder in part) flows into a hepatic portal system. The genital (spermatic or ovarian) vein enters the left ductus Cuvieri. The caudal vein when it enters the abdomen divides into a right and left branch. The former anastomoses with the right cardinal vein, and the latter, which is small, is also connected to the right cardinal. There is a renal-portal circulation. The left cardinal vein rises from the anterior part of the left kidney and is not directly connected to a branch of the caudal vein. Both cardinal veins unite anteriorly, each with the corresponding jugular vein, forming the right and left superior cavae or ducts of Cuvier. A vein—the inferior jugular—lies dorsally to the heart. It is best developed on the left side, collects blood chiefly from the inferior part of the head, and falls into the left duct of Cuvier.

The thyroid gland is broken up into lobules, and lies ventrally to the ventral aorta, but some of its lobules are found distributed for a short distance along the roots of the branchial veins. They are red in colour. The thymus is paired, and each part lies behind and dorsally to the branchial arches, internally to the supra-clavicle so-called. The kidneys are placed on either side of the vertebral centra. They enlarge anteriorly and coalesce, and are perforated by the cardinal veins. This region of the kidneys in many *Teleostei* was found by Professor Balfour to consist of a vascular lymphatic tissue, and it does not, as is generally stated, appear to be a persistent head-kidney or pronephros. In the Perch the kidneys thin out posteriorly; in the Pike they thicken and extend beyond the abdominal cavity into the caudal region. There are two ureters which rise from the ventral surface of the glands. They are fine tubes which pass ventrally downward behind the posterior end of the air-bladder, unite, and at the place of union develop a large simple urinary bladder. This structure, the form of which varies much in fish, does not correspond with the urinary bladder of higher animals, which is derived in development from the anterior (ventral) wall of the intestine, and either represents (Amphibia) or is a remnant (Sauropsida, Mammalia) of the allantois.

The testes are paired; they are rarely single in *Teleostei*. The inactive organ is semi-transparent; the active organ varies much in size, shape, and lobulation,

COMMON PERCH.

according to its state. The vas deferens, as in all *Acanthopteri*, lies on the inner (median) side of the gland in a well-marked hilus. It becomes free posteriorly, and fuses with its fellow. In the genus *Blennius* the two remain unfused. The mesorchium in the Perch is single at its origin, a rare abnormality. The tubuli seminiferi are long, simple, and radially arranged at the hilus. In the Pike they form numerous anastomoses *inter se*, as in *Cyprinoidei*, *Clupeidae*, &c. The ovary, as in some other *Teleostei*, is single. The ova is produced by lamellae arranged transversely. The oviducal canal is central in the Perch, &c., and lined by a flat or columnar epithelium. It is lateral in the Pike, *Cyprinoidei*, &c., and lined by a ciliated epithelium. When there are two oviducts they unite posteriorly. The genitalia are covered externally by a layer of flat epithelium which, according to Brock, is peritoneal. The genital and urinary ducts open into a urogenital sinus placed behind the anus, the former in front of the latter. In some instances the oviducal aperture is situate on an enlongate papilla, e.g. in *Rhodeus amarus*, which lays its eggs in the mantle cavity of the Anodon. In this instance the urinary bladder opens also on the papilla.

NOTE.—*On the ovary of Teleostei.* In *Salmonidae* and the Eels the ova are shed into the abdominal cavity, and pass out thence through pores, usually but perhaps not properly homologised with abdominal pores. In the Smelt (one of the *Salmonidae*) there are two oviducts widely open at their inner and anterior end, just as in the majority of *Ganoidei*. Each ovary has developed from its ventral edge a lamella, which curves over and partially protects the outer side of the ovary. In all other *Teleostei*, as in the Perch, the ovaries and oviducts are continuous, and this is true also of the Ganoid *Lepidosteus*. In the case of this fish, however, Professor Balfour and Mr. W. N. Parker found that a lamella similar to that of *Osmerus* was formed from the ventral edge of the ovary, and met another lamella growing from the dorsal abdominal wall. These two lamellae by their union clearly bring about the disposition of parts seen in the adult. Observations on the mode of formation of the posterior part of the oviduct were not made for want of material. The same want prevented MacLeod carrying his observations on *Teleostei* to a perfect conclusion, but he has found with reference to the ovary a state of things similar to what obtains in *Lepidosteus*. It remains to be ascertained whether the ducts, generally called ducts of Müller in Ganoids, are really so or not; whether the ducts of *Teleostei* are ducts of Müller continuous with the ovarian capsule or not; and whether in both groups alike the oviducts are not simply peritoneal folds and nothing more.

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## 17. SKELETON OF COMMON PERCH (*Perca fluviatilis*),

With Figures 8 and 9.

THE Perch belongs to the order *Acanthopteri* among *Teleostei*. It may be taken as an illustration of a highly specialised as opposed to a generalised type of organisation: combining as it does so many of the peculiarities of its own class, rather than showing affinities, as e.g. do the *Dipnoi*, to other and higher forms of life. Its skeleton is typically Teleostean.



This skeleton is well ossified. The parts of the skull may be most readily identified with the help of Figs. 8 and 9. The occipital region (Fig. 8) is composed of the four typical bones, the supra-occipital (*S.O.*), which, as usual, is here of very large size; the two ex-occipitals (*Ex.O.*), which surround the foramen magnum, each pierced by the glossopharyngeal and vagus nerves (*X.*) and offering an oblique facet (\*) for articulation with the first vertebra; and a basi-occipital (*B.O.*), which has a cup-shaped posterior surface and articulates with the same vertebra. The basi-sphenoid (*B.S.*) is small and has the Y-shape typical of *Teleostei*: the alisphenoid (*A.S.*) is placed in front and above it. Between the occipital and basi-sphenoidal regions intervenes the auditory capsule, which in *Teleostei* is very large and ossified from five centres. The bones corresponding to these centres are the epiotic (*Ep. O.*), the opisth-otic (*Op. O.*), to which are attached the upper and lower extremities of a forked bone, the post-temporal scale (not shown in the

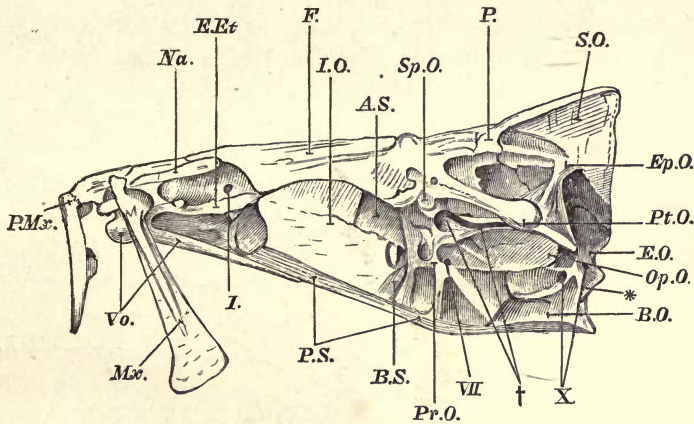


FIG. 8.—From a specimen (natural size).

figure) by which the fore-limb is connected to the skull: the pro-otic (*Pr. O.*), a large bone pierced by the fifth and seventh (VII) nerves, and two bones which attain their relative maximum development in the *Teleostei*, the pter-otic (*Pt. O.*), and the sphen-otic (*Sp. O.*), (= post-frontal of Huxley). Between these two bones above, and the pro- and opisth-otic below, are the articular cavities (†) for the two heads of the hyomandibular (*H.M.* in Fig. 9). As is often the case, the parietal (*P.*) is a very small bone, and the frontal (*F.*) a very large one. The nasal (*Na.*) is slender. In front of the ali- and basi-sphenoid a cartilage plate, the interorbital septum (*I.O.*), divides the two orbits. It represents the prae- and orbito-sphenoid regions. Anteriorly to the septum is a large bone, the ecto-ethmoid (*E. Et.*) (= the pre-frontal of Huxley), the homologue of the lateral masses of the ethmoid in a mammal, and pierced by the single olfactory foramen (*I.*). The two ecto-ethmoids are separated by a small median mesethmoid. The praemaxilla (*P. Mx.*)

is very large and dentigerous, and of a characteristic shape. The maxilla (*Mx.*), which is edentulous, lies behind and parallel to it, and does not form the margin of the gape of the mouth. This disposition of the two bones is nearly universal among *Teleostei*. The base of the cranium is underlaid by two bones—a single vomer (*Vo.*), dentigerous in front, and a parasphenoid (*P.S.*) which extends back to the basi-occipital. These two bones, as well as the praemaxilla, maxilla, nasal, frontal and parietal are preformed in membrane, the remainder belong to the cartilaginous cranium, which persists as cartilage beneath the parietal and frontal regions.

The jaw apparatus (Fig. 9) is very remarkable. It is connected to the cranium in front by the palatine (*Pa.*) and behind by the hyomandibular

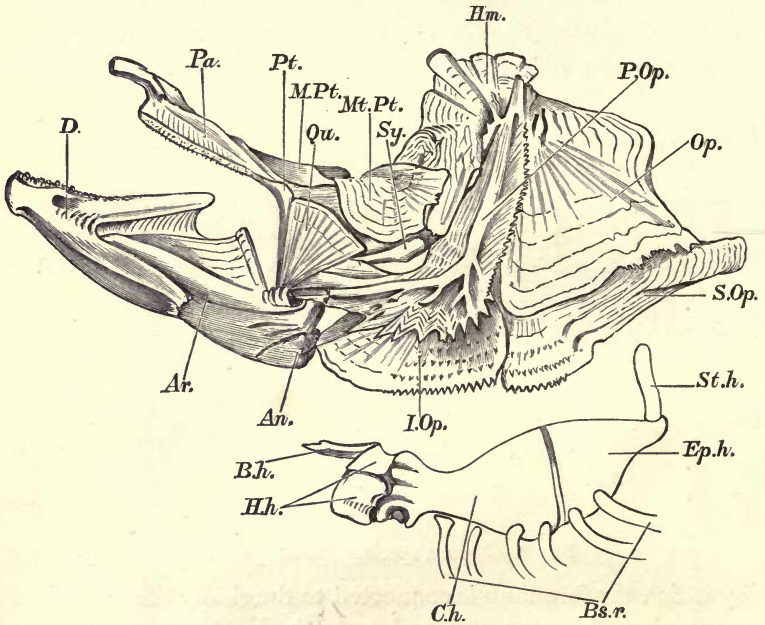


FIG. 9.—From a specimen (natural size).

(*Hm.*). The palatine (*Pa.*) is dentigerous. There is a slender pterygoid (*Pt.*) (= ectopterygoid of Huxley), which bears a few teeth anteriorly and descends along the anterior edge of the quadrate, while a thin plate-like mesopterygoid (*M. Pt.*) (= entopterygoid of Huxley) extends horizontally inwards. These bones are formed in a bar of cartilage lying in front of the mouth in the embryo. Another bar of cartilage—Meckel's arch—which lies behind the mouth segments transversely. The upper, or proximal portion, forms the metapterygoid (*Mt. Pt.*) and the quadrate (*Qu.*). The latter has a rounded articular head for the articular element of the lower jaw, and both bones are firmly united to the bones in front and behind them. The lower or distal segment constitutes the lower jaw in part. Its upper end

ossifies as the articular (*Ar.*), from which an angular (*An.*) is cut off, while the median portion remains cartilaginous and rod-like. It is surrounded by the dentary (*D.*), a bone formed in membrane, and carrying teeth. The hyoid cartilage of the embryo gives origin to a pharyngo-hyal element which ossifies as the hyomandibular (*Hm.*) and symplectic (*Sy.*) bones. They are connected with the bones of the jaw as well as with some others to be described presently. The hyomandibular has two condyles for articulation with the otic region († in Fig. 8). It is a large bone and represents, according to Kitchen Parker's most recent researches, the columella auris or stapes of higher forms. The quadrate represents the element of the same name in Amphibians, Reptiles, and Birds, and the incus of Mammals, while the malleus of the last-named group corresponds to the articular of the fish, of *Amphibia* and *Sauropsida*. A series of membrane bones well developed in *Teleostei* and *Ganoidei* are attached to the posterior edge of the hyomandibular and quadrate bones. These are the prae-operculum (*P. Op.*), the operculum (*Op.*), the sub-operculum (*S. Op.*), and the inter-operculum (*I. Op.*). They close in laterally the branchial cavity. The remaining portion of the embryonic hyoidan cartilage gives origin to the interhyal or stylo-hyal (*S. h.*) which articulates between the hyomandibular and symplectic, the epihyal (*Ep. h.*), the cerato-hyal (*C. h.*), both large flat bones, and two nodular hypo-hyals (*H. h.*). The arches of the right and left side are united by a median basi-hyals (*B. h.*) or entoglossal. A series of membrane bones, the branchio-stegal rays (*Bs. r.*), are attached to the epi-cerato-hyal. They are formed in the membranous flap, which is a continuation of the opercular apparatus to the hypo-hyal region. A thin median bone, the basi-branchiostegal (=urohyal of Huxley), not shown in the figure, projects backwards from the basi-hyal region towards the ventral ends of the clavicles, so-called, with which it is connected by ligament. It underlies the ventral aorta.

The branchial arches are five in number on each side. In the median ventral line, and immediately following the basi-hyal, are three basi-branchial bones. The first arch consists, proceeding from its dorsal to its ventral end, of a small pharyngo-branchial, or superior pharyngeal bone, an epi-branchial, to which is articulated, at a sharp angle, a cerato-branchial followed by a hypo-branchial. The three next arches have a similar composition. The pharyngo-branchials are, however, both large and dentigerous. The hypo-branchial element in the third arch is applied laterally to the last basi-branchial, and is wanting altogether in the fourth arch. The fifth arch consists of a single bone, probably homologous with a cerato-branchial. Osseous plates bearing fine teeth are implanted on the anterior and posterior aspects of the four first arches. These plates are carried by cartilaginous rods in the case of the first cerato-branchial. The rods, known as gill-rakers, are present in some fish on the following cerato-branchials. The interlocking of one

series with another, closes the gill-clefts and prevents the passage of foreign bodies of any size.

The vertebral column consists of forty-two vertebrae, of which twenty-two are dorsal and twenty caudal. There are no other regions differentiated in the backbone of a fish. Successive vertebrae articulate one with another by the edges of the centra, which are united by ligaments. In the majority of vertebrae a process springs from the base of the neural arch on each side and articulates with the arch of the vertebra preceding. The neural arches are continuous with the centra, and are prolonged dorsally into neural spines. Lateral projections, or inferior, i.e. haemal arches, as it appears from development, project from the centrum of the eighth and following vertebrae. They increase in length and are turned more and more ventrally in the posterior dorsal vertebrae. The processes of the two last dorsal vertebrae have the ribs united to them, as is the case in the caudal series, where the ventral ends of the ribs unite and inclose the caudal canal, which lodges the caudal artery and vein. This is the case as far as the last or terminal caudal vertebra, which bears solid inferior arches, to either side of which pass the two vessels into which the caudal artery and vein divide. The two last caudal vertebrae are modified. The last but one has a short expanded neural, and a long inferior arch. The last has the centrum prolonged into the urostyle—the ossified and undivided sheath of the notochord—which is bent upwards dorsally at a sharp angle and incloses the termination of the notochordal cartilage. It has a long, low neural arch and six inferior or haemal arches, expanded and flattened, divided by an interval into two groups of three arches apiece, one anterior, the other posterior. To the neural arches of these two terminal vertebrae are attached three long and somewhat broad 'false' spines, as they are called. These, with the haemal arches, carry the rays of the caudal fin. Simple curved and free ribs are carried on the lateral processes of the dorsal vertebrae except the two last. These ribs bend ventrally but do not meet, and in the Perch, as in all other fish, there is no sternum. Certain of the anterior ribs have epipleural bones attached to them at some little distance from their vertebral ends. These bones radiate outwards into the myocommata or connective tissue septa uniting successive muscular segments or myomeres.

The Perch has four fins belonging to the median or azygos system. These fins, as in all fish, are supported by fin-rays, ossified in the *Teleostei*. The four fins are the first and second dorsal, the caudal, and an anal, which is in position ventral. The dorsal and anal fins are supported by a series of bones, 'fin-bearers' or 'interspinal' bones, which in the case of the dorsal fins alternate with the neural arches; in the case of the anal fin with the inferior arches. These bones lie between the muscle-masses of the right and left halves of the body respectively. The folds of integument which constitute the fins proper, are supported by bony 'fin-rays.' There are

thirteen (or sometimes fifteen) of these in the first dorsal, and as in all *Acanthopteri* with two dorsal fins, they are stout stiff spines, hence called *entire* fin-rays. The first fin-ray of the second dorsal, and the two first of the anal fin are likewise entire, while the remaining rays as well as all the rays of the caudal fin are 'soft' and 'jointed.' The soft rays break up into filaments at their free termination, and these filaments as well as the stem to a certain extent, are jointed. The caudal fin in the Perch appears externally to be equally developed in its dorsal and ventral half. It may be termed 'homocercal.' But, anatomically speaking, the eight or nine long fin-rays which make up the bulk of the fin are all articulated to inferior arches, and the upward-bent termination of the notochord has therefore in reality the chief part of the fin on its ventral edge. The dozen or so small 'accessory' rays which belong to the dorsal aspect are inconsiderable in size; and, balanced by similar rays on the ventral aspect, complete the wedge-shaped outline of the fin. The fin is, therefore, from an anatomical point of view, as 'heterocercal' as is the caudal fin of an Elasmobranch in outward appearance as well as anatomically.

The paired fins are the pectoral and pelvic or ventral, i.e. the fore and hind-limbs respectively. A forked bone, the supra-temporal scale, connects the fore-limb to the skull. It is followed by two thin, plate-like bones, developed in membrane and properly belonging to the skin, the so-called supra-clavicle and clavicle. These two bones lie immediately below the mucous membrane of the hind wall of the branchial cavity. They are probably not represented in Vertebrata above the class Pisces. The two 'clavicles' meet in the median line where they are united by ligament. They bear on their inner and posterior face the true-shoulder-girdle. This consists of two flat bones, one, the scapula, more dorsal, small, and perforated by a foramen, the other, the coracoid, large and extending nearly to the median line. There is a thin bone, the 'post-clavicle,' which is attached proximally to the clavicle, and hides the scapula when viewed from within. It is superficial and underlies the surface of the depression internal to the pectoral limb. It has been removed on the right side. To the edge of both scapula and coracoid articulates the fore-limb. The small basal cartilages which immediately articulate with the shoulder-girdle cannot be made out in this specimen. The fin contains about ten soft rays.

The hind-limb lies immediately behind the median union of the pectoral arch. The basal part of the limb consists of a long triangular bone produced by the contact of a right and left element, which appear to be homologous with the two metapterygia (right and left), i.e. the posterior basalía of the hind-limb in an Elasmobranch. The true pelvis is therefore absent. *Teleostei* and *Ganoidei*, with the exception of *Polypterus*, which has small pelvic cartilages, agree in this respect, and differ from *Elasmobranchii*,

*Holocephali*, and *Dipnoi*, which possess a pelvis. The fin-rays are articulated to the posterior and external faces of this double bone. The first ray in each fin is entire, the remaining five are soft.

The following additional points may be noted relative to the skull. A series of suborbital bones lies beneath the eye of which the most anterior is exceedingly large. These bones are removed in this specimen. In some *Teleostei*, e.g. the Trout, there are similar bones above the eye. The optic nerve passes out of the cranium between the arms of the basisphenoid. The bone termed alisphenoid is continued forwards for a short distance by membrane which is pierced by the olfactory nerve. The two nerves separated by the interorbital septum traverse the back of the orbit and pierce the ectoethmoids on the way to the olfactory mucous membrane. An 'ocular' canal which lodges the recti muscles of the eyes passes backwards into the forepart of the basi-occipital, beneath the pro-otic and above the parasphenoid. The inner wall of the ear-capsule is replaced by thin membrane which is easily injured in dissection, and the vertical semi-circular canals then appear to lie in the cranial cavity.

The skulls of *Teleostei* in general agree closely with that of the Perch. The size of the cartilaginous cranium varies, as may be seen on comparison of a Salmon with the Perch. The amount of persistent cartilage as compared with bone also varies. Anchylosis of the bones may take place. In Cyprinoid and Siluroid fish there is no inter-orbital septal plate, but there are orbito- and pre-sphenoid ossifications in this region. In the Pike the mesethmoidal cartilage is partially ossified by two pairs of bones instead of a median one, and in the Salmon this region is not ossified but is covered by a supra-ethmoid bony plate. The Pike has a small supra-orbital bone. Praemaxillae are absent in Muraenoids. In some *Teleostei*, e.g. Pike, a small bone placed distally on the posterior margin of the maxilla appears to represent the jugal. The metapterygoid is absent in the Siluroid *Clarias capensis*. And in Siluroids generally the sub-opercular is absent. In Cyprinoids the fifth branchial arch is strongly bowed, and carries prominent teeth which work against the horny basi-occipital tooth. The group of *Pharyngognathi* is so named from the fact that the fifth pair of arches is fused into a single dentigerous plate.

When the lower jaw is connected to the cranium solely by a hyomandibular element derived from the hyoid arch as it is in *Teleostei*, in *Ganoidei* except *Lepidosteus*, in the majority of *Elasmobranchii*, it is said to be hyostylic. When it is connected not only by a hyoidean element but also by a quadrate, as in *Lepidosteus*, or by a palatoquadrate, as in *Cestracion* among *Elasmobranchii* and probably in *Holocephali*, it is said to be amphistylic; and when it is connected by a quadrate element alone as in *Amphibia* and *Sauropsida*, it is termed autostylic. In *Mammalia* the dentary element articulates with the squamosal, the articular portion of the lower jaw and the quadrate having been converted into ear-bones, i.e. malleus and incus respectively.

The azygos system of fins appears in *Teleostei* as in other fish as a continuous fold of skin supported by embryonic fin-rays which are afterwards replaced by permanent fin-rays. Such a continuous fold extending from the back of the head round the tip of the tail to the anus persists in Blennies, Eels, Congers, Soles, *Ophidiidae*, &c., among *Teleostei*, and in *Dipnoi*. But this condition in the

opinion of the late Professor Balfour has been *secondarily* acquired. The caudal fin is first differentiated from the continuous fold: then the posterior dorsal when present, unless the anterior dorsal is of a peculiar type, as in *Lophius*, when it appears before the posterior. The anal fin appears before the pelvic fins, unless the latter are of a peculiar type and adapted to special uses, as in the young of some *Gadoidei*.

The young Elasmobranch, *Lepidosteus*, and Teleostean, have at first a long pointed tail, to the tip of which the notochord extends and the lateral line as well whenever this primitive condition is retained. A caudal fin is next developed on the ventral aspect and at some little distance from the extremity of this pointed prolongation as an enlargement of the continuous fold. The prolongation bends upwards towards the dorsal aspect at the same time. The growing caudal fin, as remarked by Professor A. Agassiz, has much the appearance of a second or posterior anal. It is supported solely by enlarged haemal arches, beyond which appear at a later period the fin-rays. Such a condition persists and forms the heterocercal caudal fin of all *Elasmobranchii*, living chondrostean Ganoids, and many extinct Ganoids. But in existing bony Ganoids and the *Teleostei* the pointed prolongation atrophies until the caudal fin becomes terminal. The upward dorsal inclination is preserved in the urostyle. The part of the caudal fin formed on the neural side of the urostyle is always inconsiderable. This outwardly symmetrical caudal fin, really asymmetrical and, anatomically speaking, heterocercal, is termed homocercal. But in a few fish, such as the *Dipnoi* and the *Teleostei* above-mentioned, the backbone retains its straight course and divides the caudal fin into two equal portions, dorsal and ventral. Such fins are known as diphyercal. In the Eel and some other eel-like Teleosteans, rudimentary haemal arches exist and point to the existence at some distant period of a caudal lobe now aborted: and in them the diphyercal tail is secondarily acquired. In *Holocephali* the long whip-like tail has the groove of the lateral line continued to its apex, and a small ventral lobe represents the large caudal lobe of *Elasmobranchii*. The late Professor Balfour believed that he had found traces of caudal haemal arches in *Ceratodus*, which would indicate a lost caudal lobe in that Dipnoan. It is perhaps doubtful whether a primary diphyercal tail exists among living Pisces.

The number of haemal arches present in the caudal lobe varies much, e.g. the Cod and Stickleback have only two. The 'accessory' rays are in some instances of large size, e.g. in the Cod, and the caudal fin has then a peculiar rounded appearance.

The series of bones known as supra-clavicle, clavicle, inter-clavicle, and post-clavicle in *Teleostei* and *Ganoidei* appear one and all to be derived from the integument and mucous membrane of the branchial cavity. In the *Teleostei* they are dermal in position; in *Acipenser* on the contrary their outer surface resembles in appearance the bony plates of the integument, and the bone has also the same structure. Recent researches appear to have established the fact that the clavicle of higher forms is a process of the cartilaginous shoulder-girdle (see Götte and Hoffmann's papers referred to under Pigeon, p. 67). Such a process exists in the Sturgeon, and is named prae-coracoid in Professor W. K. Parker's Monograph on the shoulder-girdle. 'Swirski's researches on the shoulder-girdle in the Pike appear to establish the fact that the true coracoid aborts almost completely in that Teleostean, and

therefore probably in others as well, while the clavicular process (=præcoracoid process of his paper) increases in size, and forms what is generally termed coracoid. The dorsal angle of the scapula of the Pike bends inwards and downwards in development. In Cyprinoids, in the Salmon, &c., a curved bar of bone stretches from the dorsal angle of the scapula to a spot ventral to the scapular foramen. This bar in the Cyprinoid is derived, according to 'Swirski, from two processes of the scapula, a dorsal and a ventral, which meet and fuse. They appear in a late stage of development.

In the bony *Ganoidei* the proximal end of the metapterygium of the ventral fin bears a cartilaginous process. Davidoff regards this as pelvic, but Wiedersheim considers it to be part of the metapterygium. The two metapterygia are always in contact at their proximal extremities, but often widely separate distally, e.g. bony *Ganoidei*, the Pike, &c.; or a bar of bone may develop at the distal end of each metapterygium, and meet its fellow in the middle line, while a space separates the middle portion of the two bones, e.g. Salmon; or the two may be in contact throughout the whole extent of their median edges, e.g. in the Perch; or finally, complete fusion may take place.

The basal cartilages or bones which articulate with the coraco-scapular are five in number. The first is included in the first fin-ray, and represents a propterygium; the fifth is long and is a metapterygium. In some *Teleostei* the number is reduced, or the bones may be entirely lost. A row of small radial cartilages is to be found in some instances inclosed in the bases of the fin-rays. They do not seem to be present in the Perch, at least not in the adult. The fin-rays of the pelvic fins articulate directly with the metapterygium. A row of excessively small bony or cartilaginous particles representing radials is sometimes inclosed in their bases. They do not exist however in the full-grown Perch.

For the caudal canal and interspinous bones, see next Preparation, pp. 100, 101.

*Skull of Salmon.* W. K. Parker, Ph. Tr. 163, 1873; cf. Id. and Bettany, Morphology of the Skull, London, 1877. *Cod.* T. J. Parker, Zootomy, London, 1884. *Pike (and other fish).* Huxley, Lectures on Elements of Comparative Anatomy, 1864. *Investing bones of Pike's head.* Walther, J. Z. xvi. 1882. *Loricaria, &c.* Göldi, *ibid.* xvii. 1883. *Characinidae (and auditory bones).* Sagemehl, M. J. x. 1885.

*Azygos fins.* Kölliker, Über das Ende der Wirbelsäule der Ganoiden, &c., Leipzig, 1860. *Caudal.* Lotz, Z. W. Z. xiv. 1864 (Perch, p. 89); *Development of;* Agassiz, Proceedings Amer. Acad. (new series) v. 1878; vi. 1879; ix. 1882; cf. Balfour and W. N. Parker on *Lepidosteus*, Ph. Tr. 173, 1882, and Grassi, M. J. viii. 1882.

*Fatty fin of Salmonidae.* De la Valette St. George, A. M. A. xvii. 1880.

*Ichthyopterygium and Cheiropterygium.* Baur, Z. A. viii. 1885; cf. Balfour in Comparative Embryology, ii. pp. 500-511 with references.

*Shoulder-girdle.* 'Swirski, Schultergürtel des Hechtes (Inaug. diss.), Dorpat, 1880; W. K. Parker, Ray Society, 1868; Gegenbaur, Untersuchungen zur Vergleich. Anat. der Wirbelthiere, ii., Leipzig, 1865.

*Pelvis.* Wiedersheim, M. J. vii. 1881; von Davidoff, M. J. v. 1879; vi. 1880.



18. VERTEBRAE OF COMMON COD (*Gadus morrhua*).

THE anterior and posterior surfaces of the centra of these vertebrae, as in all fishes with distinct vertebrae, except *Lepidosteus*, are concave, the anterior surface being less so than the posterior. They are therefore amphicoelous. The two concavities communicate by a fine central canal. Their surfaces are marked by two sets of lines, radial and concentric, indicating the directions in which ossification has taken place. More or less wedge-shaped cavities are observable around the periphery of the centrum. There are two of especial depth on the ventral surface immediately internal to the bases of the haemal arches in the more anterior vertebrae of the series, while two shallower cavities occupy the median line. In the posterior vertebrae the lateral cavities become more and more shallow, and finally disappear, while the median cavities coalesce and deepen. These cavities in the living animal are filled by connective or fatty tissue. The neural arches are continuous with the centra and coalesce to form a median spine. At the base of each arch there are two processes on either side, an anterior broad process, with a slight groove to its outer side, and a posterior process, pointed and adapted to fit more or less closely into the groove just mentioned. The anterior process becomes more and more pronounced in the anterior dorsal vertebrae, and in the first vertebra is of huge size and articulates with the skull. The vertebrae carry well-developed inferior or haemal arches projecting outwards and downwards, and continuous with the centrum. In the median vertebrae they are broad and flat, and serve to protect the air-bladder, which is largely developed in the *Gadidae*, and devoid of an air-duct. In these same vertebrae a smaller process is developed behind, but parallel with the haemal arches. It is probably of no significance beyond assisting in the protection of the air-bladder. The haemal arches fail to be developed only in the four first vertebrae. They carry the ribs. In the region of the tail they are united with the ribs and form a caudal canal, as in the Perch.

The bones of fish are the poorest in inorganic constituents of all the five classes of Vertebrata, and the bone-cells, the characteristic microscopic structures in true bone, may in the fully formed bone be absent altogether or very rare, e.g. in the Perch or Pike. According to Kölliker, they are to be found in all *Ganoidei* and in the majority of *Teleostei* which possess an air-duct to the air-bladder.

The formation of the vertebral centra in *Teleostei* appears to take place as follows:—The embryonic chorda dorsalis, when fully formed, is composed of central vesicular cells with a thin superficial epitheliomorphic layer produced by the peripheral aggregation of the protoplasm of certain of the cells, each apparent cell containing a nucleus. A cuticula comes next: and most externally

a layer which, according to Grassi, is an *elastica externa*, but, according to Götte, is composed of flat nucleated cells in a single layer, with an abundant intercellular substance. In this substance Götte states that the first ossifications forming the primary centrum start. The chorda grows intervertebrally, and shrinks to a fibrous cord in the middle of the vertebra. Hence the amphicoelous centra. The cuticula thickens and becomes fibrous intervertebrally, as does the external layer, forming the ligaments which unite the centra peripherally. The neural and haemal arches rest with their bases on the chordal sheaths, but do not grow round the chorda as they do in the Elasmobranch. The main, i. e. secondary osseous substance, is periosteal, formed from connective tissue, which develops between the bases of the arches and imbeds them.

There are four principal types of structure in the vertebrae of adult Teleosteans. (1) Concentric laminae are laid down round the primary centrum. The bases of the arches ossify and fuse indistinguishable with the laminae; but isolated masses of cartilage, remnants of them, may persist here and there temporarily, e. g. the Cyprinoids. (2) Delicate bony radial laminae with intervening clear connective tissue, appear first of all; finally the bony matter becomes spongy, and the connective tissue is converted into a fatty medulla. The bases of the arches persist as cartilage, and form the well-known *cross*, e. g. Pike. The majority of *Teleostei* belong to this type. (3) The bony matter forms a delicate spongy mass; the intervening substance consists of small round cells with a clear, firm matrix; the bases of the arches may retain isolated masses of cartilage (*Cyclopterus lumpus*) or may ossify completely (*Chironectes* sp.?). (4) There are delicate radial united by a few concentric, bony laminae. The intervening substance is hyaline cartilage: *Monacanthus penicilligerus*, *Diodon*.

The differences depend upon (1) the persistence of cartilage in the bases of the arches or the total conversion of the latter into bone, and (2) either the total or partial conversion of the intervening connective tissue into bone; and in the latter case the persistence of the remnant as connective tissue or its conversion into either medulla or cartilage.

The neural or superior appear before the haemal or inferior arches, and both structures appear earlier in the anterior than in the posterior region of the column. In Cyprinoid fishes certain of the arches may ossify without previous chondrification. In the anterior region of the column the haemal arches may become entirely imbedded within the centrum, e. g. in the Perch; and in the posterior region they become not only more and more ventral in position, but they bend more and more towards the ventral median line. Finally they *appear* to unite, inclosing the caudal canal. The most posterior, however, attached to the terminal vertebrae fuse into solid knobs. It may be observed that in the dorsal region ribs are articulated to their ends. These ribs are developed continuously with the arches in *Elasmobranchii*, *Ganodei* so far as is known, and in some *Teleostei*, whereas in others they are developed independently, but yet in close apposition to their ends. In *Amia* and *Lepidosteus* the caudal canal is formed by the haemal arches plus ribs which are cut off from them, but which articulate with them, as in the dorsal region. And it is these ribs that unite distally, completing the canal. The presumption is, that in other cases the canal is formed by haemal arches with ribs remaining continuous with them. This view was strongly supported

by the late Professor Balfour in his paper on *Lepidosteus*, published in connection with W. N. Parker (*infra*). In some *Elasmobranchii*, e.g. *Scyllium* and some *Teleostei*, the anterior portion of the caudal canal is apparently inclosed by haemal arches, to which ribs are attached laterally. The explanation of this arrangement is as follows (Balfour):—The canal in this region is secondarily acquired: it is a prolongation forward of the posterior part which is normally developed, and it is formed by the growth of two processes—one from each haemal arch near its base, towards one another which meet and fuse, the true haemal arch being that portion of cartilage or bone which bears the rib.

In some instances, e.g. Pike, the right and left neural arches are not united by bone in the median line. It should be noted also that in the region of the trunk at least, the ribs have free ventral ends. There is no sternum.

Other structures to be noted are: (1) the ligamentum vertebrale superius which runs above the spinal cord and connects the successive vertebrae. (2) A pair of cartilages which appear in development between the ligament and the spinal cord: they project posteriorly, ossify or become surrounded by bone and become continuous ultimately with the arch. They are probably homologues of the intercalaria neuralia of the Elasmobranch which lie between the neural arches. They are present also in Ganoids. (3) The interspinal bones which support the azygos fins seen in the preceding preparation (Prep. 17). These, according to Götte, may be regarded as dissociated parts of vertebral spines, but this view is extremely doubtful. Dohrn has recently suggested, and Mayer has strongly supported his view, that the azygos fins are derived from paired rudiments; the anal and ventral element of the caudal fins, by the coalescence behind the primitive cloaca of the two ventro-lateral ridges from which the pectoral and pelvic fins originate: the dorsal fins and the dorsal element of the caudal fin from two similarly coalesced dorso-lateral ridges. If this is so, then the interspinal bones are really equivalents of the basal cartilages in the paired fins. They are not connected with the vertebral column in most *Elasmobranchii*. In Dipnoi they remain articulated to the neural spines in the dorsal region, and to the haemal in the ventral region, where in other types the anal fin is formed. They appear in the young Teleostean just above the summits of the arches, but when the latter lengthen, come to lie between them. They are developed also in regions where the azygos fins are deficient; but it must be borne in mind that this system of fins is primitively represented by a continuous fold. (4) The set of bones known as epi-neurals, epi-centrals, epi-pleurals (Fleischgräten). They are formed in the intermuscular septa (myocommata), and never pass through a cartilage stage. Götte has suggested that the series which lies on the ends of the inferior arches in the region of the trunk are ribs homologous with the ribs of Elasmobranchs owing to their position. But this view appears to have little to support it, and the mode of formation of the bones in question is against it.

It may be noted that the ribs of all fish except *Elasmobranchii* lie at the base of the myocommata, immediately below the peritoneum. In *Elasmobranchii* they extend *outwards* in the fibrous septum which separates the dorso-lateral and ventro-lateral muscle-masses, and therefore not below the peritoneum. Hence these ribs have been regarded as not homologous with the ribs of other fish. But in *Lepidosteus* the free ends of the ribs, the bodies of which are normally

placed, bend outwards into this same septum. It is possible, therefore, that the ribs of *Elasmobranchii* have undergone a change of position.

Schmid-Monnard has recently investigated the origin of bony tissue in *Teleostei*. He finds as follows. (1) The first bone is always formed *outside* the cartilage. (2) All skeletogenous tissues may take part subsequently in the formation of bone, and whether cartilage or connective tissue they ossify either directly or indirectly, i. e. by means of osteoblasts. In most parts of the skeleton bone is derived exclusively from perichondrium. (3) The first-formed bone is invariably homogeneous, containing neither bone-cells nor connective fibres. Bone-corpuscles are to be found here and there in those fish in which, according to Kölliker, they are absent, and the bone resembles dentine, e. g. Pike, Perch, *Lota vulgaris*, *Gadus aeglefinus*, &c. But true dentine, i. e. tubular dentine, appears never to be formed. The great development and regular arrangement of Sharpey's fibres probably led to the supposition, coupled with the then imperfect methods of research at command.

*Formation of vertebrae, arches and ribs in Teleostei*, Götte, A. M. A. xvii. 1879; Grassi, M. J. viii. 1882; *in Ganoidei and Elasmobranchii*, Götte, A. M. A. xv. 1878; *in Elasmobranchii*, Balfour, *Elasmobranch Fishes*, London, 1878; *in Lepidosteus*, Id., and W. N. Parker, Ph. Tr. 173, 1882.

*For discussion as to homologies of ribs and formation of caudal canal, see work last quoted.*

*Azygos fins.* Mayer, Mitth. Zool. Stat. Naples, vi. 1885.

*Formation of bone.* Schmid-Monnard, Z. W. Z. xxxix., 1883, and Kölliker, P. R. S. ix. 1859. Cf. Köstler, Z. W. Z. xxxvii. 1882.

## 19. ASCIDIAN (*Ascidia affinis*),

Dissected to show the chief features in the anatomy of *Urochorda*.

THE animal is mounted with the base of attachment or posterior end downwards, and the oral or inhalent aperture or anterior end upwards. The ventral edge is on the left hand, the dorsal on the right, and the animal's left side is therefore turned to the observer. On the dorsal edge, and somewhat anteriorly, is situated the atrial or exhalent aperture, through which a white bristle has been passed.

There is an external transparent test. This test is secreted by the ectoderm cells, and is remarkable among animal tissues for containing cellulose or a substance very closely akin to it. It is prolonged inwards for a short distance at both oral and atrial apertures. The body walls, often termed mantle, have shrunk away from the test under the action of the alcohol in which the animal is preserved. This contraction does not take place in all species of the genus, and in this instance the body walls remain firmly united to the test in the region of the two apertures. They may be seen to be fibrillated, and consist of connective tissue with bundles of muscular fibres. In the genus *Ascidia* these bundles are more or less irregularly arranged, and interlace more or less with one another, a fact to be made out easily in the part of the body walls left near the atrial aperture.

But in the genus *Cynthia* they are disposed in two layers, an outer longitudinal and an inner circular layer.

The cavities of the pharynx and digestive tract have been displayed by the removal of their own and the body walls on the left side. Close to the margin of the oral aperture may be noticed, first, the circle of tentacles which guard the entrance, secondly, behind this circle two delicate bands, the peripharyngeal bands which run circularly round the pharynx, and thirdly, the cavity of the pharynx itself. This cavity is marked by transverse and longitudinal lines at right angles to one another, inclosing innumerable square meshes. The transverse lines are the transverse vessels which run from the ventral to the dorsal edge of the pharynx, connecting the two main longitudinal bloodvessels which correspond to these two edges respectively. The longitudinal lines are the longitudinal bloodvessels which run on the inner surface of the pharyngeal cavity. They extend from the anterior to the posterior end of the pharynx, and are connected by short vessels to the transverse vessels at the spot where the two sets cross one another. The longitudinal vessels which pass from one transverse vessel to another, and lie in the same plane as they do, are very fine and inclose the stigmata or apertures which lead from the cavity of the pharynx to the peribranchial or atrial cavity. They are not visible without the use of the microscope. The cilia which beset the stigmata cause a current of water to flow from the pharyngeal into the atrial cavity. The pharynx has thus a respiratory function and is hence often termed branchial sac.

The pharynx extends on the right side of the animal to its posterior extremity, and the digestive portion of the alimentary canal is placed to its left side, an arrangement which does not occur in all *Urochorda*, e.g. *Clavelinidae*. Stretching along the dorsal edge of the pharyngeal cavity is a delicate longitudinal band, the dorsal lamina. Anteriorly it may be seen to come into contact with the peripharyngeal bands. At this point there is an opaque white spot, the nerve-ganglion which is underlaid by the neural gland, and in front of the opaque spot may be noted a crescentic curved line with the concavity turned forwards. This line represents the dorsal tubercle, so-called, or the aperture of the neural gland. When the specimen is held in a certain position as regards the light, a yellow opaque line may be seen running along the ventral edge of the pharynx internally. This line is the endostyle, which extends from the peripharyngeal bands anteriorly to the posterior end of the dorsal lamina, close to which is the aperture from the pharynx into the stomach. A black bristle has been passed down the pharynx and through this aperture.

The pharynx is attached to the body walls along the line of the endostyle, but a cavity, the atrial or peribranchial cavity, which opens externally by the atrial aperture, extends round its dorsal edge throughout nearly its whole extent to the right and left sides, separating them from the body

walls. This atrial cavity is produced by two invaginations from the exterior in the larva, the openings of which unite, forming the single atrial aperture. The atrial must not be confounded with the body cavity which, if present at all, is probably represented by blood spaces in the body walls, &c.

The stomach is posterior and ventral: the intestine rises from its anterior ventral end, runs forwards for a short space, and then turns back upon the stomach dorsally and posteriorly. It passes to the left side of the aperture of the pharynx into the stomach, and then turns forwards and dorsally to end in the anus, which may be seen just above the dorsal edge of the pharynx internally to the atrial aperture. The cavity of the intestine is partially divided by a ridge or *typhlosole* which projects from its right wall, and commencing at the pyloric end of the stomach, extends in this Ascidian to within a short distance of the anus. In the substance of the body walls, which are left along the ventral edge of the intestine close to its origin, and in the concavity of its last curve may be noticed some opaque white cords. These are probably portions of the testis.

The substance of the test is sometimes fibrillated: it contains cellular elements which wander into it from the ectoderm. These cells increase the quantity of matrix. Some of them may become pigmented and others frequently undergo extreme vacuolation, becoming little more than bladders, with a thin wall of protoplasm which contains the nucleus. Chemically, the matrix appears to be identical with the cellulose of plants.

The terms 'mantle' and 'branchial sac,' often used in speaking of the body walls and pharynx respectively, are better discarded, as it is a well-established fact that there is no relationship between the *Urochorda* and *Mollusca*.

The muscle fibres are unstriped and have the form of fusiform or filiform fibres. There is a well-developed sphincter both at the oral and atrial apertures, and the test at these spots is generally lobed—eight lobes round the oral, six round the atrial, aperture of the *Ascidiidae*. The part of the test between the thickened lobes is very thin and bendable. The mode in which the muscle fibres are disposed in the body walls is characteristic in the sub-groups of *Urochorda*. The connective tissue corpuscles of the body walls are often pigmented.

The tentacles spring from a ridge which coincides with the line in the oral aperture where the test ends. They are simple and filiform. Posteriorly to the circle of tentacles is a plane area—the praebranchial zone—limited behind by two ciliated ridges bounding a ciliated groove. The ridges are the two peripharyngeal bands. The posterior is continuous ventrally with the ridges bordering the endostyle, and the groove of the latter is continuous with the peripharyngeal groove. The posterior is also continuous dorsally with the dorsal lamina. The anterior band forms a complete circle.

The cavity of the pharynx is lined with endoderm. Its outer or atrial surface is covered by the invaginated ectoderm. The stigmata lying between the transverse vessels and the fine longitudinal vessels are usually straight, but sometimes curved. Under some conditions it appears that the direction of the ciliary current may be reversed, and water be expelled at the oral instead of the

atrial aperture. The system of internal longitudinal vessels is very well developed in *Ascididae*, and it is characteristic of the family to have a prominent papilla developed from the free surface of these vessels at spots opposite to the short vessels which connect them to the transverse system.

The endostyle is a groove, at the bottom of which are cells bearing extremely long cilia. The sides of the groove are ridged, and the ridges are caused by the large size of certain cells which appear to secrete mucus. The mucus collects into small lumps or balls which are carried forwards to the peripharyngeal groove. They traverse this groove and are then conveyed by the ciliated dorsal lamina backwards to the stomachal opening. The dorsal lamina has anteriorly a median epipharyngeal groove, the extent of which varies in different Ascidians. The free edge of the lamina is curved, usually to the right. It ends posteriorly in a low ridge continuous with the endostyle.

The ganglion is single, generally swollen at either end where it gives off an anterior and posterior set of nerves. The central part is fibrous, and the ganglion cells are placed peripherally. The ganglion lies in the body walls, and always between the oral and the atrial apertures, on the opposite side of the body to the endostyle. As to organs of special sense, the tentacles must be regarded as tactile; and in many Ascidians there are orange-coloured visual (?) spots between the lobes of the oral aperture. The sub-neural gland consists of caecal ramified tubes. They open into a duct which lies between the gland and the ganglion. This duct runs forwards and opens into a ciliated depression of the prae-branchial zone. The margins of the depression are prominent, and the aperture has usually a crescentic shape, the concavity of the crescent being turned forwards. The margins may be much modified in shape. They constitute what is often spoken of as the ciliated sac or dorsal tubercle. The gland has been homologised by Julin with the pituitary body of the brain in higher Vertebrata, and it has been suggested that it has a renal function. In some cases it has secondary ducts opening into the atrial cavity.

The digestive portion of the alimentary canal is disposed variously in different groups of *Urochorda*. The liver (?) may be represented by glandular tissue coating the stomach, and sometimes attaining considerable size, or by a system of clear tubes ramifying over the stomach and part of the intestine and opening into the pyloric portion of the former. A renal organ is probably represented by clear walled vesicles containing concretions in which uric acid has been found, and situated round the intestine and in the body walls. These vesicles have no ducts.

The heart is more or less fusiform, and is inclosed in a delicate pericardium. It lies in *Ascidia* along the posterior ventral edge of the stomach on the left side. It gives off (1) a *ventral* vessel which sends a branch through the mantle to the test and then runs forwards beneath the endostyle, and is connected to the transverse system of vessels in the walls of the pharynx; (2) a *dorsal* vessel from its opposite end which sends a branch through the mantle to the test parallel to the one above mentioned. These two branches divide in the test, end in ampullae, and intercommunicate. The remaining branches of the dorsal vessel go to the body walls; and to the stomach intestines and reproductive organs from which the blood is collected into a large vessel running along the dorsal edge of the pharynx and connected to its transverse vessels. There are

branches also (=connectives of Hancock) from the pharynx to the body walls, thence to the test and back again. When the heart pulsates so as to drive the blood from the ventral to the dorsal surface, it draws arterialised blood from the pharynx and venous only from the test; when in the opposite direction the blood it draws has previously passed through the viscera, body walls, and test. The blood itself is a clear plasma containing rounded nucleated corpuscles, many of which are pigmented, generally yellow, red, or brown, but white and blue are sometimes found.

All Urochorda are hermaphrodite, but in most instances the male and female organs are not ripe at the same time. These organs in *Ascidia* are racemose glands placed on the left side of the body between the intestine and stomach. The testis is composed of delicate white tubules, ramifying dichotomously, and spread over the ovary, stomach, and intestine. Both oviduct and vas deferens run along the dorsal edge of the intestine and open near the anus.

The Ascidian is an example of an animal which has lost, more or less completely, the structure typical of the phylum, and even, strictly speaking, of the class to which it belongs, at the same time acquiring marked peculiarities of its own. It is an instance of what has been termed by Professor Ray Lankester *Degeneration*, or 'a gradual change of structure in which the organism becomes adapted to less varied and less complex conditions of life.' *Elaboration* is the converse: but '*elaboration* of some one organ may be a necessary accompaniment of *Degeneration* in all the others: in fact this is very generally the case.' It is when the total result of both processes combined leaves the organism 'in a *lower* condition, that is, fitted to less complex action and reaction in regard to its surroundings than was the ancestral form with which we are comparing it (either actually or in imagination), that we speak of that animal as an instance of *Degeneration*.'

The causes of degenerative evolution are, according to the same authority, four in number: (1) parasitism; (2) fixity or immobility; (3) vegetative nutrition; (4) excessive reduction of size. Instances are, of the first, various *Copepoda*, e. g. *Lernaea*; of the second, a barnacle (*Lepas*); of (1) and (2) combined, the parasitic *Cirripedia* or *Rhizocephala*; of the third, the Turbellarian worm *Convoluta*; and of the fourth male Rotifers, etc.

There can be no reasonable doubt that an Ascidian is one of the *Chordata*. The structure and development of the larva suffice to establish this point fully. The central nervous system originates as a neural groove the side of which closes over to form a neural tube; there is a cerebral or myelonic eye; the caudal notochord is derived from the archenteron; the pharynx becomes a respiratory organ pierced by slits, with walls richly vascular. These structures reach a certain degree of perfection. But with the fixation of the larva a series of regressive changes sets in. The notochord disappears with the swimming tail. The nervous system is reduced to a fraction of what it was in the larva. The eye is lost. The pharynx however becomes much more complicated and enlarged relatively to the remaining organs. The larval characteristics are however more or less retained and specialised in the free swimming order *Larvacea*.

*Tunicata*. Herdman, Challenger Reports, vi. 1882; and Bronn, Klass. und Ordn. des Thierreichs, Malacozoa, iii. i. 1862.

*Notes on British Tunicata*. Herdman, J. L. S. xv. 1881. *Ascidies Simples*



*des côtes de France*, de Lacaze Duthiers, A. Z. Expt. iii. 1874; vi. 1877. Heller, Untersuchungen, &c., Dk. Wien. Akad. xxxiv. 1875; xxxvii. 1877; and SB. Wien. Akad. lxxvii. Abth i. 1878.

*Degeneration.* Ray Lankester, Nature Series, 1880.

*Various points.* R. Hertwig, J. Z. vii. 1872.

*Test.* O. Hertwig, J. Z. vii. 1872. Semper, Verhandl. Phys. Med. Gesellsch. zu Wurzburg, vii. 1875.

*Tunicin*=Cellulose. Cf. Watt's Dictionary of Chemistry, v. p. 918, and Suppl. 2, 1875, p. 271.

*Nervous System.* E. van Beneden et Julin, Archives de Biol. v. 1884. *Neural gland.* Julin, Archives de Biol. ii. 1881. Herdman, Nature, xxviii. 1883.

*Endostyle.* Fol, M. J. i. 1876.

*Tubular gland opening into stomach.* Chandelon, Bull. Acad. Royale Belgique (2) xxxix. 1875. Ulianin, on *Doliolum*, Fauna and Flora des Golfes von Neapel, x. 1884.

## 20. SHELL OF EDIBLE SNAIL (*Helix pomatia*).

WHEN the shell has its apex directed upwards, and its aperture downwards and towards the reader, its spire, as is the case with the great majority of Gasteropod spiral shells, ascends obliquely towards the right. It is in consequence termed 'dextral.' In the living animal inhabiting such a shell, the heart is on the left, the generative, respiratory and anal apertures on the right of the body. The aperture of the shell in *Helix* as in all vegetable-feeding *Gastropoda* is entire, i.e. forms an unbroken curve: in carnivorous *Gastropoda* on the contrary it is notched or produced into a canal which lodges a process of the mantle or siphon: e.g. in the Whelk. These two varieties of aperture are known respectively as 'holostomatous' and 'siphonostomatous.' The columella or pillar formed by the contact of successive whorls of the shell lies on the left side of the aperture in the angle between the first whorl and the peristome or free margin of the aperture. It is hollow and the external opening or umbilicus is partially hidden by the peristome, not wholly as it is in the Garden Snail, *Helix aspersa*. The smooth rounded off edge of the peristome shows the animal to have been adult. The shell is coarsely striated in a direction parallel to the margin of the aperture, i.e. corresponding with the lines of growth, and more delicately in a spiral direction, parallel to the five coloured bands with which it is marked. The 'apex' or 'nucleus,' the tip of the shell or the part first formed, is smooth and semi-porcellanous in appearance, thus differing, as is so often the case, from the rest of the shell. The spiral line marking the point of contact between one whorl and its successor is known as the 'suture.' The shell increases in thickness towards the peristome, and it is probable that but little addition to its substance takes place except in

that region. In this particular, as well as in being univalve and possessing a much smaller amount of organic matter, the shell of a Gastropod contrasts with that of a Lamellibranch.

There is no operculum in the *Pulmonata*, the order of *Gastropoda* to which the Snails and Slugs belong. When the snail hibernates it closes the aperture of its shell by a whitish disc, the hibernaculum or epiphragma—a structure containing much organic matter and calcareous granules of variable shape irregularly scattered. It appears to be secreted by the margin of the mantle or collar (see next preparation) rather than by the foot, as has been supposed. There are sometimes two such epiphragmata, one within the other. The moveable clausilium of the pulmonate *Clausilia*, which covers the aperture of the shell when the animal is retracted, appears to be a structure homologous with the epiphragma.

The majority of Gasteropod spiral shells are dextral. When the spire of a shell turns in a direction opposite to what is normal, it is said to be 'reversed.' In some species this is a common occurrence, e.g. in the Common Whelk; in others it is so usual that the type of shell commonly met with is sinistral, e.g. *Clausilia*. The lower whorls of the shell may, in a few instances, become loose and straggling, e.g. *Vermetus*, *Siliquaria*.

The reflection of the peristome over the umbilicus in *Helix* is due to the presence of a 'columellar lobule' or projection of the collar. When the shell is injured at the peristome before the animal is adult, both the outer non-calcareous layer 'periostracum' or 'epidermis' and the calcareous layers internal to it are repaired: when at any other spot, or after the animal is adult, only the latter, and in this case the shell is thickened internally. The colouring matter is secreted by unicellular glands of the collar. The spiral shell, as in all *Gastropoda* with few exceptions, is a *secondary* shell, i.e. formed on the outer surface of the mantle, and not from the shell-gland of the embryo. A *primary* shell, i.e. one formed by this gland, rarely persists. It is found, however, as the 'nucleus' of the shell in the pulmonate *Clausilia*, and as the internal shells of the Slugs *Arion* and *Limax*.

The shell of the *Helices* is stated by Longe and Mer to consist of an external organic cuticle or periostracum; of an outer calcareous layer containing colouring matter, and composed of (1) a thin external division with confused striation, (2) a thicker internal division which consists of vertical prisms; and of an inner nacreous layer including several laminae of prisms arranged horizontally, the axes of the prisms in the different laminae being at right angles to one another. The cuticle is formed by a cutogenic apparatus situated just behind the collar. It is composed of a pallial groove into which glandular caeca open, and an epithelial organ consisting of long bottle-shaped cells which secrete granules. The epithelial organ disappears in the adult, and the glands of the pallial groove gradually undergo atrophy. The rest of the shell appears to be formed by the edge of the mantle; the nacre from its surface in general. In *Zonites algirus*, according to Nalepa, the cells of the pallial groove develop in spring—the period at which growth of the shell takes place—into long unicellular glands, and the cells of a ridge (? = epithelial organ of Longe and Mer) just behind the groove enlarge into flask-shaped gland

cells. The cuticula is secreted by these two sets of gland cells. It is possible that the glands may be developed in *Helix*, as in *Zonites*, in the spring of the year, and that the atrophy of the organ in the adult (*supra*) merely marks a period of rest. (See Nalepa, SB. Akad. Wien. lxxxvii. Abth. i. 1883.)

A layer of nacre or mother of pearl is not generally found in the calcareous shells of *Gastropoda*. The calcareous matter is usually arranged in three layers composed of parallel lamellae, those of the outer and inner layer usually disposed parallel to the suture, of the middle layer at right angles to it. The direction of the layers is sometimes reversed. The lamellae are vertical to the surface of the shell, and each lamella is composed of calcareous prisms, all parallel to one another, but forming an oblique angle with the surface of the shell. The prisms of adjoining lamellae are disposed in contrary directions to one another. The calcareous matter is in the form of Arragonite ( $\text{Ca CO}_3$ ). Splinters of the shell are hard enough to scratch Calc-spar.

The Gastropod shell is composed chemically of about 1.5 per cent. of an organic substance (Conchiolin); of about 95-98 per cent. of Lime carbonate; with small quantities of Magnesium carbonate; phosphates; silica and alumina.

The inner whorls of the shell are in some *Gastropoda* partially absorbed. In some cases the animal withdraws from the older region of the shell. The part forsaken is closed off by a calcareous lamina secreted by the surface of the mantle. The process of withdrawal and closing off may be repeated several times.

*Technical terms, structure, &c.* Woodward, Manual of the Mollusca (ed. 3.), 1875, p. 28, p. 204. Keferstein, Mollusca, Bronn's Klass. und Ordn. des Thierreichs, iii. 2. p. 899, p. 1181. Zittel, Handbuch der Palaeontologie, Abth. 1, ii. p. 153. Leydig, Haut-decke und Schale der Gastropoden, A. N. 42. 1876.

*Structure and formation of Shell in Helices.* Longe and Mer, C. R. xc. 1880, cf. A. N. H. (5) v. 1880.

*Epiphragm.* Keferstein, op. cit. *supra*, p. 1186. Binney, Terrestrial Mollusca of United States, ii. 1851. *Analysis and source of lime.* Barfurth, A. M. A. xxii. 1883, p. 509.

## 21. EDIBLE SNAIL (*Helix pomatia*),

Dissected so as to show the position of the heart and the respiratory cavity.

THE shell, with the exception of a part of the columella or spire left *in situ*, has been removed. The foot is completely expanded and the left upper tentacle is partially protruded. A depression on the animal's right side anteriorly above the foot, marks the position of the generative aperture. The thickened collar is seen crossing the animal's dorsum. In it, on the right, is the pulmonary aperture, and below the aperture, again to the right, the columellar lobule. The pulmonary chamber has been opened by a transverse incision, and its cavity exposed by turning forward the anterior flap. Its roof is for the most part thin, and is formed by the branchial fold of the mantle, the anterior edge of which has fused, as in most pulmonate Molluscs,

with the skin of the dorsum leaving only the small pulmonary aperture. Its floor is thickened and muscular, and represents that portion of the general integument which is roofed over by the fold of the mantle. The heart, composed of a thin-walled auricle and thick-walled ventricle, is seen as in dextral Molluscs, on the left side, and below it lies in this preparation the triangular pale-coloured kidney. The vessels have been injected with a red-coloured fluid from the auricle. The right half of the roof of the pulmonary chamber is covered by vascular ramifications: the anterior part of the left side is smooth; its posterior portion corresponds to the pericardium and kidney. The pulmonary vein passes along the edge of the cut on the right side towards the auricle. It is joined, but this fact cannot be seen here, before it enters the auricle by the efferent kidney veins. The right border of the pulmonary chamber which is applied to the line of the suture in the shell is relatively thick. It is muscular, and muscular fibres pass off from it into the roof of the chamber. One of the vessels bringing venous blood to the chamber runs along this border.

When the animal is retracted into its shell by the action of the columella muscles, seen in the next preparation, air is forced out of the pulmonary chamber; conversely, when the animal expands again by the contraction of the muscular integument including the floor of the pulmonary chamber, air is drawn in. But, except during the acts of expansion and retraction, interchange of air in the pulmonary chamber with the air without must take place only by diffusion.

The foot is relatively large in most *Pulmonata*, and simple in contour. It is divided by a transverse furrow into a fore- and hind-part only in *Pedipes* and *Auricula brunnea*. The sole of the foot is ciliated, and in *Arion* its lateral walls as well. A supra-pedal gland appears to be present in all *Pulmonata*, as well as in some other *Gastropoda* (*Azygobranchia*, *Opisthobranchia*). It opens above the anterior margin of the foot beneath the head. It consists of a ciliated duct extending backwards in the substance of the foot near its coelomic surface. Into this duct open unicellular glands. Sense cells have been stated to be present in the epithelium of the duct; but it is very doubtful if the gland has the olfactory function which has been ascribed to it. A caudal aggregation of mucous glands, situated posteriorly on the dorsal aspect of the foot and opening into a depression of the integument, is found in *Arion ater* and some other Slugs. But no Pulmonate possesses a pedal gland opening near the centre of the creeping sole of the foot, such as is found in many Azygobranchiate *Gastropoda*. A supra-pedal and a pedal gland coexist in the Azygobranchiate *Cyclostoma elegans*, which leads a terrestrial life. The aperture of the pedal gland has often been taken for an aquiferous pore.

Many Mollusca possess the power of suspending themselves by mucous threads, and not only those of terrestrial habit but aquatic as well, e.g. *Limneidae*, and the marine *Litiopa* and *Rissoa parva*. In the *Limacidae* the thread appears to be derived from the mucus coating the surface of the body.

The position of the anal, renal, and generative apertures in front and on the right side of the body is due to the twist of the dorsal aspect of the body or visceral dome, which is characteristic of *Gastropoda Anisopleura*. The presence of but a single kidney and a single generative duct is nearly equally characteristic.

The pulmonary chamber must be regarded as formed by the fold of the mantle which in branchiate *Gastropoda* constitutes the roof of the branchial cavity lodging the gills or ctenidia. The latter are aborted, and the mantle-fold itself has become vascular and respiratory. The fore-edge of the mantle-fold in the aquatic Pulmonate *Limnaeus* is free, and has not undergone fusion or 'concrecence' with the dorsum, as it has in *Helix* and its allies. When *Limnaeus* inhabits the deep waters of lakes it is said to admit water to the pulmonary chamber, instead of coming to the surface at intervals for a fresh supply of air, as it does when it inhabits shallow streams and ponds. An adaptation of the branchial fold of the mantle to aerial respiration occurs also in certain streptoneurous *Gastropoda Anisopleura*: namely, in the *Pneumonochlomyda* and in the genus *Ampullaria*, among *Azygobranchia*. In the last named, which is amphibious, and is found in tropical America, Africa, and the East Indies, the left side of the branchial cavity contains the ctenidium, and is separated by a fold from the right side, the walls of which are vascularised. The *Pneumonochlomyda*, to which our English *Cyclostoma elegans* belongs, have lost the ctenidium, and respiration is carried on solely by the walls of the branchial cavity, as in the *Pulmonata*, from which order the *Azygobranchia* differ in such essential features as the twisted character of the visceral nerve-loop, and the separateness of the sexes. The view, which is advocated by von Ihering, that the pulmonary chamber in *Pulmonata* is derived from the renal organ, does not appear to be tenable.

The size and extent of the pulmonary chamber vary greatly in the *Pulmonata*.

The pericardial cavity is a portion of the coelome closed off completely from the remainder, but communicating, as in all Mollusca where it is present, with the exterior through the nephridium, with which it is connected by a ciliated nephridial tube. The aorta divides into an intestinal and a cephalic branch, the latter passing through the infra-oesophageal collar. The system of capillaries appears to be very complete in *Helix pomatia*, judging from the result of injections. The vascular system of *Zonites algirus* has been accurately investigated by Nalepa. The arteries and capillaries have proper walls, and are lined by an endothelium. The capillaries communicate by short branches with a narrow meshwork of wide blood-spaces—the 'transition' vessels, which open into the venous spaces or the coelome by infundibular orifices, seen also in *Arion ater* (= *rufus*) by Jourdain. The venous system is represented in part by the coelome, in part by vessel-like spaces, the walls of which are formed of homogeneous connective tissue with scattered nuclei, but which are not lined by an endothelium. The pulmonary vein pulsates rhythmically in *Zonites*. There is in the same Pulmonate a nervous network in the walls of the auricle, of the ventricle, and aorta, in the last two instances derived from the genital nerve. Nerves are found also in the walls of the larger vessels. Ganglion cells connected with these nervous networks appear to be rare. They are found in the walls of the heart of certain marine *Rhipidoglossa* (*Fissurella*, *Haliotis*, *Trochus*), according to Haller. See Haller, M. J. ix. 1883, p. 61; cf. Dogiel, A. M. A. xiv. 1877.

The blood of *Helix* contains haemocyanin, a respiratory substance in which copper is present in combination with a proteid. It is colourless when deoxidised, bright blue when oxidised. Hence the coelomic fluid of a *Helix* exposed to air assumes a violet tinge. The blood-plasma of the pulmonate *Planorbis* contains haemoglobin. Haematin is found in the liver-secretion of *Helix pomatia*, *H. aspersa*, *Arion ater*, and *Limax*. Amoeboid corpuscles occur, but rather sparingly, in the blood.

The shape of the nephridium varies in *Pulmonata*. It has a long tubular duct in *Helix*, &c., opening near the anus; whilst in other *Pulmonata*, such as *Arion*, it has a simple round opening. Its cavity is large, and its walls are lamellate. It really consists of a urinary chamber into which open acini of very large calibre. These acini are bound together externally by connective tissue. The renal cells are ciliated, and urates of Ammonium and Calcium are found in them and in the cavity of the sac. Free uric acid and Guanin occur in *Zonites* as well as Ammonium urate. The nephridium of *Helix pomatia* is supplied with arterial blood from the pulmonary chamber and by the renal arteries; by the latter alone in *Zonites*.

*Gastropoda*. Ray Lankester, 'Mollusca,' Encyclopaedia Britannica (ed. ix.), xvi. 1883. Keferstejn, Bronn's Klass. und Ordnungen des Thierreichs, iii. 2. 1862-66. (*Pulmonata*, p. 1160.)

*Pulmonata*. Semper, Z. W. Z. viii. 1856-57. Leidy, in Binney's Terrestrial Air-breathing Mollusca of the United States, i. 1851, p. 198. For the Slugs, see literature to Plate v (*post*).

*Helix pomatia*. Cuvier, Mémoires pour servir à l'histoire, &c. des Mollusques, 1871. (Annales du Muséum, vii. 1806.) *H. aspersa*. Howes, Atlas of practical Elementary Biology, 1885, Pls. xiii. xiv. Taylor, Journal of Conchology, iv. 1883, pp. 102-105. *Zonites algirus*. Nalepa, SB. Akad. Wien. lxxxvii. Abth. i. 1883. *Ancylus*. Sharp, Proc. Acad. Nat. Sc. Philadelphia, 1883. *Onchidium* (Marine Slug). Bergh, Challenger Reports, x. 1884, p. 126, and M. J. x. 1885.

*Muscles and locomotion of snails*. Simroth, Z. W. Z. xxx. Suppl. 1878; xxxii. 1879; xxxvi. 1882.

*Glands of foot*. Houssay, A. Z. Expt. (2) ii. 1884. Carrière, A. M. A. xxi. 1882. *Supra-pedal gland*. Sochaczewer, Z. W. Z. xxxv. 1881. Id. and Simroth, *ibid.* xxxvi. 1882. Sarasin, Arb. Zool. Zoot. Inst. Wurzburg, vi. 1883.

*Mucous threads spun by Mollusca*. Martens, Z. A. i. 1878. Eimer, *ibid.* Tye, Quarterly Journal of Conchology, 1878.

*Pulmonary chamber*=*a uropneustic apparatus*. Von Ihering, Z. W. Z. xli. 1884; criticisms of view, see Semper, Arb. Zool. Zoot. Inst. Wurzburg, iii. 1876-77; cf. Simroth, Z. W. Z. xxvi. 1876, p. 337 et seq.

*On Ampullaria*. Jourdain, C. R. 83, 1879. Sabatier, *ibid.* and A. N. H. (5), iv. 1879.

*Vascular system and pulmonary vessels*. Nalepa, *op. cit. supra*. *Apertures of capillaries in Arion ater* (= *rufus*). Jourdain, C. R. 83, 1879. *Haemocyanin, properties and distribution*. Halliburton, Blood of *Decapoda* (*Crustacea*), Journal of Physiology, vi. 1885. MacMunn, Q. J. M. xxv. 1885. *Haemoglobin in Mollusca*. Ray Lankester, P. R. S. xxi. 1872; cf. Sorby, Q. J. M. xvi. 1876. *For colouring matters in general*, see Krukenberg, Vergleich. Physiol. Vorträge, iii. 1884. MacMunn, Proc. Birmingham Philosoph. Soc. iii. 1881-83. Cf. Moseley, Q. J. M. xvii. 1877.

*Connection between nephridium and pericardium in Helix.* O. Nüsslin, Beiträge zur Anat. und Physiol. der Pulmonaten, Tübingen, 1879. Cf. Haller, Marine Rhipidoglossa, M. J. xi. 1886.

## 22. EDIBLE SNAIL (*Helix pomatia*),

Dissected so as to show its digestive and reproductive, together with portions of its circulatory and respiratory organs.

THE body has been detached from the shell, and the greater part of the mantle and skin has been removed. The coils of the right lobe of the liver (hepato-pancreas), which occupy the upper whorls of the shell and lodge the hermaphrodite gland, are arranged with the rest of the reproductive organs on the right hand: the left lobe of the liver, intestine, heart and respiratory chamber lie to the left: the nerve-collar, buccal mass and stomach occupy the centre. Between the latter and the parts to the left lies at a lower level the sole-shaped 'foot' upon which the animal creeps. A black bristle has been passed between the cerebral or supra-oesophageal ganglia and the buccal mass which contains the crescent-shaped chitinous jaw and the lingual ribbon or radula, structures invisible here. The buccal mass is somewhat retracted, as it is when the snail 'draws in his head.' On the left side of the buccal mass may be seen the sheath which contains the connectives from the cerebral to the infra-oesophageal ganglia, a small portion of which with numerous nerves proceeding from it is also visible. From the base of the buccal mass projects the small conical 'sac' of the radula below, while the oesophagus and ducts of the salivary glands enter it above,—the oesophagus between the two salivary ducts. The oesophagus expands into the stomach which is embraced by the salivary glands. The right and left bile ducts, from the right and left lobes of the liver respectively, enter one on either side the pylorus, and at this spot there is a small projecting median caecum. Just below the heart, which has been exposed in the pericardium, and above the aorta cephalica, which has been cut transversely, the intestine passes on to the convex surface of the left lobe of the liver. It reappears on the left side of this lobe in the preparation, on the right side in the natural position of the parts in the living animal, and passes straight to the anus. A white bristle has been placed in the anus through the pulmonary aperture. To the right side of the terminal segment of the intestine is seen the wall of the pulmonary chamber with its network of vessels.

The hermaphrodite gland or ovo-testis is lodged in the concavity of the penultimate and ante-penultimate coils of the right lobe of the liver, which occupy the lowest portion of this preparation on the right hand. From the gland a convoluted hermaphrodite duct passes up to a spleen-

shaped body, the albuminiparous gland, and from this spot the duct passes upwards again as a much thicker tube consisting of two parts—one, oviducal or uterine, much plicated; the other granulated, the vas deferens. These two parts are not separated completely from one another internally, but at the level of a cylindrical muscular organ, the dart-sac, they become independent. The vas deferens passes to the left, turns round the right upper tentacle, and then passes back again to the base of the penis at the point where the flagellum or organ for secreting the spermatophore also joins it. The retractor muscle of the penis is attached to it near this same point. The flagellum is of great length, and to its right lies a duct of similar, perhaps correlated length, terminated by a bulb. This is the receptaculum seminis or spermatheca, an appendage to the female organs. Lying below the penis and dart-sac are the two bundles of multifid vesicles, which enter the female duct close to the dart-sac. The generative aperture is on the right side of the head.

The integument varies in thickness in different parts of the body. In the *Pulmonata* with external shells it is exceedingly thin and delicate where it lines the coils of the shell. It is thicker where it forms the roof of the pulmonary chamber, and thickest of all on the exposed parts of the body. The epidermis consists of a single layer of cells. These cells are columnar and provided with a very delicate cuticula, thickened in certain spots on the tentacles and oral lobes (*infra*, p. 121-2). The terrestrial differ from the aquatic *Pulmonata*, and from aquatic *Gastropoda* in general, in the restricted extent to which cilia are present. In aquatic forms they are as a rule found over the whole of the exposed surface of the body; in the terrestrial *Pulmonata*, on the contrary, they occur on the sole of the foot but sometimes not over its whole surface; occasionally along its lateral margins (*Arion*); round the aperture of the supra-pedal gland and that of the pulmonary chamber in some instances (e. g. *Helix nemoralis*, *Limax marginatus*)<sup>1</sup>. The cells occasionally contain pigment. Among them are scattered on the exposed surface of the body, sensory cells (*infra*, p. 121), small goblet cells, and the apertures of mucous, pigment, and calcareous, glands. The mucous glands are unicellular, but project inwards into the cutis. The mucus varies in character, but not infrequently contains whetstone-shaped bodies. The glands are especially large on the collar. Pigment-producing glands are either richly pigmented epidermic cells, e. g. on the collar where they secrete the colouring matter of the shell, or long irregular bodies composed of more than one cell, extending outwards between the cells of the epidermis, inwards into the cutis, where they are said by Leydig to become continuous (?) with the pigmented networks there present. The glands which produce calcareous matter resemble the irregularly-shaped pigment-producing glands, and, like them, open externally and are continuous (?)

<sup>1</sup> Inter-cellular passages are said to exist between the epidermis cells, and are supposed to be the passages by which water enters the blood. They have been described and figured in *Helix* by Nalepa, SB. Akad. Wien. lxxxviii. Abth. 1. 1883. For absorption of water in Mollusca, see Schiemenz, Mitth. Zool. Stat. Naples, v. 1884. Cf. Sarasin, C. F. and P. B., 'Directe Communication des Blutes,' &c., Arb. Zool. Zoot. Inst. Wurzburg, viii. pt. 1, 1886.



internally with the cells of the cutis which contain calcareous matter. The pigment and calcareous glands do not extend over the surface of the foot. The latter are especially numerous on the collar, and round the margins of the foot in *Helix*.

The body-wall consists of connective tissue and muscle-fibres. Its surface in the exposed parts of the body is raised into ridges and tubercles. The muscle-fibres are non-striated long cells. They occasionally appear striated, but the cause of the striation is not known. The connective tissue consists of plasma-cells, a matrix, and fibrils. The plasma-cells are richly developed in all Mollusca, but especially in *Pulmonata* where three kinds are distinguishable. These are: (1) oval or round in shape with a transparent protoplasm and a round nucleus; (2) irregular cells containing refractile granules which are not fatty in nature; and (3) cells with granules of lime carbonate, which are immeasurably fine in the interstitial tissue of the upper coils of the visceral dome, coarser elsewhere. These cells are imbedded singly or in masses in a matrix which contains stellate cells, and connective tissue fibrils, the latter much more scanty than in other Mollusca. The matrix is sometimes much reduced, and the first kind of plasma-cells then appears to form sheaths round various organs, e.g. nerves, but the stellate cells of the matrix may still be detected among them. The connective tissue membranes are generally pierced by apertures, many of which are bounded by refractile rings, the product of several cells which encircle the aperture. Glycogen has been detected in the plasma-cells of the first kind both in *Anodon* and *Helix* (Blundstone, P. R. S. xxxviii. 1884-85). Branched pigment-cells are found in the cutis and sometimes extend inwards to its deeper layers. Changeable chromato blasts have been observed by Leydig in *Limax variegatus* and *L. (= Amalia) carinatus* (A. M. A. xii. 1876, p. 541).

The buccal mass consists chiefly of an odontophore, using that term in a wide sense to include the muscular and cartilaginous apparatus in connection with a chitinous (?) radula or lingual membrane bearing transverse rows of teeth. The radula is developed within a radular sac and is perpetually growing throughout life. The sac is essentially a ventral diverticulum of the buccal cavity, and its lining cells are continuous with the oral epithelium. It is crescentic in transverse section. At the blind end of the sac the lining cells are differentiated into odontoblast cells, which form a transverse ridge broken up in correspondence with the number of teeth present. This ridge contains in vertical section four to five large cells in *Pulmonata* and *Opisthobranchia*; a number of elongated cells in other *Glossophora*. The singly refractile core of each tooth is secreted by these cells, the doubly refractile enamel-like outer layer by the cells lying immediately dorsal to the odontoblast cells, whilst the membrane or matrix uniting the bases of the teeth is formed by a single cell in *Pulmonata* and *Opisthobranchia*, by several in other *Glossophora*, placed in each case just ventral to the odontoblast cells. These matrix cells split up at their free ends into fibres. The radula is carried by a subradular membrane, developed by the cells of the ventral wall of the sac. The membrane is borne upon cartilaginous pads, and the whole is worked by a system of muscles, protractor and retractor. Other muscles flatten the radula or convert it into a groove. And in some cases the subradular membrane with the radula slides backwards and forwards to a limited extent over its cartilaginous supports.

The chromogen, called myohaematin by MacMunn, is found in the buccal muscles (and in the heart) of *Helix*, *Arion*, *Limax* and of other *Pulmonata*. According to Ray Lankester, haemoglobin occurs in the buccal mass of some Mollusca.

The form and number of the teeth in a transverse row are very variable in the *Glossophora*. In *Pulmonata* a median tooth may be distinguished from an indefinite number of admedian teeth. Such a dentition may be formulated thus— $\infty . 1 . \infty$ , and is termed myrioglossate. Various technical terms have been applied to the variations in number and arrangement of the teeth already alluded to. A median tooth may be present or absent: so too admedian teeth: and in the arrangement known as rhipidoglossate lateral may be distinguished from admedian and median teeth. The size and shape of the teeth themselves are also extremely variable. In the *Pulmonata* each tooth is provided with a recurved hook, usually simple, but sometimes denticulated<sup>1</sup>.

The more or less chitinous jaw lies on the dorsal aspect of the oral cavity. In most *Helices* it is a crescentic plate; its free surface provided with antero-posterior ridges. The form of the jaw varies in different *Pulmonata*: in aquatic *Pulmonata* it may consist of more than one piece, and in a few terrestrial forms it is absent, e. g. *Testacella*.

The salivary glands vary in form and size in different *Pulmonata*. They are compound glands, but the ultimate acini are composed of a number of unicellular glands. They receive bloodvessels and nerves, the latter from the buccal ganglia. An additional salivary gland lies imbedded in the buccal mass in *Helix pomatia* round the entrance of the main salivary ducts. It consists of unicellular glands, partly opening into the salivary ducts, partly uniting and opening by ducts of their own into the oral cavity. The salivary extract converts starch into sugar. The muscular coats of the digestive tract are an external circular, and an internal longitudinal coat. The longitudinal ridges of the internal surface are formed by the longitudinal muscles. The epithelial cells possess a cuticle, and cilia are present in places; in young *Helices* over the whole surface of the stomach. Goblet cells are present in *Zonites* and apparently in *Helix*; and in the former Nalepa observed small cells at the base of the other cells, which they are apparently destined to replace. The liver or hepato-pancreas is a compound acinous gland. Its acini are held together by connective tissue, ramifying bloodvessels and nerves. The epithelium forms a single layer. In the ducts are found columnar cells, sometimes ciliated, but not in *H. pomatia* (Barfurth), as well as mucous-cells: in the acini three kinds of cells—liver-cells (Barfurth) or granular-cells (Frenzel); ferment-cells (Barfurth), club-cells, or club-shaped ferment-cells (Frenzel); and calcareous-cells. The granular cells contain each a vesicle which incloses a number of more or less coloured highly refractile granules, fat globules variable in size,

<sup>1</sup> The character of the dentition is especially useful for classificatory purposes in the Azygobranchiate *Gastropoda*. The names in use are chiefly the following. The formulae indicate the presence or absence of median, admedian, and in *Rhipidoglossa* of lateral teeth. *Rachiglossa*, 0. 1. 0, e. g. *Volutidae*: *Hamiglossa*, 1. 1. 1, e. g. *Murex*, *Buccinum*: *Toxoglossa*, 1. 0. 1, e. g. *Conidae*: *Taenioglossa*, 3. 1. 3, e. g. *Cerithium*, *Natica*, *Littorina*, *Paludina*: *Cteno-* or *Pteno-glossa*,  $\infty . 0 . \infty$ , e. g. *Ianthina*: *Rhipidoglossa*,  $\infty . 4-7 . 1 . 4-7 . \infty$ , e. g. *Turbo*, *Nerita* (also *Haliotis*, *Fissurella*, among *Zygobranchiata*). There are forms of dentition which do not fall under any of the above-written terms, e. g. *Patella Vulgata*, the Limpet, with 3. 1. 4. 1. 3.

and albuminous bodies. In *Helix* the granules are clear yellow in colour ; sometimes, as in *Arion*, they are the only coloured constituent of the cells. These granular cells are absent in *Cephalopoda*. The ferment-cells vary in appearance in different Mollusca. They are absent in *Chiton*, *Patella*, *Fissurella*, and *Pteropoda* ; doubtfully present in some azygobranchiate *Gastropoda* and some *Lamellibranchiata*. In shape they are like a club or pear, with the larger end turned towards the cavity of the acinus. They contain each a vesicle inclosing more or less coloured fluid, viscous or semi-solid bodies, fat and albumen globules. The refractile index of the contents of the vesicle is low in *Helix* and *Cephalopoda*, and their colour is similar to that of the granule-cells. It is generally more or less different in the *Opisthobranchia* and *Azygobranchia*. It is similar in intensity in *Pulmonata*, more intense in other groups (Frenzel). The calcareous cells are wanting in *Lamellibranchiata*, *Pteropoda*, and in *Natantia* (= *Heteropoda*) among *Gastropoda*, and other isolated instances in this Class. Their size is great, and they are more or less triangular with the base external, and the apex not reaching the cavity of the acini. They contain the so-called calcareous globules, which vary in chemical characters. Lime is always an ingredient, and, according to Barfurth, in combination with phosphoric acid, a view opposed by Frenzel. Barfurth has shown that the percentage of inorganic ash obtainable from the liver of *Helix pomatia* varies at different seasons. In May the amount averaged 20.24 per cent. ; in September 25.72 per cent. ; after the breaking and repair of the shell it fell at once to 16.99 per cent. ; and after the formation of the epiphragma to 10.26 per cent., the normal figure during the winter rest of the animal. It may be added that the quantity of phosphates in the epiphragma is 5.52 per cent. as opposed to 0.85 per cent. in the shell. The mucus of *Helix* contains lime, and to a very large amount in *Arion*. The secretion of the liver is acid, and has been found to have a diastatic and a peptic action in *H. pomatia*. It contains enterochlorophyll in *Helix pomatia*, in many other *Gastropoda*, some *Lamellibranchiata*, and haematin in various *Pulmonata*, e. g. *Helix pomatia*, *H. aspersa*, and *Arion ater*, &c. Glycogen is found in the liver ; in *Helix*, in the plasma-cells of the connective tissue which are abundant ; in *Limax*, in the liver-cells, the connective tissue being scanty. For the distribution and mode of occurrence of glycogen in the other tissues of *Gastropoda*, as well as in the tissues of other animals, the very valuable paper of Barfurth's, A. M. A. xxv. 1885, should be consulted.

The hermaphrodite gland or ovo-testis consists of a number of cylindrical follicles opening into a common duct. The ducts from the various groups of follicles unite in their turn with the chief duct of the gland, which is lined by a non-ciliated squamous or columnar epithelium. The ova and spermatozoa are formed from the lining epithelium of the follicles, but at a different time. The albumen gland is a racemose gland. It opens by a common duct, which with its branches is lined by a ciliated epithelium. The ovi-spermi-duct is lined by a ciliated epithelium, and both portions are beset with glands. The free portion of the oviduct is also ciliated, but not the vas deferens, as is the case also with the penis and flagellum. The latter organ, with the hinder part of the penis, secretes the 'capreolus,' or spermatophore, a structure formed of hardened mucus. It is more or less elongated and its edges folded so as to form a groove in which a mass of spermatozoa are lodged. In copulation it is transferred to the duct of the recepta-

culum seminis, and in this species it is said to undergo resolution in ten days after transference. The dart-sac, which has extremely muscular walls, contains a pointed cuticular style, with much calcareous matter in its composition. Its use appears to be a preliminary excitant to copulation, after which act it has been found within the body. A new dart is speedily formed after the loss of the old one. The multifid vesicles secrete a highly refractile fluid, which is poured out during copulation, and is formed by the epithelium. The duct of the receptaculum seminis has occasionally a tubular diverticulum appended to it. The latter is constantly present in many species of the genus *Helix*, e. g. *H. aspersa*, and may possess a terminal bulb like the receptaculum itself. The genital organs are richly supplied with nerves and bloodvessels. In aquatic *Pulmonata* the male and female apertures open separately from one another externally.

Of the accessory organs present in *Helix pomatia*, the flagellum is absent in all the American species of the genus, and both dart-sac and multifid vesicles, common in the European species, are rare in them. A dart-sac is found in the American slug *Tebennophorus*; and glands resembling the multifid vesicles are appended to the male organs in *Veronicella*. With these two exceptions the organs in question are confined to the genus *Helix*.

The eggs have, like those of other *Helices*, of *Arion* and some other terrestrial *Pulmonata*, a hard calcareous shell inclosing a quantity of albumen and a small ovum. Those of some terrestrial (*Limax*), and of all aquatic *Pulmonata*, are devoid of a calcareous shell, and the surface of the albumen is simply hardened. The eggs of *H. pomatia* are large, nearly a quarter of an inch in size, and are laid in earth as are those of other terrestrial *Pulmonata*, in masses, but not united, as are those of many species of *Limax* and of all aquatic *Pulmonata*. A few terrestrial *Pulmonata* are viviparous (certain species of *Clausilia* and *Pupa*, *Helix rupestris*, *Achatinella*, a *Vitrina*). The larva has but slight traces of the typical Molluscan velum; in that point differing from its aquatic congeners, where it is well developed, and *Arion* and *Limax*, where it is wanting. There is no operculum. A remarkable contractile pedal sinus is present. A paired provisional tubular renal organ appears to be found in the larva of all *Pulmonata*.

*Integument.* Leydig, A. N. 42, 1876. *Epithelium.* Flemming, A. M. A. vi. 1870. *Connective tissue (interstitial)*, Brock, Z. W. Z. xxxix. 1883.

*Odontophore. Mechanism.* Geddes, Tr. Z. S. x. *Radula*, Rössler, Z. W. Z. xli. 1885. *Description of various forms of dentition and nomenclature*, Gray, P. Z. S. 1853; A. N. H. (2), xii. 1853; Troschel, Das Gebiss der Schnecken, Berlin, i. 1856-63; ii. parts i-vi. 1866-79. *Myohaematin in odontophore muscles*, MacMunn, Proc. Physiol. Soc. in Journal of Physiology, v. 1884; P. R. S. xxxix. Novr. 1885.

*Salivary glands, &c.*, see Nalepa (op. cit. ante, p. 112). *Sugar formation.* Bonardi, Boll. Sc. Pavia, Anno 5, 1883. *Liver* Barfurth, A. M. A. xxii. 1883; Id. Biol. Centralbl. iii. 1883-84; Frenzel, Biol. Centralbl. tom. cit.; Id. A. M. A. xxv. 1885; *its physiological action*, Krukenberg, Untersuchungen Physiol. Inst. Heidelberg, ii. 1882, pp. 4 and 13; Fredericq, Bull. de l'Acad. Royale de Belgique (2), 46, 1878. *Pigments.* MacMunn, P. R. S. xxxv. 1883, and xxxviii. 1884-85; Krukenberg, Vergleich. Physiol. Studien, ii. (2) p. 63, 1882. *Glycogen*, Barfurth, A. M. A. xxv. 1885.

*Genital organs*, Baudelot, A. Sc. N. (4) xix. 1863. *Histology of accessory organs*, Batelli, Atti Soc. Toscana Sc. Nat. (Mem.), iv. 1880; cf. Journal Royal Micr. Soc.

(2) i. 1881, p. 435. *Development*, Rouzaud. C. R. 96, 1883; Jourdain, Revue Sc. Nat. Paris and Montpellier, viii. *Physiology*, Dubrueil, Revue des Sci. Nat., Paris and Montpellier, i. 1873; ii. 1874; cf. Jourdain in A. N. H. (4) viii. 1871. *Dart of British Helicidae*, Ashford, Journal of Conchology, iv. 1883.

*Sperm.* Leydig, Untersuchungen zur Anat. und Histol. der Thiere, Bonn, x. 1883, p. 118; *development of*, Blomfield, Q. J. M. xxi. 1881; Nussbaum, A. M. A. xxiii. 1884, p. 206; cf. Von Brunn, *ibid.* p. 459; Platner, A. M. A. xxv. 1885. *Ova and Development*. Fol, A. Z. Expt. viii. 1880.

### 23. EDIBLE SNAIL (*Helix pomatia*),

Dissected so as to show its nervous system.

THE collar has been divided to the right of the pulmonary aperture, to the left of its columellar lobule, which is left *in situ* on the right side. The attachment of the mantle below the collar to the integument of the body has been divided from right to left, and again along the right margin of the pulmonary chamber. The mantle-fold or roof of the pulmonary chamber thus freed from its connections has been turned over to the left and displays the terminal portion of the intestine at its edge, the pulmonary vessels, the triangular kidney, and the pericardium, the latter opened to show the heart. The integument covering the head and neck has been divided in the middle line, and the floor of the pulmonary chamber continuous with it removed. The whole of the viscera have also been removed, leaving only the buccal mass, the nerve-collar and the columellar muscles cut short. The buccal mass is much retracted, as it is when the animal's head is drawn in. At its base are seen, the origins of the oesophagus and salivary ducts above, and the sac of the radula below. A stout black bristle has been passed under the right cerebral ganglion. From the anterior edge of this ganglion a nerve passes to the right upper tentacle which bears the eye: a similar nerve, not visible here, passes to the lower tentacle. From its posterior edge a nerve passes along the buccal mass to a small stellate ganglion, the buccal ganglion, which lies below the salivary duct and innervates the buccal mass; a fine black bristle has been placed beneath it. There are two such ganglia, right and left, connected by a commissure below the oesophagus. The right cerebral is united to the left by a commissure passing across the buccal mass: it is united to the infra-oesophageal ganglion below the buccal mass by a broad band. This band contains two nerve-connectives (not visible here), one to the anterior or pedal portion, the other to the posterior or visceral (parieto-splanchnic) portion of the infra-oesophageal ganglion. From the posterior margin of this ganglion three nerves pass backwards to the body walls; a fourth, which accompanies the aorta cephalica, has been removed together with that vessel. Bundles of nerves may be seen passing down from the anterior or pedal portion of the

ganglion to the foot. The cut ends of the columellar muscles are visible in a bundle below the buccal mass. These muscles are attached on the one hand to the columella of the shell, on the other to the foot, to the buccal mass, tentacles, and nerve-collar on either side. They therefore serve as retractors of these organs.

There are two pairs of cephalic tentacles in nearly all terrestrial *Pulmonata*, the superior pair bearing the eyes at their apex: hence the name *Stylommatophora* applied to this section of the order. They are hollow, and in- and e-vaginable. The exceptions are the Australian genera *Janella* and *Aneitea*, in which the eye-bearing tentacles alone are present, and the slugs *Onchidium* and *Vaginulus*, in which the tentacles are solid but extremely contractile. The aquatic *Pulmonata*, on the other hand, have but one pair of tentacles, solid and contractile, with the eyes placed at the inner side of their bases: hence this section of the order is termed *Basommatophora*.

The bands of nerve-fibres uniting the various ganglia are termed 'commissures' when they unite the ganglia of the same pair, e.g. the cerebral; 'connectives' when they unite ganglia of different pairs, e.g. cerebro-pedal connective between the cerebral and pedal ganglia of the same side. The nervous system of *H. pomatia* has been worked out in detail by Böhmig. Each cerebral ganglion is divisible into three regions: from one there arise the commissure to the other cerebral ganglion, the various connectives, and six nerves, one to the upper tentacle, the mouth, lip, pharynx, lower tentacle, and on the right side to the penis: from the second arises a nerve to the upper tentacle and eye: from the third nothing. The two pedal ganglia are each divisible into two regions, from which 8-9 nerves pass to the foot, and from one of the ganglia branches proceed to the connective tissue surrounding the uterus. The parieto-splanchnic region consists of a right and left pleural (= commissural) ganglion which are in union with the connectives to the cerebral and pedal ganglia, and with the remaining ganglia of the visceral system. These are a right and left visceral ganglion and a median abdominal. The right visceral ganglion gives origin to two pallial nerves inclosed in a common sheath; the left to a single pallial nerve. The abdominal ganglion gives origin to three nerves; one distributed to the heart, nephridium, liver and (?) sexual organs; another to the neighbourhood of the anus, and the third to the integument. The buccal ganglia supply the pharynx, intestine and salivary glands with four nerves. Although the divisions between the pedal and the various ganglia of the visceral system are not visible externally in *Helix* and other terrestrial *Pulmonata* as they are in the aquatic Pulmonate *Limnaeus*, several facts may be noted which clearly show without further analysis the compound nature of the infra-oesophageal ganglion. These are (1) the distribution of the nerves given off by it; (2) the passage of the aorta cephalica through its centre; (3) the relation of the otocysts to the region termed pedal; (4) the presence of double connectives on each side between it and the cerebral ganglia, which can be clearly discerned through the common connective tissue sheath.

In *Zonites algirus* two pedal nerves run backwards in the foot nearly parallel one with another. They are connected by transverse commissures from place to place, and posteriorly they break up into a number of branches which anastomose with one another. Minute ganglia occur at the nodal points of this network, but are

not common in the course of the two main nerves. The nerves to the margins of the foot originating from the pedal nerves form a similar network with nodal ganglia. In *Vaginulus*, according to Semper, the pedal nerves run parallel to one another, and are provided at stated intervals with ganglia from which spring transverse commissures. The similar transverse commissures of *Limax* appear from Simroth's description to be rather irregular, and they give origin to a network of fibres with nodal ganglia which unite them together. The nerves passing across the foot in *Helix* anastomose, but they are very irregular in arrangement; and in *Arion* they break up into a fine network, and there is nothing to compare with the commissures of *Limax* either in the direction or in the size of the nerves; but the networks of nerve-branches are furnished as usual with nodal ganglia both in *Helix* and *Arion*. The regular arrangements of transverse commissures in *Zonites* and *Vaginulus* recall the ladder-like structure of the pedal nervous system in *Chiton*, *Haliotis* and *Fissurella* among marine *Gastropoda*. It is not certain, however, whether or no they are strictly comparable with one another.

The ganglion cells of *Helix* vary from 0.4 mm. in the visceral ganglia to 0.16 mm. or 0.007 mm. in the cerebral. Some of the larger cells have a connective tissue capsule. The majority are unipolar, but bi- and multi-polar cells are also found. The central region of the ganglia is occupied by Leydig's 'Punkt-substanz,' which is composed really of a network of very fine fibres derived from the ganglion cells. The nerves are composed of an outer sheath of vesicular connective tissue, and an inner membranous sheath continuous with internal septa dividing the nerve-fibrillae into bundles. The fibrillae and fibrillar bundles originate from the 'Punkt-substanz.'

The organs of special sense are sensory epidermic cells, the tentacular ganglia, the ganglia of the oral lobes, the eyes, and the otocysts. The sensory cells are most numerous on the tentacles, oral lobes, and on the sides of the foot, where they have the form of cylinders with a fine point composed of delicate hairs, which do not project above the level of the cuticle of the ordinary epidermic cells. At the actual edge and on the sole of the foot, parts covered by mucus, the hairs are distinctly separate, and project beyond the cuticle of the surrounding cells. Hence there is a closer resemblance with the 'Pinselzellen' of aquatic *Pulmonata* and other Mollusca in which the cell is terminated by a distinct head and a bundle of long projecting hairs.

The nerve which enters each tentacle ends at its summit in a knob composed of nerve-fibrils and ganglion-cells, the whole surrounded by a muscular sheath derived from the retractor muscle of the tentacle. There are masses of small ganglion-cells underlying the epidermis, which is modified in the region of this terminal ganglion. The ordinary epidermic cells acquire an exceedingly well-developed cuticle vertically striated. A few goblet cells occur among them, and numerous sense-cells connected each with a fibril from a ganglion-cell. The sense-cells are flask-shaped, and end (?) either in a single point or several hairs. They do not reach as far as the cuticle of the epidermic cells. These tentacular organs appear to be olfactory in function. As long as one or both pairs are present the snail recoils from strong-smelling liquids, e.g. turpentine. If both pairs are removed it creeps into them. The ganglionic structures in the large oral lobes or lips, and the smaller series of oral lobes are similar to the tentacular ganglia. The

overlying epidermic cells have also a very thick cuticula. A tentacular ganglion is found on the outer side near the bases of the two tentacles of *Basommatophora*, and an oral ganglion in the oral lobes, e. g. of *Limnaeus*.

The eyes are situated close to the apex of the upper tentacles, a little to their inner side. The optic nerve is a branch of the tentacular nerve in the *Stylommatophora*, an independent nerve in the *Basommatophora*. The retina is composed of a single layer of cells derived by invagination from the epidermis. The cells are of two kinds, pigmented and non-pigmented, both continuous basally with the nerve-fibrils derived from a peripheral optic ganglion. The pigmented cells are widest at their inner, the non-pigmented at their outer ends. The inner ends of the non-pigmented cells end in a flask-shaped (*Stylommatophora*) or a fine (*Basommatophora*) visual rod. The inner ends of the pigmented cells form transparent processes. Each non-pigmented cell is surrounded by a zone of pigmented, and the visual rods are encased in the transparent processes of the latter. The retina is continuous at its anterior margin with a layer of transparent cells which lines the cornea (=pellucida). The optic cavity is filled by a structureless substance, the vitreous body (Carrière), commonly called the lens. By Hilger a vitreous body is distinguished from a lens in all the *Gastropoda* he examined except the *Stylommatophora*, which, according to him, possess a lens but no vitreous body. It is probable that the lens, so called, is a differentiated portion of the vitreous body, and not an independently formed structure. The cornea consists of an outer layer of transparent cells with underlying connective tissue.

The otocyst is small in size, and is to be found on the pedal ganglion close to the spot where the anterior bundle of pedal nerves quits it. To the naked eye it appears like a minute white dot. It consists of a connective tissue capsule nearly, but not quite, spherical, and an epithelial lining with a central cavity. The latter contains a fluid and a number of otoliths, as is usual in *Gastropoda*. The otoliths are more or less oval, and consist of a small quantity of an organic substance and a large quantity of calcium carbonate. The cells of the epithelium are not clearly separated from each other in the fresh state, according to Leydig. At the spot opposite to the auditory nerve (or the auditory canal) they are of larger size. All the cells are ciliated, and the cilia are short. It is doubtful whether or not long auditory or sensory hairs are present such as are found in *Natantia* (= *Heteropoda*) and in *Cyclas* (a Lamellibranch). Leydig believes them to be present. The otoliths are in constant motion in the living animal. The otocyst is connected to the cerebral ganglion by a delicate filament. This, according to Leydig, as in some other *Gastropoda*, is a narrow canal lined by cells, and continuous with the cavity of the otocyst. Nerve-fibrillae are therefore not present. But if this is the case, it is difficult to see in what way auditory impulses can affect the nervous system. And, judging from the analogy of other Mollusca, auditory nerve-fibrils are probably present. The connection of the otocysts with the pedal ganglia is only accidental. Both sets of structures are enveloped by a common investment of loose connective tissue.

An osphradium or olfactory organ in connection with the organ of respiration has not been detected in *Helix pomatia* and many of its allies. In *Helix personata* Sarasin found a nerve arising from the region of the right visceral ganglion which passes beneath the epithelium of the pulmonary chamber, the cells being more



columnar where the nerve is in contact with them than elsewhere. It bends round the anterior edge of the pulmonary aperture, and at the spot where it bends swells into a small ganglion with large ganglion-cells. A nerve extends from the ganglion to the glandular cells of the epidermis (?) of the collar. The homologous nerve, but devoid of a ganglion, is present in *Succinea amphibia*, *Bulimus detritus*, *B. decollatus* and *Limax cinereoniger*. It is distributed to the glandular epithelium as in *H. personata*. The corresponding nerve is apparently present in *H. pomatia*<sup>1</sup>. The osphradial apparatus is well developed in the aquatic Pulmonates, *Limnaeus*, *Planorbis*, and *Physa*. In the first of the three, which has a dextral shell, the nerve is derived from the right visceral ganglion; in the other two, which have sinistral shells, from the corresponding left ganglion. The nerve ends in a ganglion with large ganglion cells, in connection with a ciliated canal or depression in the pulmonary chamber above and behind its orifice. In branchiate *Gastropoda* the nerve is also derived from the visceral ganglion, and ends in a similar ganglion lying immediately beneath the epidermis close to the ctenidium. The epidermic cells above this ganglion are large and columnar. The apparatus is paired when the ctenidia are paired. See general account of the Class.

*Nervous system*: of *Helix pomatia* and *Limnaeus*, Böhmig, Inaugural Dissertation, Leipzig, 1883; of *terrestrial Pulmonata*, Leydig, A. M. A. i. 1865; of *aquatic Pulmonata*, De Lacaze Duthiers, A. Z. Expt. i. 1872; of *Mollusca*, von Ihering, Vergleich. Anat. des Nervensystems, &c. der Mollusken, Leipzig, 1877.

*Homology of the ganglia*. Spengel, Z. W. Z. xxxv. 1881. Cf. Ray Lankester, 'Mollusca,' Encyclopaedia Brit. (ed. ix.) xvi. p. 636, and Fig. 1 D.

*Pedal nerves*: of *Zonites*, Nalepa, SB. Akad. Wien. lxxxvii. Abth. 1. 1883, p. 282; of *Limax*, *Helix*, *Arion*, Simroth, Z. W. Z. xxxii. 1879, pp. 304-318; of *Vaginulus*, Semper, A. M. A. xiv. 1877, p. 123.

*Histology*. See Böhmig, op. cit. *supra*; Vignal, A. Z. Expt. (2) ii. 1883. Cf. Haller, Marine *Rhipidoglossa*, ii. M. J. xi. 1886.

*Organs of special sense*. *Sensory epithelium*. Flemming, A. M. A. v. 1869. *Tentacular ganglion*, &c., Id. A. M. A. vi. 1870; Sarasin, Arb. Zool. Zoot. Inst. Wurzburg, vi. 1883. *Oral ganglion* (=Semper's organ), Sarasin, op. cit. *Eye*, Hilger, M. J. x. 1885. Carrière, Sehorgane der Thiere, Leipzig, 1885; Z. A. ix. 1886. *Otocyst*. Leydig, A. M. A. vii. 1871. Cf. Simroth, Z. W. Z. xxvi. 1876, pp. 278-281; De Lacaze Duthiers, A. Z. Expt. i. 1872. *Osphradium* (=olfactory organ): of *Mollusca*, Spengel, Z. W. Z. xxxv. 1881; of *aquatic Pulmonata*, Simroth, Z. W. Z. xxvi. 1876, p. 308; De Lacaze Duthiers, A. Z. Expt. i. 1872 (=organe nouveau d'innervation); of *terrestrial Pulmonata*, Sarasin, op. cit. *supra*.

*Regeneration of eye, &c. in Pulmonata*. Carrière, Studien über die Regenerationserscheinungen bei den Wirbellosen, i. Wurzburg, 1880.

<sup>1</sup> Simroth has described (Z. A. v. 1882, and with figures in J. B. Mal. Gesellsch. x. 1883), in the slug *Parmacella Olivieri*, a groove with projecting edges extending from the pulmonary aperture forwards to the left, and lying in the furrow between the edge of the mantle-fold and body. Ganglion cells underlie the groove and its edges, which are supplied by the right pallial nerve, as well as by a branch from the left pallial nerve. The position of the organ external to the pulmonary chamber appears to render an homology with the osphradium impossible. *Zonites* has a sac opening close to the pulmonary aperture and lying in the roof of the pulmonary chamber. It is beset with gland-cells and supplied by the 'olfactory' nerve, which is, however, devoid of a ganglion (see Nalepa, op. cit. *ante*, p. 239).

24. SHELL OF FRESH-WATER MUSSEL (*Anodonta cygnea*).

THE shell of *Anodonta* and of all *Lamellibranchiata* is bivalve. The two valves correspond to the two sides, right and left, of the body, and they resemble one the other. The shell is therefore equivalve. Each valve presents a short straight margin, the hinge-line, along which it is united to its fellow, and which coincides very nearly with the whole of the dorsal aspect of the animal, whilst the long curved margin coincides with its ventral aspect. The external surface is marked by concentric lines parallel with the margin and usually considered to mark distinct periods of growth—a point which cannot be regarded as certain. The areas inclosed by the lines diminish progressively in size. The smallest area corresponds to the original shell. This region of the shell is sometimes remarkably prominent and is known as the beak or umbo. If a line be drawn to the ventral margin from the centre of the umbo and perpendicularly to the hinge-line, it divides each valve into a smaller anterior and a larger posterior portion. Hence each valve is inequilateral. Those *Lamellibranchiata* which move from place to place by means of their distensible foot, move invariably with the anterior part of the shell-valves foremost, and never in the reverse direction. The shell of the *Brachiopoda* is also bivalve: but it contrasts with that of *Lamellibranchiata* in several points: the valves are dissimilar, i. e. the shell is inequivalve: they are divisible into symmetrical right and left halves, i. e. are equilateral: and finally one valve is dorsal, the other ventral according to the usual view. At any rate they are not right and left as in *Anodonta*. The larger or ventral valve is perforated by a peduncle of attachment, and is uppermost in the natural position of the Brachiopod.

The shell of *Anodonta* surpasses in size the shells of all other European fluviatile bivalves. It also shows with remarkable distinctness the three layers of which the Lamellibranch shell is usually composed—the epicuticula or periostracum, the prismatic layer and the layer of nacre or mother-of-pearl. The epicuticula is purely organic and is composed of conchiolin like the organic substratum of the rest of the shell. It is laminated, and the ridges on the outer surface of the shell are formed by it alone. It constitutes the free border of the shell which is flexible in the natural condition. The prismatic layer is calcified and is visible as a dark border on the inner surface of the shell close to the margin. With a lens it has a shagreen-like appearance due to its division into minute polygonal spaces. The calcareous matter is in the form of more or less regular prismatic needles. The nacre covers the whole inner surface of the shell within the dark border mentioned above. It is iridescent in appearance owing to the diffraction of light by the irregular free edges of the many delicate calca-

reous lamellae which enter into its composition. The calcareous lamellae alternate with organic layers.

An elastic ligament unites the two valves along the hinge-line. It serves to open the shell and is antagonised by the two adductor muscles. See next preparation.

The inner surface of each valve is marked by three principal muscular impressions, as they are termed, two anterior and one posterior, placed somewhat dorsally. Of the two anterior impressions, the larger is due to the attachment of the anterior adductor muscle, as well as of the anterior retractor of the foot; while the smaller, placed nearer the free margin of the shell and more dorsally, corresponds to the protractor of the foot. The larger portion of the posterior impression gives attachment to the posterior adductor muscle, but its irregular process, extending dorsally towards the hinge-line, denotes the point of attachment of the posterior and larger retractor of the foot. A continuous line extends between the impressions of the two adductors parallel to the margin of the shell and at some little distance from it. This is the pallial line. It gives attachment to a series of muscular filaments which extend outwards into the free edge of the mantle, and are attached to the spot where the epicuticula commences. The epicuticula being flexible, contraction of these muscles brings the edges of the epicuticular layers of both valves into firm contact, and at the same time retracts somewhat the free edges of the mantle lobes. As the pallial line describes an even curve throughout its whole extent, *Anodonta* is said to be integripalliate.

Muscles pass up from the foot and are attached to the ridge which borders the ligament internally, and in shells with hinge-teeth (*infra*) to the teeth, which are merely developments of the ridge present in *Anodonta*. A muscle also passes across from the ridge of one to the ridge of the other valve. And small muscular bundles are attached also to the inner part of the ligament.

The valves of the shell are inequivalve in the *Ostreidae*, one valve being smaller than the other. Each valve is nearly equilateral in some of the Pectens, e.g. *Pectunculus*. It is a rare thing for the anterior portion of the valve to be larger than the posterior. *Anodonta*, like some of its immediate congeners and some of the oldest *Lamellibranchiata*, geologically speaking, is devoid of 'hinge-teeth' on the inner aspect of the valves. The hinge-teeth consist of 'cardinal-teeth' placed below the umbones: of 'anterior lateral teeth' in front of the 'cardinal' teeth and 'posterior lateral' behind them, and below the ligament. *Unio*, which belongs to the same family as *Anodonta*, and, like it, inhabits the freshwaters, possesses anterior and posterior lateral but no cardinal-teeth. The presence of these interlocking teeth gives a dissimilar appearance to the two valves when viewed from within. The variations in the character and arrangement of the hinge-teeth have furnished recently a basis for the classification of *Lamellibranchiata* (Neumayr).

In those *Lamellibranchiata* which possess siphons, the pallial line is incurved beneath the impression of the posterior adductor muscles, forming a bay or sinus. Such shells are said to be sinupalliate.

The epicuticula varies in thickness in different *Lamellibranchiata*, and it is sometimes complicated in structure as in *Mytilus edulis*. It is rather thin in *Anodonta*. The prismatic layer consists of more than one layer of calcareous prisms, which vary in size and external shape. The different layers of prisms are held together by remains of the organic substance (conchiolin) in which the calcareous prisms are deposited. At their first appearance these bodies are, in *Anodonta* at least, more or less rounded and irregular in shape, and at some distance apart. They increase in size, and at the same time new prisms appear between those first formed. In some instances, e.g. *Cyprina islandica*, the prismatic layer consists chiefly of a mass of granular calcareous matter: in other instances it is very distinctly lamellate, like the nacre, e.g. *Astarte borealis*. It may closely resemble the Gastropod shell, and consist of vertical laminae, e.g. *Cardium*. The nacre consists of alternating lamellae of conchiolin, and of conchiolin containing calcareous deposits, which appear exactly in the same manner as the prisms of the prismatic layer. In the region of the various muscular impressions it is 'transparent,' and here the muscular fibres are directly continuous with the shell-substance, and not separated from it by an epidermis. According to F. Müller, the inner surface of the nacre is covered by a soft layer.

The *Cyclas cornea* of the freshwaters differs from other *Lamellibranchiata* in the structure of its shell. There is no prismatic layer, and the organic portion of the nacreous layer is reticulate. Short wide unbranched canals extend into the substance of the shell and are lined apparently by extensions of the mantle. In this point they differ from the branching canals so often found in the substance of the shell in other *Lamellibranchiata*, which, according to Kölliker, are due to algal parasites. Ehrenbaum, however, who mentions them in various genera, says nothing as to their contents.

The structure of the calcareous parts of the Lamellibranch shell does not appear to be by any means so uniform as is often supposed.

The ligament in *Anodonta* consists of an outer and inner part. The outer is laminated and passes gradually into the epicuticula. The inner is striated radially, and consists of radial fibre composed of two different alternating substances refracting light differently. Hence in cross sections this inner part appears to be laminated like the outer: but the mode in which it splits proves its real radial structure. It must probably be regarded as continuous with the nacreous layer. Where it borders the nacreous layer internally there is a distinct nacreous ridge, the homologue in *Anodonta* of the region which is produced into teeth in *Unio*, &c., and, like the teeth, giving attachment to muscles ascending from the foot (F. Müller). The border of the ligament itself is connected with numerous isolated bundles of muscles; and just as the 'transparent' portion of the nacre in the muscular impressions is continuous with muscle fibres, so here the fibres of the inner part of the ligament are continuous with muscle fibres.

The relations of the ligament to the shell-valves show that, strictly speaking, the valves ought to be regarded as parts of a continuous structure. The dorsal region of this structure does not undergo calcification, or only to a very slight extent, inas-

much as the economy of the animal requires that it should remain flexible. It is an adaptation of an originally univalve shell.

The whole shell is generally regarded as a cuticular secretion, the cells near the edge of the mantle forming the epicuticula; those of the part a little remote, the prismatic layer; and those of the general surface the nacre. Tullberg appears to take the view that the organic part of the shell is produced by a fibrillation of the cells. F. Müller believes that it increases by intus-susception, and states that in *Anodonta* the surface of the mantle is separated from the shell over a large space extending from the pallial line and adductor muscles as far as the attachment of the muscles to the ridge bordering the ligament (*supra*). Judging from analogy it is more reasonable to class the shell as a cuticular formation. This conclusion is borne out by Osborn's experiments on the Oyster. He studied the formation of shell by snipping away portions of the already formed shell, and placing on the exposed surface of the mantle a disc of thin glass such as is used in microscopic work. He found that a gummy film was formed on the surface of the glass by the columnar cells of the mantle, which hardened in forty-eight hours into a tough leathery membrane. Crystals of lime, for the most part scaly, appeared in this membrane, which became stony in six days. It is probable that the gummy films formed by the mantle-cells are charged with lime carbonate, which eventually crystallises, its crystalline form being modified by the organic matter of the films, as is the case with crystalline products formed in the presence of colloid matter.

The calcareous substance of the shell is chiefly composed of Calcium carbonate. Traces of Calcium phosphate, silica, alumina are sometimes found. The carbonate of lime is sometimes in the form of Calc-spar, e.g. *Ostrea*, *Pecten*, and such shells retain their integrity when fossilised. It is sometimes in the form of Arragonite, in the nacreous layer only, e.g. *Pinna*, or in the prismatic also, as in a very large number (Sorby). The Arragonite usually dissolves away when the shell is fossilised, and then either the inner layer only or both layers are lost as the case may be, leaving a stony nucleus or cast.

The thickness of the shell does not depend upon the amount of lime in the waters in which the animal dwells, but rather on the workings of its tissues, modified by surrounding influences, whether chemical or non-chemical. This may be readily seen by a comparison of the dense shell of a Pearl Mussel (*Unio margaritifera*), from the mountain-streams of Westmoreland, with the thin shell of *Anodonta* from Oxford waters so much richer in lime.

*Structure of the shell.* Ehrenbaum, Z. W. Z. xli. 1884; F. Müller, Z. A. viii. 1885; in *Anodonta*, F. Müller in Schneider's Zoologische Beiträge, Breslau, i. pt. 3, 1885; cf. Bronn, Klass. und Ordnungen des Thierreichs, iii. 1, p. 330: and Sorby, Presidential Address, Geological Society's Journal, xxxv. 1879; of *Cyclas cornea*, Leydig, Archiv f. Anat. und Physiol. 1855, and F. Müller, op. cit. *supra*.

*Hinge teeth.* Neumayr, SB. Akad. Wien. lxxxviii. Abth. i. 1883.

*Formation of shell in Oyster.* Osborn, Biological Studies from the Laboratory of Johns Hopkins University, ii. 1882; cf. on *Embryo Oyster*, Ryder in Bull. U. S. Fish Commission, ii. 1883. p. 383.

On 'Molecular Coalescence' and on the effect of Colloids upon the form of Inorganic Matter, Ord, Q. J. M. xii. 1872, and St. Thomas's Hospital Reports (N. S.), ii. 1871.

*Formation of Pearls.* Pagenstecher, Z. W. Z. ix. 1858, von Hessling, Die Perlmuscheln und ihre Perlen, Leipzig 1859, and in Z. W. Z. ix. 1858, p. 453.  
*Composition of shell in relation to lime in water, &c.* Voit, Z. W. Z. x. 1859-60.  
*Vegetable parasites in shell, &c.* Kölliker, Z. W. Z. x. 1859-60.

## 25. FRESH-WATER MUSSEL (*Anodonta cygnea*),

Removed from its shell and suspended so as to show the general external features of the animal.

THE animal is suspended by the anterior adductor muscle, and the two folds (right and left) of the mantle have been turned back and fastened over the dorsal area. The mantle-folds are free throughout their whole extent, but they are united indirectly at the posterior end behind the foot by the attachment of the branchiae. The mantle cavity is in this way divided into two chambers, an inferior large infra-branchial chamber, and a superior small supra-branchial chamber. In the living animal the ventral edges of the mantle-folds are applied more or less closely to one another, even when the foot is protruded, and water finds its entrance to the infra-branchial chamber through the inferior siphonal notch. The edges of this notch are covered with tentacles, and hence the portion of the mantle in question is readily recognised. It is posterior, and lies immediately below the attachment of the branchiae. The supra-branchial chamber opens above the attachment of the branchiae by the superior siphonal notch, which has smooth non-tentaculate edges. A white bristle is passed into it in this specimen. The two notches in many *Lamellibranchiata* are prolonged, the inferior into the inhalent, the superior into the exhalent, siphon. The two chambers, however, in the *Anodon* communicate one with the other, not only indirectly through the cavities of the branchiae, but directly also along the posterior part of the base of the visceral mass, where, as may be seen in this specimen, the innermost branchial lamella has a free edge. In some *Lamellibranchiata* with an aborted foot this gap does not exist, and consequently the two chambers do not communicate directly.

The free edges of the mantle folds are thickened, and correspond to the collar in the Snail. Two main lips, best developed posteriorly, run along the free edge, and they inclose two somewhat smaller ridges not always discernible. The outermost ridge is prolonged round the superior siphonal notch, and unites at some distance from it on the dorsal surface with its fellow to form the dorsal ridge or raphe.

The foot projects in the middle line. It is continuous with the visceral mass, which contains coils of the digestive canal, liver (=hepato-pancreas), and generative organs, and is much dilated. The foot proper is purely muscular, and may be distinguished by its yellow tint and comparative

thinness. At its anterior edge a black bristle has been passed into the mouth. A ridge or lip above the mouth, and another below it, are prolonged respectively into the right and left pairs of labial tentacles, which project like wings in this specimen. Behind these tentacles, at the sides of the visceral mass, and between it and the mantle-folds, are the branchiae or gills. There are two gills or ctenidia on each side. Each gill is composed of two lamellae, an outer and an inner. The inner lamella of the inner gill is attached most anteriorly to the side of the visceral mass above the outer tentacle. It is then free for a part of its course, but posteriorly unites with its fellow, as may be seen in this specimen. The junction of these two inner lamellae *inter se* separates the infra- from the supra-branchial chamber, and is the cause in part of the posterior indirect union of the mantle-folds (see also Preparation 26). The outer lamella of the outer gill is fused in its whole extent to the mantle, and it assists where the ctenidial axis becomes free posteriorly in dividing the supra- and infra-branchial chambers, and in causing the indirect union of the mantle-folds.

The internal surface of the mantle is covered with ciliated epithelium, and the plasma-cells (p. 115) of its connective tissue contain glycogen. In many forms its ventral edges coalesce or 'concesce' leaving an aperture for the foot; or the process may be carried even further when that organ is aborted, e. g. in *Aspergillum*, and then the only entrance to the mantle cavity is through the inhalent siphon. When an *Anodonta* is removed from its shell, there is seen (best in a fresh specimen) a reddish streak running from near the anterior to near the posterior adductor. This streak is the red-brown organ of Keber, the pericardial gland of Grobben. According to the latter, it consists of a series of caeca communicating with the pericardial cavity and lined by a continuation of its epithelium. The homologous structure in *Cephalopoda* forms an appendix to the branchial heart, is similarly formed, and a portion of its epithelium, that in the peripheral caeca, is excretory in structure.

The foot is in some *Lamelibranchiata* aborted, e. g. Oysters. In others it is very small, and its shape varies much within the limits of the class. The ventral edge has, according to Griesbach, in the *Anodonta* three pores of fair size, one placed anteriorly, two somewhat posteriorly. He states that water finds its way through them to the vascular lacunae, a fact disputed by other authorities. Similar pores exist in other *Lamelibranchiata* and *Mollusca* (?). Water has been supposed to find its way into the blood-system in one of three ways—through the nephridium into the pericardium, through special pori aquiferi, and through intercellular passages between the ectoderm cells or epidermis. But the great distension of the foot in *Anodonta*, when protruded from the shell for the purposes of locomotion, is due apparently to the action of a circular muscle surrounding the vein which conveys the blood from the foot on each side of the body to the median infra-cardiac sinus. By this means the return of the blood is prevented whilst the heart at the same time continues to drive blood into the foot. Certain

regions of the mantle appear to act as blood-reservoirs from which a store of blood may be drawn under these circumstances (Fleischmann). It may be added that in *Solen* (*Ceratisolen*) *legumen*, where some of the blood-corpuscles are tinged with haemoglobin, these corpuscles do not escape from the blood even when the animal is greatly irritated and consequently strongly contracted. Any direct passage of water from without into the blood, or escape of blood, must consequently be regarded as an extremely doubtful occurrence. In some specimens of *Anodonta* there exists a small pit on the posterior margin of the foot. This, according to Carrière, is a remnant of the byssus gland, which is so well developed in *Dreissena* among fresh-water Bivalves. The young *Anodonta* (= *Glochidium*) has a byssus filament, but the gland which secretes it disappears, and the true byssus gland appears later. The filament referred to is adhesive, and clings to anything which it touches.

The labial tentacles are vascular, richly supplied with nerves, and ciliated. Their opposed surfaces are covered with fine parallel ridges. The upper tentacles appear to rise in part from the mantle, the lower from the sides of the visceral mass, but the two tentacles of the same side undergo partial concrescence of their surfaces, and the furrow between them does not extend back between the mantle and visceral mass. In some instances they are of very large size. Embryology does not favour an homology with gills. Professor Ray Lankester however has suggested that they with the gills are homologues of the prae- and post-oral ciliated bands of the Echinoid and Ophiurid larva, *Pluteus*, or the *Tornaria* larva of *Balanoglossus*.

The gills require careful examination. In *Anodonta* they appear to be profoundly modified from their original structure. Each gill consists of two lamellae, an outer and an inner. The inner lamella of the outer gill and the outer lamella of the inner gill arise close together and along the line between them run the afferent and efferent blood-vessels. This line represents the original (ctenidial) axis of the gill. Posteriorly the axis is free for a short distance, but anteriorly it is part of the under side of the organ of Bojanus and the side of the body. The space between the two lamellae, i. e. outer and inner, of each gill, is the 'interlamellar' space, and examination shows that it is crossed by numerous 'interlamellar' junctions. If the surfaces of the lamellae be regarded attentively, they are seen to be perforated by many series of apertures. Hence the lamellae resemble a fenestrated membrane, but may be regarded as composed of a number of parallel vertical filaments united from place to place by 'interfilamentar' junctions. The latter is the view justified both by a comparison with certain other forms as well as by embryology. *Nucula* and *Yoldia* (*Arcacea*) have each ctenidial axis bearing two series, an outer and inner, of gill-filaments which are lamellate in shape. In *Mytilus* and other bivalves they are filamentous, and the filaments of the outer series are folded on themselves, the folded part being external, while the inner filaments are similarly folded, but the folded part is internal. The filaments are also united laterally in *Mytilus*, *Arca*, &c., by peculiar long cilia into a lamella, the component filaments of which are easily separated. Solid interlamellar junctions are sparingly developed. Further steps in complication are, the development of tubular interfilamentar junctions, e. g. in *Dreissena*, the union of the reflected portions of the filaments to neighbouring parts and *inter se*, and the great development of interlamellar junctions. The



individual filaments, originally tubular, become nearly solid at the same time by the development of rods of a condensed gelatinous tissue in their interior. The vascular channels then run chiefly in the junctions. These changes are carried to a great extent in *Anodonta*. The surfaces of the filaments are clothed with cilia. The ciliated cells are distinguishable into three sets: *frontal*, with medium-sized cilia; *lateral-frontal*, forming a single row of large cells with very long cilia; and *lateral* with much the shortest cilia. The vascular channels in the gills have been stated by Kollmann to possess an endothelium. This is certainly the case in many forms, e. g. *Arca*; but Bonnet has failed to prove the fact in *Anodonta*. The vascular channels have a very complex arrangement in *Anodonta*, and have been fully described with figures by the last named author. The tissue of the branchiae in the *Unionacea* (*Unio*, *Anodonta*, &c.), contains a very large amount of lime carbonate. Hence the brittleness of these structures.

From the account given above it is clear that the two gills so-called of each side in the Lamellibranch are really parts of a single gill, a highly complex and modified ctenidium.

The cilia covering the surfaces of the gills cause the currents of water to flow from the outer free surfaces into the interlamellar spaces and thence outwards through the superior siphonal notch. The cilia at the margins of the lamellae are said however to cause currents towards the mouth and thus subserve alimentation.

*Lamellibranchiata*, Bronn, *Klass. und Ordn. des Thierreichs*, iii. 1. 1862; *Do. with Anodonta as a type*, Ray Lankester, 'Mollusca,' *Encyclopaedia Britannica* (ed. ix), xvi. 1883; cf. Haren Noman, *Niederländ. Archiv für Zool.* i. Suppl. 1881-82.

*Anodonta*, Howes, *Atlas of Practical Elementary Anatomy*, London, 1885.

*Keber's organ*. Grobben, *Arb. Zool. Inst. Wien.* v. 1883, p. 40; cf. Griesbach, *A. N.* 43, 1877.

*Absorption of water*, &c. Schiemenz, *Mitth. Zool. Stat., Naples*, v. 1884 (with lit.); cf. Schüller, *A. M. A.* xxv. 1885. *Movements of foot in Lamellibranchiata*, Fleischmann, *Z. W. Z.* xlii. 1885; *for valve of vein from foot*, see p. 419, and Fig. 5, p. 420.

*Byssus gland*. Carrière, *Arb. Zool. Zoot. Inst., Wurzburg.* v. 1882. *Mode of attachment*. Cattie, *Tijdschr. Nederl. Dierk. Vereen*, vi. 1882-85.

*Gills*. Posner, *A. M. A.* xi. 1875; Peck, *Q. J. M.* xvii. 1877; Mitsukuri, *Q. J. M.* xxi. 1881; *circulation and endothelium of*, Kollmann, *Z. W. Z.* xxvi. 1876; *A. M. A.* xiii. 1877, and *Festschrift zur Feier des 300-jährigen Bestehens der Universität zu Wurzburg*, 1882, p. 42 (with lit.); Bonnet, *M. J.* iii. 1877. *Rods of gills*. Bonnet, *op. cit.* p. 321; cf. Kollmann, *SB. Bayer. Akad.* 1876, p. 163. *Development of gills*, De Lacaze-Duthiers, *A. Sc. N.* (4) v. 1856.

*Ciliary-currents*, Sharpey, *Encyclopaedia of Anat. and Physiol.* i. 1835-36, p. 621.

26. FRESH-WATER MUSSEL (*Anodonta cygnea*),Dissected so as to show the viscera *in situ*.

THE animal is suspended by the apex of its foot and fastened on its left side. The mouth is superior, the anus inferior; the heart to the left hand, and the foot to the right. The right mantle lobe, gills, and body wall have been removed to show the stomach, coils of intestine, liver, and reproductive glands *in situ*. The mouth lies between the anterior adductor muscle and the base of the foot. It is fringed by the upper and lower lips, which are prolonged into the corresponding labial tentacles, not visible here. The oesophagus is wide, and leads into the stomach, which has a small cavity on its dorsal wall, and in front of the pylorus a depression, the entrance to a small diverticulum, or caecum, generally, but incorrectly, said to lodge the 'crystalline style.' This organ lies in the stomach, and reaches its full development at the approach of autumn. The liver, or hepato-pancreas, surrounds this portion of the alimentary canal. It looks in this preparation white, owing to the removal of its natural dark colouring matter by the action of the alcohol. Its ducts open into the stomach. A black bristle is passed along the first or descending segment of the intestine which passes straight towards the foot. The first coil curves round towards the dorsal or haemal aspect. The second coil reverses this direction, and curves concentrically and ventrally by the side of the first and beyond it anteriorly. The third coil passes over the first segment of the intestine on its right side, and ascends towards the dorsal aspect between the first segment and the first coil. It then runs along the dorsal surface, perforating the ventricle of the heart, and finally opens by an anus behind the posterior adductor muscle into the supra-branchial chamber. A ridge or 'typhlosole' runs along the posterior wall of the first or descending segment of the intestine. Another commences by a swollen or club-shaped end on the ventral or neural wall of the ascending segment, at the spot where it bends abruptly towards the heart, and is continued as far as the anus, as may be seen here. The ingestion of food depends solely on the currents of water set up by the ciliated epithelium lining the alimentary canal from mouth to anus. The generative gland, in this preparation yellow, is mixed up with the liver, surrounds the coils of the intestine with the exception of a small portion of the second coil, and extends between the ascending and descending segments, and even behind the latter. It must be borne in mind that both liver and genital gland are paired organs. The sexes are separate in *Anodonta*, and, like other *Lamellibranchiata*, it has no accessory organs of generation such as occur in the Snail.

The cut edges of the ventricle of the heart, which surround the

intestine, may be seen just behind the spot where the ascending segment of the intestine bends backwards. The lower wall of the ventricle is particularly evident, and there is a well-marked space (ventricular cavity) between it and the intestine.

A portion of the pericardial space is visible as a triangular cavity ventrally to, .i. e. to the right in this preparation of, the ventricle. Still more to the right is the organ of Bojanus or nephridium. The two parts of its cavity may be seen in section. Next to the pericardium is the non-glandular thin-walled duct, the walls of which are more closely apposed than in nature, leaving a mere chink. The glandular portion of the organ with its lamellae extends far forwards; it surrounds the tendon of the posterior retractor pedis muscle, which is seen just in front of the posterior adductor muscle, and reaches to the anterior edge of this muscle and even a little to its ventral surface. Behind the posterior adductor the attachment of the left gill to the mantle is displayed. It corresponds to the junction of the tentaculate and non-tentaculate portions of the mantle which constitute the inferior or inhalent, and the superior or exhalent, siphonal notches respectively.

The muscular portion of the foot is well seen in partial section. In locomotion it swells up and protrudes from the shell into the soft mud of the streams and ponds inhabited by these creatures. The rate of motion is slow, and the animals, as they move along, leave a deep furrow behind them.

The two adductor muscles, as seen in this preparation, are equal in size; hence the name *Isomya* applied to the great group among *Lamellibranchiata* to which *Anodonta* belongs. In others, e.g. the freshwater *Dreissena*, the anterior adductor is small compared to the posterior, hence *Heteromya*; and in a third order, the *Monomya*, to which the Oyster and Scallop belong, the anterior adductor is absent altogether, though it is present in the Oyster when the shell and muscles first develop. The anterior adductor is formed in the mantle region above, and in front of the mouth. The posterior adductor may perhaps correspond to the columellar muscles of the Snail.

The crystalline style occurs among *Monomya* only in *Anomia*, but is found in most other *Lamellibranchiata*, either in a special caecum or in the intestinal tract, as in the *Unionacea*. It is transparent in most instances. Hazay has recently made some researches on its formation and function in the *Unionacea*. He finds that from spring to autumn the stomach is full of a gelatinous mass in which the crystalline style is slowly differentiated, a process complete by October. The remaining jelly, apparently superfluous food-material, passes into the first section of the intestine, and by November the stomach is empty of it. In the intestine the jelly becomes a thick, compact hyaline body, which is gradually consumed during the winter months. The style appears to act as a stopper, closing the entrance of the pylorus, but it is itself gradually consumed; any remains serve

as the nucleus of a new style. The chemical reactions of both bodies prove their albuminoid nature.

The liver in *Lamellibranchiata* secretes a diastatic as well as a peptic or tryptic ferment; of the two latter, sometimes apparently only the former, as e.g. in the Oyster and Edible Mussel, or both, as in the Scallop (*Pecten Jacobaeus*) in which the extract is active in alkaline, neutral and acid solutions alike. The liver contains no calcareous cells, only granular and ferment cells (see pp. 116-117).

The heart consists of a median, thick-walled ventricle, and a thin-walled auricle on either side. The auriculo-ventricular apertures are valved. An aorta arises from both ends of the ventricle; the anterior passes above, the posterior below the intestine. The blood spaces are for the most part lacunar, but vessels are found in the walls of the intestine, labial tentacles, and gills (?). There is a median venous sinus lying between the two nephridia. From it blood passes to the nephridia, thence to the gills, and so to the auricles. The blood is colourless, and has colourless corpuscles. The pericardium surrounds the heart. It communicates with the glandular portion of the nephridium, two apertures at the anterior end leading one into each gland. It is thus directly connected with the exterior.

The renal organs or nephridia (=organs of Bojanus) are paired. They lie ventrally to the pericardium, and are divisible into a duct or non-glandular, and a secreting or glandular portion. The former opens by a pore at the side of the body, and is covered by the inner lamella of the inner gill, where it is attached to the side of the visceral mass. It lies under the pericardium, and opens posteriorly into the glandular portion which underlies it. There is a communication anteriorly between the ducts of opposite sides. Other communications have been stated to exist between the ducts and the organ of Keber. The glandular portion contains numerous lamellae, and is greenish in life. It communicates anteriorly with the pericardium (*supra*). The outer surface of the ducts has a cylindrical epithelium; the inner has an epithelium, of several layers, the outermost cells rounded and ciliated. A similar ciliated epithelium exists in the glandular portion of the organ. The superficial cells of the latter contain yellow-brown urinary concretions. Guanin not uric acid is stated to be found in them. The relations of the organs are illustrated in Pl. vii. fig. 4. Kollmann has recently described ciliated funnels (nephro-stomata?) on the lamellae of the glandular portion of the organ. Their number appears to be great, as many as 200 in an *Anodonta* specially examined from this point of view. The funnels, however, appear to be blind, and not to lead into any system of canals or into the blood-lacunae of the lamellae into which their blind ends project.

The generative organ of each side opens by a pore in front of the opening of the nephridium. The organs are simple racemose glands, and alike in both sexes. They can only be distinguished by the characters of their products. The testis, however, is whitish in colour; the ovary reddish. In the few hermaphrodite forms the gland may be divided into a distinct male and female part, e.g. *Cyclas*; or the two elements, male and female, may lie side by side in the same caeca as in *Ostrea edulis*. In the case of the Oyster the two generative products ripen at different times, and hence self-impregnation does not occur, a rule which obtains in most hermaphrodite animals. *Anodonta* appears to be occasionally hermaphrodite.

In the *Unionacea* an external difference of shape between the male and female individual is noticeable, and this difference may be considerable.

*Structure and strength of adductor muscles.* Coutance, De l'énergie et de la structure musculaire chez les Mollusques Acéphales, Paris, 1878. Von Ihering, Z. W. Z. xxx. Suppl. 1878. Plateau, A. Z. Expt. (2) ii. 1884. *On attachment of muscles in Anodonta.* F. Muller, Schneider's Zoologische Beiträge, i. pt. 3, 1885. *Action of nerves on adductors.* Pawlow, Plüger's Archiv, xxvii. 1885.

*Crystalline style.* Hazay, Malacozool. Blätter, iii. 1881, p. 196. Krukenberg, Vergleich. Physiol. Vorträge, ii. p. 63, 1882, Heidelberg.

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*Differences between male and female shells.* Bronn, Klass. &c., iii. 1. p. 406. Hazay, Malacozool. Blätter, iii. 1881, p. 170.

## 27. FRESH-WATER MUSSEL (*Anodonta cygnea*),

Dissected to show the nervous system and the route along which the ova pass from the generative gland into the interlamellar cavity of the external gills, where, as in the pouch of a marsupial mammal, they are lodged, and go through certain stages of their development.

PART of the foot has been removed on the animal's left side to show the pedal ganglia *in situ*; the union of the inner lamellae of the inner gills behind the foot has been divided, and the glandular portion of the nephridium opened to show the nerve cord uniting the left cerebro-pleural to the left visceral ganglion in its entire length.

The left cerebro-pleural ganglion is seen lying upon the tendon of the retractor pedis anterior muscle, and just anteriorly to that of the protractor pedis muscle. It is connected to the ganglion of the same name on the right side by a commissure passing above the mouth, under which a slip of blue paper has been placed. It is united by a connective which passes obliquely to the left hand with the pedal ganglion of its own side. The right and left pedal ganglia are united closely *inter se*. They lie within the periphery of the 'visceral mass,' a division of the body which in these Molluscs is less sharply marked off from the 'foot' proper than in many other members of the phylum. Four or five delicate nerves may be seen passing off from the ganglion into the muscular portion of the foot. The auditory vesicle may be found appended close to the line limiting the

viscera from their muscular envelope. Its nerve in *Anodonta* is derived from the cerebro-pedal connective (*infra*). It is not seen here.

A second connective passes backwards (downwards here) to the visceral ganglion, which lies upon the inferior surface of the posterior adductor muscle. It passes, first, between the fibres of the anterior retractor and of the protractor pedis muscles; and secondly, after skirting the inner edge of the orifice of the reproductive gland, through the glandular portion of the nephridium externally to the common tendon of the posterior retractor pedis muscles. The corresponding connective of the other ganglion, i. e. that of the right side, comes into view in front of as well as behind this last mentioned tendon. A slip of blue paper has been passed under both cords just before they enter their respective halves of the ganglion. The visceral ganglion is really paired, but its two parts are closely united in the median line. It gives off posteriorly to the right and left a stout pallial nerve which skirts the mantle. Similar nerves are given off by the cerebro-pleural ganglia, but are not seen in this preparation. Both sets of nerves unite in a circumpallial plexus with ganglia here and there. Other nerves (not visible) pass to the anus which lies in the median line behind the posterior adductor muscle, and to this muscle itself. Anteriorly the ganglion gives off two stout nerves right and left to the gills. These nerves are beset in reality with ganglion cells, and are in relation with a modified epithelium. The whole represents the osphradium or olfactory apparatus of Spengel. There are no ganglia in a Lamelli-branch corresponding to the buccal ganglia of the Snail; but ganglia may be developed along the course of the pallial nerves, and on the siphonal nerves in those genera where siphons are well developed.

The lamellae of the glandular portion of the nephridium, the interlamellar space of the outer left gill, its interlamellar and interfilamentar junctions, and a large bloodvessel running between the outer and inner gills at their base, are all well seen (see *ante*, pp. 130-31).

The ova must be extruded from the generative organ in part by the contraction of the foot compressing the visceral mass. They escape from the generative orifice where the inner lamella of the inner gill is attached anteriorly to the visceral mass, and thence pass on probably as follows. The free portion of the inner gill lamella is converted into a canal by the apposition of the visceral mass to its edge. Behind the foot the ova pass between the united inner lamellae of the inner gills of opposite sides below and the organ of Bojanus above, into the cloaca. This space is small in the *Unionacea* relatively to their ovaries: it must fill rapidly with ova under pressure, and the shell being closed, there is no other path for them to take but the one which leads into the interlamellar space of the outer gill. This space is open to the cloaca behind the limits marked by the osphradia. Spermatozoa are sometimes found free in

the interlamellar spaces of the gills, and as the animals are usually dioecious, it is probable that they are drawn in by the currents of water inhaled by the female, and that the ova are impregnated after their extrusion. The ova may be found in great abundance during the autumn and winter months. They are nourished by a substance formed by the epithelium of the spongy interlamellar junctions, and develop into the *Glochidium*. This *Glochidium* is eventually set free from the parent. It possesses a shell triangular in outline with an incurved tooth in the centre of the free edge of the valve. The margin of each lobe of the embryonal mantle has four sense organs, and a long embryonal byssus filament protrudes from between the valves, by means of which the young animal attaches itself when it quits the egg-membrane. It eventually fixes itself to the fins, tail, &c., of fish, e. g. Stickleback, by means of its valve-teeth. The epidermic cells of its host grow round and enclose it, and it then undergoes a metamorphosis. The permanent mantle is formed, and the rudimentary byssus gland, homologous with the byssus gland, e. g. of *Pinna*, appears. The embryonal byssus gland of the *Glochidium* is not homologous with the permanent gland as usually supposed. The nerve ganglia and the otocysts are derived from the ectoderm. The single adductor of the *Glochidium* disappears; and the two adductors of the adult are new formations, as is also the shell of the adult.

According to Spengel, the supra-oesophageal ganglia of the Lamellibranch represent the cerebral *plus* the pleural ganglia, i. e. portions of the parieto-splanchnic ganglia so-called in the Snail, and independent ganglia in *Limnaeus* and many other *Gastropoda*. It is a noteworthy point that in *Lamellibranchiata* there is no connective between the pedal ganglia and the ganglia here called visceral. Supposing that the latter ganglia were the homologues of the pleural and visceral ganglia of e. g. *Limnaeus*, as ordinarily maintained, the absence of such a connective would be an abnormality. It would not be, on the supposition that the pleural ganglia are fused to the cerebral. The homology of the visceral ganglia with the ganglia of the same name in *Gastropoda*, is also probable from their connection with an osphradial apparatus.

As to organs of special sense. Certain of the epidermic cells are modified into tactile cells, continuous basally with nerve filaments and furnished at their outer free ends with a bundle of fine projecting tactile hairs or setae. These tactile cells are most plentiful on the papillae of the mantle edge, especially in its siphonal region. They are more sparingly present round the edge of the cloaca, on the edge of the fore part of the mantle, on the labial tentacles, inner surface of mantle, and on the foot.

Eyes are not present in *Anodonta* at any period of its existence, whether larval or adult. Many larval *Lamellibranchiata* possess larval eyes at the base of the velum close to the oesophagus. For the eyes of adult *Lamellibranchiata*, see general account of the Class.

An otocyst or auditory organ lies near to each pedal ganglion. It is sur-

rounded by plasma-cells (p. 115), and consists of a fibrillated connective tissue coat, within which is a nervous layer (?) formed by the auditory nerve, and most internally a layer of ciliated epithelium. Whether special auditory hairs are present, as in *Cyclas* and some *Gastropoda*, is uncertain. The cavity of the vesicle contains a fluid in which floats a spherical calcareous otolith, single as in all *Lamellibranchiata*. The nerve is derived from the cerebro-pedal connective, according to Simroth, not from the pedal ganglion, as ordinarily stated. See Z. W. Z. xxvi. p. 270, Pl. xvii. fig. 56; and for otocyst, Pl. xviii. figs. 62 and 68. It is not certain if the auditory nerve is similarly derived in other Bivalves. It is in other Mollusca. The only specimens of *Anodonta* at my command were not sufficiently fresh to enable me to decide whether or no the nerve-supply is invariably derived as Simroth describes. It is possible that in some cases the nerve passes through the pedal ganglion, but without being derived from it.

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*Otolithic vesicle.* Leydig, Lehrbuch der Histologie, 1857, p. 278, with references, p. 283. Simroth, Z. W. Z. xxvi. 1876.

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*Passage of ova to gills.* Von Baer, Meckel's Archiv. (Archiv. f. Anat. und Physiol.), 1830. *Possible passage of ova from one Mussel to another.* Von Hessling, Z. W. Z. x. 1859-60, p. 358. *The different parts that act as Marsupia.* Bronn, Klass. &c. iii. 1, p. 442.

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## 28. COMMON COCKROACH (*Periplaneta orientalis*), FEMALE,

Dissected to show its digestive, renal, nervous, and reproductive systems,

AMONG external features characteristic of the class Insecta, the head with the antennae, the three pairs of jointed thoracic limbs, and the segmented abdomen may be noted. The short tegmen or wing-cover of the female of this species is visible above the second limb on the right side, and posteriorly, on the same side also, at the extremity of the abdomen, one of the two short jointed cerci anales found in many *Orthoptera*, &c.

The dorsal body walls or terga, and the fat body which abounds between the viscera, especially in the abdomen of these insects, even in their



adult state, have been removed, and the digestive tract fastened out upon the left side of the body.

The digestive tract is divisible into three regions, which correspond to the stomodaeum, archenteron, and proctodaeum of the embryo. The first of these includes oesophagus, crop and gizzard, the second, the chylic stomach and caeca, and the third, the intestine and rectum. The narrow oesophagus expands directly into the crop, which occupies about three-fourths of the entire length of the body, and is distended with food. The digestive tract as a whole, however, is little more than twice as long as the body, a comparative shortness compensated partly by the character of the food, and partly by the large quantities devoured. A muscular subconical gizzard follows the crop. This organ is not developed in the larvae of Insecta with a perfect metamorphosis, e. g. *Coleoptera*, in those species which possess it when adult, but is developed in larval *Orthoptera* as well as *Odonata*. The posterior end of the gizzard is elongated and projects into the chylic stomach. Eight 'pyloric' caeca arranged in a whorl mark the commencement of this region, and a very much larger number of long and slender Malpighian or renal tubes its termination. Pyloric caeca are found in most *Orthoptera*, and in the *Plecoptera*. Their walls are glandular, and the size of the caeca varies with their state of distension. The intestine consists of a short, narrow 'ileum,' and a long, somewhat dilated colon. The ileum is not clearly visible in this preparation. The colon is ridged and beaded owing to the contraction of its muscular coats. It ends in a rectum, which shows six longitudinal ridges alternating with furrows.

The lobed labial salivary glands are to be seen on either side of the anterior end of the crop: and on the right side in this preparation the right salivary receptacle, a pellucid bladder reaching a little further back than the gland.

An azygos *nervus recurrens*, derived from the 'ganglion impar' or 'frontale' of the stomatogastric system, lies on the dorsal wall of the crop, and ends in a triangular ganglion placed a little way in front of the middle point of its length. From this ganglion a nerve may be traced passing down the sides of the crop to the gizzard. The paired ganglia of the system are not to be seen. The six terminal ganglia of the ventral chain are visible in the abdomen. The two first are more closely apposed to each other than are any of the succeeding four. The last ganglion is more or less cordiform, larger than those which precede it, and gives off nerves to the lower portion of the digestive and generative tubes.

Each ovary consists of eight ovarian tubes or ovarioles inserted in pairs, on the inner edge of the oviduct, one set of tubes along its ventral, the other on its dorsal margin. The tubes are beaded, owing to the swellings caused by the ova. These ova increase in size the nearer they are to the oviduct. The tips of the ovarioles are in the natural state united

by short filaments to a common ligament. This ligament is probably attached, as in other Insecta, near the heart. The two oviducts open beneath the last ganglion of the ventral chain into a short vagina. The spermatheca consists of a short peduncle terminated by two slightly curled vesicles. It opens into the vagina behind the last nerve ganglion. And opening in turn behind it are the right and left colleterial glands, often, but wrongly, termed sebaceous. They secrete the material which forms the cocoon.

The Cockroach, according to Cornelius, moults seven times before it becomes adult. The first moult occurs immediately after hatching; the second a month later; and the remaining moults at intervals of a year. The adult stage is reached in the fifth year. The young animal differs from the adult principally by inferiority of size, by the smaller number of facets in the cornea of the eye, by the absence of wings, imperfection of the genitalia, and in this family by lightness of colour, a feature, however, in which great differences exist between adult individuals of this species. The absence of a quiescent stage and of a period of abstention from food, such as exist in Insecta with a perfect metamorphosis, is probably the reason why the fat body persists, instead of being utilised as a storehouse of force during the internal changes undergone by the organism.

A Gregarine *Clepsidrina blattarum* is often found in the body cavity of the Cockroach, and some remarkable Flagellate Protozoa in its intestine.

The body is divisible, as in all adult Insecta, into a head, thorax, and abdomen.

The head is broad transversely, and compressed antero-posteriorly. It is carried vertically, not horizontally as in many forms. Its dorsal surface or *Epicranium* is convex, and is marked by a Y-shaped *epicranial suture*, as in the Earwig. This suture is in some specimens indistinct. The branches of the Y end in a translucent spot of unknown function placed superiorly to the inner side of the articulation of the antennae. The front of the head (= clypeus) is flat and broad, and a labrum is moveably articulated to it, closing in the mouth anteriorly. The antennae are long, filiform and many jointed. The joints are beset with hair (i.e. are setose), and the basal joint is attached to a soft membrane, which closes the socket. For the minute anatomy of antennae, see p. 145, *infra*. Behind the antennae are the reniform compound eyes. There are no ocelli.

The mouth is constructed for biting, and consists of three pairs of jaws: the mandibles, the maxillae, and the labium. Each mandible is of one piece, triangular, attached by two condyles to the head. Its inner edge has at the base a grinding surface or mola, and in front of the mola and at the tip strong teeth. Neither teeth nor mola are fashioned alike in the two mandibles. They appear to interlock more or less perfectly. Each maxilla is composed of (1) a basal part, the *cardo*, placed horizontally and articulating with the head; (2) a *stipes*, which is placed vertically, and bears (3) a five-jointed *palpus* on its outer edge articulated to a basal piece representing the palpiger of some Insecta; (4) a hood-shaped *galea* in

front, which is articulated by a distinct joint to the stipes; and (5) a *lacinia*. This lacinia is attached to the stipes by an imperfect joint; it ends with two stout conical teeth, at the base of which there rises on the internal edge a finger-shaped process, terminated by three or four recurved blunt teeth. Its inner edge is beset with stout hairs. The labium closes in the mouth posteriorly. It consists (1) of a large basal *sub-mentum*, to the fore-edge of which is moveably articulated (2) a *mentum*; (3) of two three-jointed *palpi* attached each to a basal prominence, representing a palpiger borne on the external angle of the mentum; and (4) a *ligula*. The ligula is divided almost completely by a median cleft, at the base of which is a small triangular piece. Each half of the ligula bears two processes articulated to it: an outer, the *paraglossa* or lamina externa of Gerstäcker (= galea?), and an inner, the smaller of the two, the lamina interna of the same author (= lacinia?). A labium of this character is to be regarded as primitive. It is found in many *Orthoptera*, in *Termes*, *Perla*, *Aeschna*, and the incomplete stages of *Ephemeroidea*, and shows clearly the origin of the labium from a pair of limbs fused medianly. The antennae are processes of the pro-cephalic lobes: while the mandibles, maxillae, and labium belong to three fused segments distinct in the embryo. The head of the insect is consequently often regarded as formed of four segments, one prae-oral and three post-oral.

The labrum (*supra*) is formed in some Insecta by the fusion of two processes. They are, however, hardly to be regarded as limb-rudiments. The antennae are not modified limbs like the remaining appendages of the head, and are compared by Balfour with the paired processes of the prostomium in the Chaetopod *Polychaeta*. The embryonic rudiments of the labium are extremely large, and in some Insecta are turned backwards parallel to the thoracic limbs.

The epipharynx, which lies on the internal surface of the labrum, is not traceable in *Periplaneta* as a distinct process. The hypopharynx (= lingua), on the contrary, is very large. It lies on the inner or oral surface of the labium, and the salivary duct opens towards the base of its posterior surface.

The thorax is composed of three limb-bearing segments—pro-, meso-, and meta-thorax. A distinct neck<sup>1</sup> intervenes between the thorax and the head. The pro-thorax has a large tergal (dorsal) plate, the pro-notum, which overlaps the head in front and the meso-thorax behind. Its sternal element is small, as are the two lateral elements, epi-merum, and episternum, which lie in front of the articulation of the limb. These parts are larger in the two segments behind. The tergal elements (meso- and meta-notum) of the meso- and meta-thorax are sub-equal in the Cockroach. In most *Orthoptera*, some *Neuroptera*, the meta- is larger than the meso-thorax, a condition the reverse of what obtains in most Insecta. The limbs increase in length progressively from before backwards. Each limb is made up of ten joints—a large coxa articulating with the thoracic ring, a small trochanter followed by a femur, a tibia, and a tarsus of six joints. The last tarsal joint is minute, and furnished with *two* claws, as is usual in Insecta that possess claws. The meso- and meta-notum carry wings. Those of the first pair in the male are

<sup>1</sup> In the neck there are certain chitinous pieces, or *cervical sclerites*, one dorsal and median, with a longitudinal depression, two ventral and transverse, and two lateral. The first and second elements are inconspicuous, the third large. They are placed obliquely. Their significance is doubtful. See Huxley, *Anatomy of Invertebrated Animals*, p. 403.

stiff, semi-opaque, and coriaceous in texture. They act as wing-covers or *tegmina*, and extend so far as to cover the fifth abdominal somite. Those of the second pair are membranous and large: each wing has an anterior triangular area of stiff texture and a thin posterior area. In repose, the base of the posterior portion closes like a fan, and then the remainder of the wing is folded once lengthwise, the edge of the fold being internal, the anterior firmer area of the wing lying uppermost and protecting the thinner posterior area. In some Cockroaches the tip of the wing is folded transversely. The base of attachment of both pairs of wings is broad. In the female there is a pair of short *tegmina*, while the hind pair of wings is represented only by two small triangular areas of the meta-notum marked by a few ridges. Certain Cockroaches, e.g. *Polyzosteria*, are wingless in both sexes.

The abdomen is flattened dorso-ventrally. Its outline is somewhat different in the two sexes. It is made up of a number of distinct segments or *somites*, composed each of a dorsal *tergum* and a ventral *sternum* connected at their margins by a soft *pleural* membrane, hidden by the projecting free edges of tergum and sternum alike. The portions of the terga and sterna exposed to light and air are hard and dark, but the membranes which connect successive terga and sterna are colourless and pliable. The first seven terga in both sexes are well developed, the 8<sup>th</sup> and 9<sup>th</sup> very narrow, and generally hidden by the 7<sup>th</sup>; the 10<sup>th</sup> is triangular and projecting. The 1<sup>st</sup> sternum is rudimentary, and represented by a narrow band at the base of the 2<sup>nd</sup> sternum. This and the succeeding sterna to the 7<sup>th</sup> inclusive are well developed in both sexes. In the male the 8<sup>th</sup> and 9<sup>th</sup> sterna are external, and the last named has articulated to its free margin a pair of unjointed setose styles, while the 10<sup>th</sup> sternum is internal, and has developed in connection with it variously shaped copulatory processes, which surround the aperture of the vas deferens. In the female the 7<sup>th</sup> sternum is very large, and its posterior extremity is cleft medianly in the adult (*imago*). The two halves are boat-shaped, and are connected by a distensible soft skin. They retain the egg-capsule, which the female carries about for a long time. The 8<sup>th</sup> and 9<sup>th</sup> sterna are internal, and bent at an angle *inter se*. The 8<sup>th</sup> has the vaginal aperture. There are three pairs of processes in connection with these sterna, homologous with the parts of the oripositor in e.g. a Cricket, or of the sting of a Bee. The first pair, according to Huxley, are developed from the 8<sup>th</sup>, the second and third from the 9<sup>th</sup> sternum. The 10<sup>th</sup> sternum in the female appears to be obsolete. The anus opens terminally in both sexes, and lies between two triangular *podical* plates, probably representing an 11<sup>th</sup> somite, as in the Dragonfly. At the outer angles of these plates arise two many-jointed setose appendages, the cerci anales, or cercopoda, supposed by Packard to represent a pair of rudimentary abdominal legs.

The nervous system consists of a supra-oesophageal ganglion supplying the antennae, translucent white spots, eyes and labrum, and connected by very short commissures to an infra-oesophageal ganglion supplying the mandibles, maxillae, and labium. The ventral chain consists of three thoracic and six abdominal ganglia, united by double commissures. The oesophageal commissures have under the neurilemma a continuous layer of ganglion cells, and from them spring the two roots, one on each side, of the *ganglion frontale*. The ventral commissures also contain ganglion cells<sup>1</sup>. The stomatogastric system consists (1) of an azygos ganglion

<sup>1</sup> According to Nussbaum a ridge of cells is developed from the hypoblast in the embryo *Peri-*

frontale, triangular in shape, lying in front of the supra-oesophageal ganglion, and giving off posteriorly a nervus recurrens, which courses along the dorsal wall of the oesophagus and crop ; (2) of a couple of paired ganglia, lying on either side of the nervus recurrens anteriorly, and connected to the under side of the supra-oesophageal ganglion and to the nervus recurrens ; (3) of a triangular ganglion terminating the nervus recurrens, from which two nerves, one on either side, run obliquely down the walls of the crop, and end in the muscular walls of the gizzard. Each nerve, near its termination, has a small ganglionic enlargement. There is also a sympathetic system in connection with the ventral chain. A fine nerve springs from either the right or left commissure, connecting successive ventral ganglia, and about midway between the ganglia. It runs dorsally between the commissures, and just above the ganglion behind its place of origin it divides. Each branch swells into a long spindle-shaped ganglion, and then joins the lateral nerve of the same side coming from the ventral ganglion.

With the exception of the chylific stomach, the digestive tract is lined by a chitinous cuticula, which is for the most part beset with setae. The chitinous coat is continued into the salivary ducts and receptacles. In the ducts it is striated, as in the tracheae (*infra*). The finest branches of the ducts in the acini of the gland are smooth-walled, and their terminal dilatations are lined by a coat which is not chitinous. The walls of the digestive tract consist of an external membrane underlain by an outer layer of circular, and an inner layer of longitudinal<sup>1</sup> striated muscle-fibres. Then follows a layer of connective tissue cells, and a layer of columnar cells, which secrete the internal cuticula where it is present. The chylific stomach is lined by columnar cells, with a striated border and rounded glandular cells lying in depressions. The gizzard has on its internal surface six longitudinal projections or teeth, and behind each tooth two cushions, the first with an uneven, the second with an even surface. In the interval between two teeth are three parallel folds, and between each of these and the teeth a smaller fold. The posterior part, which projects into the chylific stomach, contains six principal folds in a line with the cushions, and between each of them a small accessory fold. The circular muscle layer is strongly developed, and according to Wilde, longitudinal fibres run from the teeth to the cushions, and on the outer surface of the posterior part, whilst radial fibres are found only in the anterior and posterior parts. The same authority states that in some *Orthoptera* the internal cuticula is cast off at each moult. According to Krukenberg (*Untersuchungen Physiol. Inst. Heidelberg*, ii. 1882, p. 26), the salivary glands secrete a purely diastatic ferment, the chylific stomach both diastatic, peptic and tryptic ferments. The ridges in the rectum consist of elongated hypodermis cells, underlain by a mass of connective tissue cells, richly supplied with tracheae. They are structures highly developed in the larvae of Dragon-flies. These animals take in and expel water from the rectum, which thus becomes an important respiratory organ.

The Malpighian vessels consist of an outer homogeneous layer, a single layer

*planeta*, immediately beneath the ventral nerve-chain. These cells eventually ensheath the nervous structures. Nussbaum suggests that the ridge represents the chorda suprascapularis in *Lepidoptera* ; cf. *infra*, p. 160.

<sup>1</sup> There is apparently a contradiction in Basch's paper (cited below) as to the position, &c. of these 1 yers. Cp. pp. 241, 249, 252 of his paper.

of gland cells with large ramified nuclei, and internally a porous chitinous (?) membrane. The secretion contains (1) yellow-brown globules, which if numerous make the vessels opaque; (2) clear white globules; (3) uric acid crystals. The tubes open in *Periplaneta* into the lower portion of the chylific stomach, but in most Insecta into the intestine. Rathke, however, states that in *Blatta Germanica* they arise as outgrowths from the intestine.

The corpus adiposum, or fat body, is a whitish glistening tissue, arranged more or less in masses, and consists of cells containing oily drops, albuminous bodies, and in some cases uric acid. This tissue originates by proliferation from a layer of cells within the hypodermis, if the observations of Wielowiczski on *Corethra* are to be trusted. Sub-hypodermic cells have been described also by Viallanes in the larval *Eristalis* and *Musca*.

If the abdominal terga are removed as a connected piece, the heart and surrounding tissues may be found on its inner surface. The heart consists of a tube, divisible into an anterior aortic membranous portion, which runs forward into the thorax, and a posterior muscular portion ending blindly behind, and divided into a series of chambers by lateral apertures. Its muscles are arranged circularly or spirally, and at the apertures in a figure of  $\infty$ . The apertures are valved. The chambers contract successively from behind forward, and according to Cornelius, there were eighty such contractions in a minute in a *Blatta* which had just undergone ecdysis. The heart is suspended to the back of the abdomen by muscular fibres. Its walls are connected to a network of elastic fibres and interposed pericardial cells, which resemble the cells of the fat body, and the whole is limited on the surface turned to the viscera by a tissue partly fibrous and partly composed of the paired alary muscles. These muscles are striated, and arranged segmentally in fan-shaped bundles. The handle of each fan is attached laterally to one of the terga; its expanded portion is spread out below the heart, and the muscle-fibres end in tendons reticularly arranged. The whole structure, as pointed out by Graber, forms a pericardial sinus, which expands and contracts rhythmically like the heart. Numerous tracheae ramify in it and upon the heart. A very similar structure, with alate muscles, covers over the ventral nerve cord, and forms a pulsating sinus, but the contractions run from the anterior to the posterior extremity.

There are nine stigmata, or respiratory apertures, two thoracic, and seven abdominal. According to Bela Deszo, the stigmata and apertures into the heart correspond numerically in *Insecta*, *Myriapoda*, and *Arachnida*. This statement can, however, only be true as far as concerns the abdominal stigmata. The two thoracic stigmata are situated, one in the meso-, the other in the meta-thorax, in front of the articulation of the coxa. The abdominal stigmata are placed immediately under the lateral expansions of the terga, upon conical papillae. With the exception of the first, these papillae are concealed by lateral prolongations of the sterna. The last of the series is the largest. The entrance into the trachea, which rises from each stigma, is protected (1) by hairs which cross the aperture, (2) by a special apparatus for closing the tube, which in the *Orthoptera* is continuous with the lips of the stigmatic aperture. These lips are prolonged inwards as two valves. A process arises on the outer, i.e. visceral surface of each of these valves. A muscle passes from one to the other process round one of the margins, and when it contracts, squeezes the valves together, and thus narrows the aperture. The details

of the structure appear to differ somewhat in the thoracic and abdominal stigmata. In most Insecta the apparatus for closing the trachea is separate from the stigmatic lips. It is apparently absent in the *Rhynchota* and abdominal stigmata of *Diptera*.

The tracheal wall consists (1) of a layer of polygonal cells continuous with the hypodermis of the body walls; (2) of an external supporting membrane; and (3) of an internal chitinous coat or intima secreted by the cells. This chitinous coat, except at the ultimate terminations of the tracheae, and in certain tracheal dilations, is marked by fine transverse lines, which, as usually explained, are due to a spiral thickening of the coat with intervening thin membranous portions. But Macloskie has adduced reasons for believing that the spiral thickenings are really spiral crenulations, i.e. tubular or channel-like folds open to the trachea by a slit or fissure. He points out that such an explanation is in harmony with the structure of the pseudo-tracheae in the proboscis of *Musca*, and would also account for the lengthening and shortening of the tracheae themselves during the respiratory expansions and contractions of the abdomen.

The testes undergo atrophy in the adult male. In the wingless, i.e. immature, male they are to be found as numerous pyriform vesicles placed dorsally, as is usually the case with the genitalia of Insecta. They are attached by short pedicles to a common duct. The ductus ejaculatorius opens on the 10<sup>th</sup> sternum. It is dilated anteriorly, and to the dilated portion two glands are attached,—one, a mushroom-shaped gland composed of short caeca with viscid granular white contents, the other composed of dichotomous moniliform tubes, united by a common investment into a long mass overlying the last ganglion. The spermatozoa have straight rod-like heads and long flagella or tails.

For the female generative organs, see description of Plate viii. and literature cited there.

#### NOTE ON THE STRUCTURE OF ANTENNAE.

Hauser has recently investigated the function and structure of antennae. He concludes upon experimental grounds (effect of strong-smelling substances; the power of finding odorous food or in certain instances the female; according as the antennae are present or removed) that antennae possess an olfactory function. The sensory apparatus consists (1) of a conducting antennary nerve arising from the supra-oesophageal ganglia in connection with certain lobes (Bellonci, Flögel); (2) of a hypodermis-cell, in union basally with a nerve-filament, and terminated by a freely projecting rod, but varying in other respects in different groups; (3) of a supporting and protective apparatus in the shape of either a groove or a chitinous cone, open round the base of the projecting sensory rod to the cavity of the antennae, and hence filled with blood plasma. The cone is generally open at its tip. The groove is in some instances (*Orthoptera*, *Apis*) closed by a superficial delicate membrane but when it is freely open, escape of liquid is impossible, by reason of the minute size of the aperture. In the *Diptera* a number of sensory cells are contained within one common depression. In some *Hymenoptera*, grooves and cones occur side by side. The organs are generally restricted to certain joints of the antennae, e.g. third joint in *Diptera Brachycera*, terminal joints in *Lepidoptera Rhopalocera*. Hauser points out that the number and perfection of the organs are in correlation with the habits of the insects examined. The *Syrphidae* (*Diptera Brachycera*)

with larvae feeding on vegetable food, &c., have but few (one to four); those with larvae feeding on dung have many; the Honey-bee has 14,000 to 15,000 grooves and 300 cones on one antenna, Ichneumon 3000 grooves: but in the phytophagous subsection of the *Hymenoptera* grooves are absent, and cones are present in comparatively small numbers. The Lamellicorn beetles have vast numbers on the foliate expansions of the joints, e.g. male Cockchafer about 39,000, female 35,000. Hauser was unable to find any organs in the antennae of *Hemiptera* and *Neuroptera* (*Chrysopa*), nor in the *Carabidae*, but in the latter and in other *Coleoptera* he found identical structures on the maxillary and labial palpi. They may, however, in these situations have a gustatory rather than an olfactory function. Cones especially appear to be present in larvae, not only on the antennae, but also on the palpi. In many instances, however, the organs appear to be absent.

Cone-like structures occur on the antennae of *Lithobius forficatus* and *Julus terrestris* among *Myriopoda*; see also Bourne (G. C.) on *Sphaerotherium*, J. L. S. xix. Dec. 1885.

*Insecta*, MacLachlan, Encyclopaedia Britannica (ed. ix.) xiii. *Anatomia degli Insetti*, Camerano, Turin, 1882. *Die Insekten*, Graber, 'Naturkräfte' series, xx., Munich, 1877. *Elementary Text-book of Entomology*, W. F. Kirby, 1885. *Introduction to Entomology*, Kirby and Spence, 4 vols. (vols. iii. and iv. 1826, which contain orismology and anatomy, have never been reprinted). *Guide to the study of Insects*, Packard (ed. 3), Salem, 1872. *Modern Classification of Insecta*, Westwood, 2 vols., London, 1839. *Entomologist's Text-book*, Idem, 1838.

*Orthoptera*. *Orth. Europaea*, Fischer, Leipzig, 1853; see for Family *Blattinae*, pp. 84-88. *Recherches anatomiques, etc., sur les Orthoptères*, Léon Dufour, Mémoires, etc., des savants Étrangers, Acad. Roy. de France, 1841. *Classification of Orthoptera and Neuroptera*, and *Genealogy of Insects*, Packard, American Naturalist, xvii. 1883.

*The Cockroach*. *Beiträge zur näheren Kenntniss von Periplaneta orientalis*, Cornelius, Elberfeld, 1853; cf. Hagen, Stettin. Entomol. Zeitung, xv. 1854, p. 378; and Huxley, Anatomy of Invertebrated Animals, 1877, p. 398.

*Structure, movement, and function of Insectan limbs*. Dahl, A. N. 50, 1884. *Adhesive organs*. Simmermacher, Z. W. Z. xl. 1884; cf. Dewitz, Z. A. vii. 1884; viii. 1885; and Reviews by Emery and Graber in Biol. Centralbl. iv. 1884-85. *Glands of feet*. Dahl, A. M. A. xxv. 1885.

*Folding of wings*. Scudder, American Naturalist, x. 1876; De Saussure, A. Sc. N. (5) x. 1868. *Circulation in wings of Blatta*, Moseley, Q. J. M. xi. 1871.

*Thoracic muscles*. Luks, J. Z. xvi. 1883; *Structure of muscle*. von Limbeck, SB. Akad. Wien, xci. Abth. 3, 1885.

*Somites of head*. Packard, American Naturalist, xvii. 1883.

*Structure of antennae*, Hauser, Z. W. Z. xxxiv. 1880. *Mouth-parts of Insecta*. Brullé, A. Sc. N. (3), ii. 1844; Chatin, A. N. H. (5), xiv. 1884.

*Brain of Cockroach*. Newton, Q. J. M. xix. 1879. *Of Locust*. Packard, American Naturalist, xv. 1881. *Stomatogastric and sympathetic systems*. Köstler, Z. W. Z. xxxix. 1883. *Nervous system of Insects in general*. Leydig, Vom Bau des Thierischen Körpers, Tübingen, i. 1864 and Atlas. *Lobi olfactorii*, Flügel, Z. A. vi. 1883, p. 539; Id. Z. W. Z. xxx. (Suppl.) 1878, described under *Blatta*, p. 566.

*Digestive tract, &c.* Basch, SB. Akad. Wien, xxxiii. 1858. *Salivary glands*. Kupfer,



Festgabe zur Karl Ludwig, 1874. *Gizzard of Orthoptera*. Wilde, A. N. 43, 1877. *Appendices pyloricae*. Graber, SB. Akad. Wien, lix. Abth. i. 1869. *Rectum*. Chun, Abhandl. Senck. Gesellsch. x. 1875.

*Malpighian tubes*. Schindler, Z. W. Z. xxx. 1878.

*Corpus adiposum*. Targione Tozzetti, Bolletino della Soc. Entomol. Ital. iii. 1871; iv. 1872. *Its formation in Corethra*. Wielowicjski, Z. A. vi. 1883.

*Heart*. Graber, A. M. A. ix. 1873. *Ventral pulsatile sinus*. Id. op. cit. xii. 1876. *Blood corpuscles*. Id. SB. Akad. Wien, lxiv. Abth. i. 1871. Cf. *on heart*. Poletajewa, Z. A. ix. 1886.

*Stigmata*. Krancher, Z. W. Z. xxxv. 1880; Landois and Thelen, Ibid. xvii. 1877 (for *P. orientalis*, see Taf. xii. fig. 12). *Primary number in Insecta*. Packard, American Naturalist, viii. 1874. *Tracheal System of Insecta*. Palmén, Morphologie des Tracheensystems, Leipzig, 1877. *Minute Anatomy of Tracheae*. Macloskie, American Naturalist, xviii. 1884.

*Testes of Periplaneta*. Rajewski in Hoffman and Schwalbe, Jahresbericht für Anat. und Phys. 1875, p. 425. *Male genital armature of same*. Huxley, Anatomy of Invertebrated Animals, 1877, p. 406.

*Female organs, &c.* see end of description of Pl. viii.

*Histology, Histolysis, and Histogenesis of Insecta*, Viallanes, A. Sc. N. (6), xiv. 1882. Cf. Ludwig, Untersuchungen zur Anat., &c. der Thiere, Bonn, 1883, passim.

*Development of Blatta germanica*. Rathke, Meckel's Archiv (Arch. für Anat. und Physiol.), 1832. Cf. *A Note on same*, Patten, Q. J. M. xxiv. 1884.

## 29. LARVA OF PRIVET HAWK MOTH (*Sphinx Ligustri*).

THIS and the two following preparations are intended to illustrate the various points of external anatomy in which the larva, pupa, and imago of a Lepidopteron, an insect with perfect metamorphosis, differ from one another. The larva (or caterpillar) belongs to the eruciform type of Packard. It possesses a distinct head, but it has a somewhat vermiform appearance owing to the great *homonymy* or similarity of the remaining somites, and the fact that the segmentation of the antennae and feet, and the form of the mouth-parts are not obvious to the unassisted eye.

The greater part of the covering of the head is made up by the two large 'parietal scales' of Lyonet, corresponding to the epicranium of the imago. A triangular plate, the 'frontal scale' of the same author, the representative of the clypeus, lies anteriorly between them. The parietal scales are each marked laterally by a dark stripe, at the inferior end of which may be found the six ocelli usually present in a caterpillar, as six whitish spots. The antennae and mouth-parts may be seen with the help of a lens. The antennae are three-jointed, and are situated below and internally to the ocelli. The joints can be retracted one within the other.

There is a pair of large toothed mandibles, but the structures corresponding to the maxillae and labium of the Cockroach are here fused into a plate which closes the mouth behind. The plate consists of a median and two lateral lobes. Each lateral lobe represents a maxilla and carries a jointed appendage, probably the maxillary palp. The median lobe, representing the labium, carries a pair of jointed appendages, the homologues apparently of labial palpi, and a central tubular projection, the spinneret, upon which opens the common duct of the two silk glands.

The three first somites carry each a pair of five-jointed limbs. They represent the thoracic region of the imago, while the remaining ten somites represent its abdomen. Of these ten, the two first somites have no appendages but like the first body-somite (pro-thorax), and unlike the second and third (meso- and meta-thorax), are pierced on each side by a respiratory foramen, the *spiracle* or *stigma*. The succeeding four somites also possess spiracles and carry unjointed, sucker-shaped limbs, armed terminally and on the inner side with spines, and known as 'pedes spurii,' or 'prolegs.' The two following somites have spiracles but no prolegs, and the last of the two (the eighth abdominal) carries a dorsal horn characteristic of the family *Sphingidae*, with the exception of a few species. The body is terminated by two somites, of which the first, representing the large ninth abdominal somite of the imago, is a narrow ring difficult to make out; while the last, the thirteenth larval somite reckoning from the head, is perforated by the anus and carries a pair of anal prolegs. The anus itself is covered by a triangular anal valve.

The action of the spirit has destroyed the natural colour of the caterpillar. In life it is of a bright green colour, with yellow spiracles, the dorsal horn black above and at the tip, yellow below, and the abdominal region ornamented by seven oblique stripes, lilac above and white below. It feeds upon the privet, ash, &c., and exists in the larval condition from the end of July to the middle or end of September. During this period, it changes its skin six times, increasing much in size after each moult, notably the last. When full grown it has a brief period of quiescence, and then becomes very restless. Its colour, especially on the dorsal surface, tends to a brownish pink, and the pulsations of the heart become very visible and rapid. At last it buries itself in the earth, penetrating to a depth of six to eight inches. Here it hollows out a smooth-walled and waterproof chamber by moistening the soil with the secretion of its silk-glands, and pressing it with its body. It lines the chamber with silk and in about three days' time throws off the caterpillar skin and appears as a pupa or chrysalis.

The labrum is represented by two tubercles connected by a soft skin lying in front of the mandibles. In *Pieris* it is a corneous plate hinged upon the frontal

scale. The mandibles of *Sphinx* are only slightly toothed. In the embryo the maxillae and labial limbs are separate as in other Insecta. A few Lepidopterous larvae are apodal, e.g. *Micropteryx* among *Tineinae*. The coxa and trochanter of the thoracic limbs are but slightly indicated. The tarsus is neither jointed nor clawed. In these points the limb contrasts strongly with the limb of an insect with an active pupa stage, e.g. Cockroach, which closely resembles that of the imago. In a few instances, e.g. in *Stauropus Fagi*, the second and third pairs of limbs are large with conspicuous joints. The prolegs vary much in number and character. In the embryo *Sphinx Populi*, as figured by Kowalewsky (Mém. de l'Acad. Imp. St. Pétersburg (7), xvi. 1871, Pl. xii. fig. 10), there is a pair to each of the ten abdominal somites. In the Caterpillar they may be reduced to the last and the anal pairs (*Geometridae*), or to the anal pair alone (some *Tineinae*). They are as a rule armed with hooks, alternately long and short, arranged either in a complete circle round the terminal disc or only on its inner side. The anal pair is produced in the Puss Moth (*Cerura vinula*) into a pair of long whip-like processes, each containing a protrusible filament, used to drive away Ichneumons. Abdominal limbs are also found in the *Thysanura*, in the larvae of *Panorpatae*, of *Tenthredinidae* among *Hymenoptera*, and of some *Coleoptera* (?).

Many larval *Tenthredinidae* closely resemble caterpillars. They differ from them in the following points: the ocellus is single; the antennae are 3-jointed and conical, but 7-jointed in the genus *Lyda*; the maxillae are membranous, bilobed and furnished with 3-5-jointed palpi; the labium is small, fleshy, and provided with 3-jointed palpi and a spinneret. The majority have prolegs which vary from 6-8 pairs in number. These legs have no hooks, and there is a pair on the second abdominal somite, which never bears one in the *Lepidoptera*. The larvae of the autumnal brood rest in the cocoon without pupating through the winter. Such a phenomenon is rare among *Lepidoptera*.

The duration of a caterpillar's life varies. It may extend only to a fortnight, or to three years in *Cossus*. The number of moults is generally three or four. In this process the old cuticle as a rule splits on the back of the thoracic somites, and the split extends to a variable degree both forwards and backwards. The three scales of the head may separate also. The cuticle of the oesophagus and intestine appears to be cast at least in the final moult. Previous to pupation the caterpillar may suspend itself either by the anal prolegs, e.g. *Vanessa*, or secure itself by the anal prolegs and a band of silk round the thorax, e.g. *Pieris*; or may fashion a silken cocoon with or without an admixture of foreign bodies; or else it buries itself as do the majority of *Sphingidae*. A few members of this family, however, e.g. *Chaerocampa Nerii*, form a cocoon on or near the surface of the ground.

Note the following points of internal anatomy. The nervous system comprises a supra- and an infra-oesophageal ganglion and a series of ten ventral ganglia, of which three are thoracic and seven abdominal. The tenth is often double, e.g. in *Acherontia*. The commissures between the three thoracic ganglia are generally divaricated. The respiratory sympathetic system consists of a nerve running on the dorsal aspect of the nerve-chain from one ganglion to the ganglion next following. In the abdominal region this nerve branches to right and left just in front of the ganglion, with which two short filaments connect the branches at their origin. The branches are the nervi transversi or respiratorii, and supply the tracheae and

stigmata. In the thoracic region the nerve breaks up into three primary branches. The median divides right and left as in the abdominal region, and supplies the longitudinal trunk which unites the prothoracic to the first abdominal stigma, as well as the tracheae it gives off. Each side branch runs backwards and unites with the ganglion, first of all giving off a lateral branch, the *nervus lateralis transversus* of Cattie, which joins the first nerve given off by the ganglion. The stomatogastric system consists, according to Newport, of a ganglion frontale and *nervus recurrens*: and of two ganglia in connection (like the paired system of the Cockroach) with the posterior aspect of the supra-oesophageal ganglion. The latter supply nerves to the tracheae of the head. The ocelli, as usual, have each a single lens. Beneath the lens lies a number of black pigment cells imbedding a crystalline body composed of several parts (Carrière).

The stigmata possess a complete apparatus by which they may be closed. The tracheal stems arising from them are all connected on each side by a longitudinal trunk which in the meso- and meta-thoracic somites gives off an external branch furnished with the usual closing apparatus of a stigma. No external indications of stigma, however, are visible in these somites in *Sphinx*, but Prof. Westwood possesses a dried specimen of *Cossus* in which they are clearly visible. W. Müller-Blumenau has found an aquatic Lepidopterous larva (*Cataclysta pyropalis*) living in Brazil, in which all the stigmata are closed and respiration is carried on by filamentous branchiae, but there are two closed thoracic stigmata, which he places between the pro- and meso-thorax and between the meso- and meta-thorax. He states that he has also found them in many terrestrial larvae. The wings arise in close connection with the meso- and meta-thoracic branches. There are three pairs of cephalic stigmata in the embryo (Hatschek).

The digestive tract consists of an oesophagus, and an intestine and rectum lined by a cuticle, and a chylic stomach or mesenteron. There are six Malpighian tubes with a beaded exterior which open as usual into the beginning of the intestine. Two short salivary glands open into the mouth, and a pair of sericteria or silk glands by a common duct on the spinneret<sup>1</sup>. The rudimentary genital organs lie one on either side the heart under the fifth abdominal tergum. A delicate filament may be traced from each organ round the intestine. Herold figures these filaments as extending in *Pieris Brassicae*, in the male to the anterior border of the ninth somite; in the female to the anterior border of the eighth somite, and into connection with two oval bodies at its posterior border. An abundant fat body fills the body-cavity, or coelome. The blood is acid as in all caterpillars with one exception hitherto examined, and contains amoeboid blood-corpuscles. It is green, and the colour is due to metachlorophyl (Poulton).

There are two types of larval (or young) Insecta: one known as Campodeiform, from a more or less close resemblance to the genus *Campodea* among *Thysanura*; the other as eruciform, of which a caterpillar may be taken as a good example. The Campodeiform larva has the typical regions of the body clearly defined, mouth parts adapted for biting, well developed ambulatory thoracic limbs, and frequently terminal abdominal jointed appendages. The outlines of the body

<sup>1</sup> Poletajew (Z. A. viii. 1885) states that the silken thread is single in the *Tenthredinidae*, but double and twisted in *Lepidoptera*. Hence he disputes the statement that the ducts of the sericteria have a common outlet.

are even, and the series of somites follow one another without any abrupt change of shape. Such a larva is seen, more or less adapted of course, in most *Ametabola* and *Hemimetabola*. The condition of the adult insect is acquired in a graduated series of moults, whilst organs such as wings make their appearance; and others, e.g. the genitalia, are brought to maturity. It is also seen in some *Metabola*, as in certain families of *Coleoptera*, e.g. *Cicindilidae*, *Dytiscidae*, &c.; in some *Neuroptera*, e.g. *Sialidae*; some *Megaloptera*. In these instances it is occasionally highly specialised, e.g. in the Ant-lion. It appears in others as a *first* larval form, subsequently modified in accordance with a change of habit in the direction of the eruciform type, constituting what is known as Hypermetamorphosis. Such a change occurs in *Mantispa* among *Panorpatae*, in the *Strepsiptera*, and in various *Meloidae* among *Coleoptera*, e.g. *Meloe*, *Sitaris*, *Hornia*, *Epicauta*, *Cantharis*. In *Mantispa* the second larval form is only sub-eruciform: in the *Meloidae* there is a number of forms one after the other more and more degraded. (See Packard, American Naturalist, vii. 1883, pp. 938-944; Riley, op. id. xii. 1878, pp. 213, 282.)

The eruciform type of larva is very generally found among *Metabola*. It may succeed, as just mentioned, a Campodeiform larva, and in its simplest shape, e.g. in *Trichoptera*, which may be termed sub-eruciform, it is little more than a persistent embryonic form such as is observable in the earliest stages of most *Insecta*. The caterpillar of the *Lepidoptera*, of the *Panorpatae*, of *Tenthredinidae* among *Hymenoptera*, and the grubs of some *Coleoptera* are typical examples of the type. The head is well-defined, but the somites of the body are simple and cylindrical (homonomous), and the animal has a vermiform aspect. Nevertheless a thoracic region with articulated limbs is distinguishable, and what is more the abdomen (except in *Coleopterous* forms) possesses functional abdominal limbs. Such limbs, but not functional, exist in *Thysanura*, and as rudiments in the embryos of most *Insecta*, e.g. in *Hydrophilus* (*Dytiscidae*), which has a modified Campodeiform larva. The limbless grub of *Aculeate Hymenoptera*, and still more the maggot of *Diptera*, must be regarded as degenerate examples of this type: and where limbs are present in a *Dipterous* larva they are probably *secondary* and *special* developments. The larvae of all existing *Insecta*, and even the primitive *Ametabolous* order *Thysanura* have been modified to a greater or less extent by Natural Selection. The embryo however has a type of structure which is readily modified in the direction of one of the two larval types; and it is not surprising to find larval forms, such as those of *Trichoptera*, which may be regarded as actually transitional between the two.

*Larvae of British Lepidoptera and their Food plants*, Wilson, London, 1880. *Figures* in Horsfield and Moore, Catalogue of *Lepidopterous Insects* in East India House Museum, 2 vols., 1858-59, and in Dewitz, *Jugendstadien exot. Lepidoptera*, Nova Acta, 44, 1883. *Aquatic Lepidopterous larvae*. Müller-Blumenau, A. N. 50, 1884; Maurice, Bull. Scientifiques du Département du Nord, iv.

*Anatomy*. Cossus, Lyonet, *Traité anatomique de la Chenille qui ronge le bois du Saule*, Hague, 1762. *Sphinx*, Newport (and also as to pupa and imago) 'Insecta'; Encyclopaedia of Anat. and Phys. ii., London, 1836-39.

*Skin glands*. Klemensiewics, Verhandl. K. K., zool. bot. Gesellschaft, Wien, xxxii. 1883. *Glandular hairs*. Dimmock, Psyche, iv. 1885.

*Muscles*. Lubbock, on *Pygaera bucephala*. Tr. L. S. xxii. 1859.

*Stigmata*. Krancher, Z. W. Z. xxxv. 1881.

*Serictaria*. Helm, Z. W. Z. xxvi. 1876; Lidth van Jeude, Z. A. i. 1878; Joseph, Z. A. iii. 1880.

*Nervous system*. Newport, Ph. Tr. cxxii. 1832; cxxiv. 1834 (includes *Vanessa Urticae*); Cattie, Z. W. Z. xxxv. 1880.

*Blood*. E. B. Poulton, P. R. S. xxxviii. 1885.

*Protective coloration and markings*. Poulton, op. cit.; ibid. xl. 1886, and Trans. Entomol. Soc. 1884 and 1885; Weismann, Studies in Theory of Descent (translated by Meldola), London, 1880-82; Cameron, on *Smerinthus*, Trans. Entomol. Soc., 1880. *On colour*, see also Hagen, Proc. American Acad. (2) ix. 1882; F. Müller, Kosmos, xii.; Wallace, Tropical Nature, London, 1878, pp. 158, 249.

### 30. PUPA OF PRIVET HAWK MOTH (*Sphinx Ligustri*).

THERE are two forms of *quiescent* pupae among Insects: one in which the antennae, mouth-parts, limbs and wings are free, the other in which they are coherent to one another and to the body. Of the first kind of pupa two varieties are distinguishable. In one the larval skin is simply thrown off. It is known as *incomplete*, *exarate* or *libera*, and occurs in the *Neuroptera*, *Coleoptera*, *Hymenoptera* and some *Diptera*. In the other variety, known as *coarctate*, and occurring only in *Strepsiptera* and *Diptera*, the larval skin is retained, and it either preserves the form of the larva, e.g. *Strepsiptera*, *Stratomyidae*, or contracts into a barrel-shaped structure, e.g. *Muscidae*. The second form of quiescent pupa, known as *obtectad*, *larvate*, or *signate*, is characteristic of *Lepidoptera*. The cohesion between the limbs, &c., as seen here, is due to the hardening of a sticky fluid which covers the surface at the moment when the caterpillar skin is thrown off.

The obtectad pupa is either angular, as in the majority of *Lepidoptera* with club-shaped antennae (= *Rhopalocera*), and then often brightly tinted; or it is conical, as in *Sphinx* and other *Lepidoptera* with the antennae fashioned after various types (= *Heterocera*). It is then, with rare exceptions, dark-brown in colour.

The pupa is plainly divisible into three well-marked and dissimilar regions, head, thorax, and abdomen. The head is globular and deflexed. The long antennae take origin from it laterally, and are bent backwards ventrally and towards the middle line. A lunate convexity below and in front of the base of the antennae marks the eye. A small median square piece in front is the labrum, and the angle projecting forwards from the convex surface that bears the eye, i.e. the gena, is formed under the larval mandible. It touches the outer inferior angle of the labrum. The pupal maxillae are large in size, and take origin below the labrum. Each has at its cephalic extremity a horn-like projection, the two projections uniting in the middle line. These projections usually but wrongly identified with the whole tongue, antliae, or maxillae of the imago, are absent in some *Sphingidae*, e.g. *Acherontia*, *Macroglossa*, and of great size in others, e.g. *Sphinx Convoluti*.

The maxillae expand into an angle below the eyes, and are then prolonged as narrow bands lying side by side in the median ventral line, as far as the tips of the wings. The labium is hidden by the maxillae. Between the maxillae and antennae may be seen the tibial and tarsal portions of the pro- and meso-thoracic limbs, whilst the metathoracic are completely hidden by the wings. The mesothoracic, or first pair of wings, are large, and hide the metathoracic pair completely, save at their dorsal origin. Both wings and maxillae extend to the middle of the sternal region of the fourth abdominal somite.

The mesothoracic tergum, viewed dorsally, is of great size, whilst the prothoracic, and especially the metathoracic, are much reduced. A depression behind the outer angle of the prothoracic tergum leads to the spiracle.

The abdomen consists of ten somites. The first and the ninth in particular are small. The first spiracle is completely, the second partially hidden by the wings. The third to the seventh spiracle inclusive are large, but the eighth is denoted only by a well-marked scar. The tenth somite is prominent. It bears a dorsal spinous projection, the *cremaster*, which is differentiated within the anal valve of the caterpillar, and is covered with spines which vary much in different specimens. It is used by the pupa as a prop when it works its way up from its underground chamber previous to the emergence of the imago. A longitudinal depression, ventral to the cremaster, marks the anus; and the ridges on either side of it (=sustentors of Riley) correspond to the anal prolegs of the caterpillar. Irregular scars, more or less evident on the ventral aspect of the third to the sixth somites, denote the position of the other prolegs of the caterpillar.

In a male pupa the ring of the ninth somite is interrupted ventrally, and a depression with a more or less prominent tubercle on either side, marks the future aperture of the vas deferens. In a female, the eighth somite (as well as the ninth) is interrupted ventrally and bears a depression, the future aperture of the bursa copulatrix. These depressions appear to be constant in all *Lepidoptera*.

When June approaches the pupa becomes restless and writhes in its chamber. It works its way up to the surface of the ground by means of the abdomen, the only part of the body which possesses the power of motion. The last abdominal somites of the moth become free first of all from the pupa-skin: this skin then becomes brittle and is fissured longitudinally in the dorsal region of the thorax. A split runs ventrally along the fore-edges of the wings. The moth emerges early in the day and suspends itself vertically while its wings expand and dry. In two to three hours it becomes capable of flight.

The newly-formed pupa is soft: in colour creamy-white, and all its appendages contain large cavities filled by a blood-plasma which is extremely milky owing to

the resolution of the fat body. A pupa preserved in alcohol at this stage retains its light colour. One in the possession of Mr. Poulton, has clearly defined though feebly coloured streaks, corresponding to the coloured streaks of the caterpillar. Under natural conditions the pupa hardens and becomes dark-brown. As this change of colour takes place underground, it cannot be due to the action of light.

Swammerdam was the first to point out that the appendages are readily separable in a newly-formed pupa, or may be dissected out from under the caterpillar skin when it is ready to be moulted. The operation is easy if the pupa or caterpillar are preserved in alcohol.

In the caterpillar it will then be found that the angle of the gena already mentioned in the pupa corresponds to the mandible: that the pupal antennae and maxillae are folded upon themselves: that the wings are mere tubercles. All these parts expand and assume their proper position as the caterpillar skin is being cast off.

It will also be found that the horn-like projection of the pupa consists of a right and left division, one belonging to each maxilla: that its labium consists of two backwardly turned lobes united basally, and of great size in *Pieris*: that the coxa of the limbs are united to the thorax, the trochanter inconspicuous: that the femur and tibia are bent at an angle on one another, the former concealed by the latter, and that the joints of the tarsus are not differentiated. Though the first abdominal spiracle is hidden by the wings, it retains the character of an open functional spiracle.

If the horn-like projection of *Sphinx Ligustri* is opened when the moth is nearly ready to emerge, the bases of the antlia of the imago will be found to fill it imperfectly. Each base forms a thick band or ribbon attached anteriorly to the head, lying under the outer surface of the projection, inside which it is folded back once upon itself. It then runs on into the straight median portion of the pupal maxilla. It appears to me likely that it is differentiated from a part, and not the whole of the outer wall of the pupal maxilla, but the histological details of the process are still wanting. Owing to the fact that the antennae, antliae, &c., of the imago are formed within the corresponding organs of the pupa, and are withdrawn from them leaving them empty when the imago emerges, the pupal organs have been spoken of as 'cases' or 'thecae,' e.g. *Ceratotheca*, *Glossotheca*, &c. But it must be borne in mind that just as the change from caterpillar to pupa takes place by a moult, and the pupal organs are formed within the corresponding organs of the caterpillar, from which they differ essentially in shape and size, so it is with the change from pupa to imago. Indeed there is reason to believe that more than one moult takes place during the pupal stage. In *Sphinx Ligustri* and in some others (?) a thin pellicle may be raised from the inner surface of the last pupal skin; and Professor Westwood has drawn my attention to a passage in Curtis (*British Entomology*, Description of Plate 147), where that author records the fact that an imago of *Acherontia Atropos* cast off a complete and thin pellicle *after emergence* from the pupa-skin. The pellicle in question appears to be homologous with the thin skin cast by the sub-imago of *Ephemeridae* after it has taken flight from the water, having already just emerged from another skin.

The pupal state of *Sphinx Ligustri* lasts for forty-two to forty-three weeks. During this period changes take place affecting all the internal organs. Changes in the nervous system continue for the first four weeks, but are then suspended until March. They have been worked out in this moth and in *Vanessa Urticae* by New-



port; whilst Herold has worked them out in *Pieris Brassicae*, as well also as the changes undergone by the digestive system and the evolution of the male and female organs.

In some pupae, e.g. of *Cossus*, the edges of the abdominal somites are fringed with short spines or *adminicula* to aid the movements of the animal. The apex of the cremaster varies much in character. The duration of the pupal state differs much. In small species it lasts only a few days. In *Lepidoptera* with two broods in a year, e.g. *Papilio Machaon*, the pupal state of the first brood lasts thirteen days, of the second from September to June. In the broods of various *Pieridae*, &c., the same differences may be observed. The pupal state of *Sphinx Ligustri* is occasionally extended for a year beyond the normal: and this is often the case in some other genera. It is a very common thing for a larval *Tenthredinidan* (*Hymenoptera*) to delay assuming the pupal state within its cocoon, but it is an extremely rare occurrence in *Lepidoptera*. It is said, however, that if the *Cossus* larva makes its cocoon in autumn, the caterpillar does not become a pupa till after winter has passed: if it makes it in June, it becomes a pupa at once and emerges as an imago in three to four weeks.

*Note.* The wings make their first (i.e. outward) appearance in the pupa stage of insects with a perfect metamorphosis. In the newly-formed Lepidopterous pupa they are hollow sacs with a cavity continuous with the coelome. These sacs swell out as the larval skin is being cast. But wings appear from the first as external processes, gradually increasing in size with successive moults in insects such as the Earwig, Ephemeron, Cockroach, i.e. in *Insecta Ametabola*, and *Hemimetabola*. Dewitz (Berlin. Entomol. Zeitung, xxv. 1881) has found in very early stages of larval *Trichoptera* and *Lepidoptera* a pair of small meso- and meta-thoracic involutions of the hypodermis cells containing an internal chitinous lamella continuous with the cuticle. These involutions increase in size at every successive moult, and acquire a more or less perfect investment of mesodermic cells derived from the sheaths of either the tracheae or the nerves. They are evaginated *previously* to the last moult by the withdrawal of the internal chitinous lamella, and when the last larval skin is stripped off they appear as external sacs (*supra*).

The homology and first origin of wings are points of great obscurity. There are no traces of them in the most primitive Insectan order known, the *Thysanura*, a survival of forms existing apparently before the acquisition of wings. Wings are to be considered as *secondary* or *acquired* structures. It is tempting to regard them as modified tracheal gills, which they much resemble in structure, and which are also organs secondarily acquired. But it is impossible to suppose that all *Insecta* with a very limited number of exceptions are descended from ancestors which took to aquatic habits; 'took,' because the first *Tracheata* were without doubt terrestrial forms. And the only supposition that appears feasible is that respiratory structures similar to tracheal gills were of use to terrestrial *Insecta* living under conditions long passed away. The larval *Calotermes rugosus* (F. Müller, J. Z. ix. 1875), one of the *Termitidae*, animals of subterranean habit, develops peculiar dorsal appendages devoid of tracheae on the pro- and meso-thorax. The pair on the prothorax disappears: that on the mesothorax acquires tracheae, and grows into the mesothoracic pair of wings. The metathoracic pair of wings develops in a similar manner but at a later period. It must be remembered that the oldest fossil *Insecta* known, even

the Silurian *Blatta*, possess wings, so far as can be judged, of the ordinary structure. The first origin of these organs dates back therefore to a period and to conditions of which we have no record.

*Pupa and Imago of Cossus.* Lyonet, Recherches sur l'anatomie et les métamorphoses de différentes espèces d'Insectes. Ouvrage posthume, Paris, 1832.

*Changes in nervous and digestive systems, and Evolution of reproductive organs.* Herold, Entwicklungsgeschichte der Schmetterlinge, Cassel, 1815. *Changes in nervous system.* Newport, Ph. Tr. 1832 and 1834. *In reproductive.* Bessels, Z. W. Z. xvii. 1867.

*Formation of antennae of Imago.* Dewitz, Biol. Centralbl. iii. 1882-3. *Of wing,* Id. Berliner. Entomol. Zeitung, xxv. 1881. Pancritius, Z. A. vii. 1884.

*Philosophy of Pupation.* Riley, American Entomologist, iii. 1880.

### 31. IMAGO, MALE AND FEMALE, OF PRIVET HAWK MOTH (*Sphinx Ligustri*).

IN the imago or Moth, *Sphinx Ligustri* reaches the last stage of its life-history, the sexually mature insect. The dissimilarity between the head, thorax and abdomen, which first appears in the pupa, is now far greater, but the outlines of these three heteronomous regions are much softened and obscured by the thick coat of hair and scales that clothes the body. The small head distinguished by its light colour carries in this stage large sensory organs,—convex, black, pigmented eyes and antennae. As the food consists of the liquid nectar of flowers the organs of the mouth are reduced and modified, the only conspicuous parts being the *spiritrompe* or *antliae*, the homologues of the galeae in the biting mouth, which are extended in one of the specimens, and the hairy labial palpi which are, as in all *Lepidoptera*, turned forwards beneath the head. The thorax is broad and clothed dorsally with black-brown hairs, with a streak of white hairs over the roots of the wings. These organs are composed of a thin membrane supported by thick *nervures*, the whole surface being covered with thickly set and variously coloured scales, arranged in distinctive patterns and characteristic of *Lepidoptera*. The fore- and hind-wings on each side are connected by a hook and bristle. The bristle springs from the fore-margin of the hind-wing near its root and ends in a tuft of stiff black hairs. The hook springs from the under surface near the margin and at the root of the fore-wing. The three pairs of thoracic-limbs are of but secondary importance as organs of locomotion and are used chiefly for support. The tarsi end with strong claws. The abdomen is large and pointed posteriorly. Its first somite is clothed dorsally with black hairs, a few white being intermingled. The remaining somites bear a longitudinal median dorsal grey-brown band with a central dark line; and each somite except the last has to either side of the median band a transverse bar of pink hairs, and a fringe

of black hairs to its posterior margin. This black fringe encroaches more and more on the surface of the somites at the expense of the pink band the further back the somite is in the series.

The female differs from the male as follows. The antennae are more slender, and want the setae-like hairs on the brown surfaces of the joints: the thorax is rounder in front and the fore-wings have generally a more curved anterior border and less acute apex: there is no hook developed on the fore-wings for the bristle. There are five pink bands on the abdomen instead of six: the last somite is broad basally, conical and as long at least as the two preceding somites, whereas in the male the abdomen tapers gradually to a point and is terminated by two valves with a vertical slit between them.

The *Lepidoptera* are often divided into two chief sub-groups—the *Rhopalocera* with the antennae ending in a club, and the *Heterocera* to which *Sphinx* belongs. The *Heterocera* have various types of antennal structure. They frequently possess the retinacular apparatus binding the fore- and hind-wings together, and their posterior tibiae have four instead of two spines.

The *Sphingidae*, the family of which *Sphinx* is the type, are characterised by the prismatic shape of the antennae and the long bristle-like character of their terminal joint; by a three-jointed very hairy labial palp with a minute terminal and two broad compressed basal joints; by a one-jointed maxillary palp; a robust body and relatively small wings. Their mode of flight is peculiar and sustained. Hence the popular name of Hawk-moths given to these insects. Ocelli are generally stated to be absent, but Cattie affirms their existence in *Acherontia Atropos*.

To see the form and composition of the regions of the body it is necessary to divest it of hairs and scales by careful brushing. The head has no sutures. The prothorax is ring-like and is hence often termed 'collar.' Its tergum carries at each outer angle a vesicular dilatation clothed with long hairs, the patagium of Kirby and Spence. The prothorax is united to the mesothorax by membrane, but the latter and the metathorax are firmly connected. The mesothorax is very large. Its tergum is broken up into a large scutum and a lozenge-shaped scutellum behind. The fore-wings are attached to it, but their roots are covered by concavo-convex shields, the tegulae or wing-covers<sup>1</sup>. The metathorax is small. Its scutum is narrowed medianly where the scutellum projects forward. It bears the hind wings. The nervures of these organs become plain when the scales are brushed off. They contain extensions of the tracheae and blood-channels. For their arrangement, as well as the composition of the lateral walls of the thorax, the student must consult the larger works on Entomology. The limbs consist of the same parts as in the Cockroach. The anterior coxae are free; the median and posterior are closely attached to the thorax. The trochanter is small; the femur short. The anterior tibiae have at their proximal end a peculiar enlarged moveable spine. The median

<sup>1</sup> The terms 'patagium' and 'tegula' are often misapplied. They are defined as in the text above by Kirby and Spence in the *Orismology*, Vol. iii. of the *Introduction to Entomology*. Patagia are structures peculiar to *Lepidoptera*, whereas tegulae are found in various other orders.

tibiae have a pair, the posterior two pairs, of distal posterior spurs. The tarsi are six-jointed, and not clothed with hairs like the rest of the limb.

The abdomen consists of ten somites. Each consists of a strongly chitinised tergum and sternum united laterally by a soft pleural membrane. The first of the series in both sexes, the ninth and tenth in the male, the seventh to the tenth in the female, require more notice. The first is firmly united to the metathorax. It is constricted, and its tergum is divided into a median and two lateral pieces, a division brought about apparently by the attachment of muscles. A slight groove and a difference in the chitin mark its separation from the second tergum. Its sternum is incurved and continuous with the second sternum.

The ninth somite in the male is inclosed by the eighth. It consists of two narrow lateral chitinous bands which meet with expanded ends dorsally and ventrally. Each band consists of a median, a dorsal and a ventral piece, the whole forming an S-shaped figure. Strong muscles are attached to these pieces. The *valves* which inclose the male genital organ and the anal papilla are attached to the posterior edges of the ventral pieces. Each valve is trigonal, concave internally, its margins fringed with long hairs. Near the ventral edge of its inner surface is a curved chitinous lamella, feebly toothed,—the *harpe* of Gosse (?=*harpagon* of White). To the posterior edges of both dorsal pieces of this ninth somite is articulated a stout decurved pointed process terminating in two hooks, the *uncus* of Gosse or *tegumen* of White. It immediately overhangs the slender anal papilla. A band of chitin connected with the base of the uncus, and continuous from side to side, curves under the same papilla, and from its mid ventral-point project two slender rods which appear to correspond to the *scaphium* of Gosse. The penis projects from the cavity below, i. e. in front of these rods, and above, i. e. behind the ventral union of the pieces of the ninth somite. The uncus appears to correspond to the cremaster of the pupa, the anal valve of the caterpillar. The bar curving below the anus may be *either* a chitinisation in the tenth or anal somite, *or* a dissociation from the ninth.

In the female the seventh somite is much elongated. Its sternum is small and triangular, its pleural membranes large and meeting posteriorly and ventrally. Somites eight, nine, and ten are inclosed by it. The eighth is short dorsally, long ventrally. It has a small pleural membrane. Its sternum is strongly chitinised, grooved ventrally, and the groove narrows anteriorly, serving as a guide to the large orifice of the bursa copulatrix. The ninth somite is soft in texture. A very narrow band represents its dorsal and lateral regions; its ventral region is thickened with a linear ventral groove. The tenth somite is represented by a large papilla slit vertically. Its sides are thickened, rough and pilose, and in the slit the anus opens above and the vagina below<sup>1</sup>.

<sup>1</sup> De Lacaze Duthiers, in his series of classical papers on the genital armature of female Insecta, places the aperture of the bursa copulatrix of the *Lepidoptera* behind the sixth somite, instead of behind the seventh in the sternal region of the eighth, its ordinary position in Insecta (see the table on p. 230, A. Sc. N. (3) xv. 1853), except in *Ephemeridae*, where it lies in the seventh intersegmental membrane. De Lacaze Duthiers does not recognise the altered first somite nor the exact position of the orifice of the bursa. Newport recognises the first somite, but has not described the differences between the male and female. His figures (Figs. 391, 392, pp. 922, 923, Article Insecta, cited below) are from a male. The correctness of the view taken above may be gathered partly from the account given of the pupa, partly from the relations of the spiracles (*infra*).

The structure of the body as above described is probably typical of the *Lepidoptera*, but the subject is one that calls for investigation. The region of the first abdominal somites seems the most variable.

The spiracles are vertical slits as in the previous stages. The last abdominal spiracle, the eighth, is aborted. A slight scar indicating its position may sometimes be found in the male. The remaining spiracles are the prothoracic and seven abdominal. The former is situated in the soft skin between the pro- and meso-thorax, nearer to the prothorax. The first abdominal is the largest of the whole series. It lies in the pleural membrane under the edge of the lateral piece of the first tergum, i. e. on the abdominal side of the thoraco-abdominal constriction<sup>1</sup>. The other spiracles are all situated in the pleural membranes of their respective somites. If the interior of the pupa skin is examined, the cuticle shed from the first portions of the tracheae may be found attached to all the pupal spiracles, with the exception of the eighth abdominal, thereby shown to be closed.

As to the mouth parts there is a labrum forming a narrow band with a median process and a lobe covered with hairs at each outer angle<sup>2</sup>. Mandibles are absent as articulated pieces, a characteristic feature, according to Walter, of all the *Lepidoptera* save *Microlepidoptera* (*Tineinae*, &c.). But from investigations made upon caterpillars about to assume the pupal condition, it seems to me that two stout pointed projections of the genae, lying to the outer side of the lateral lobes of the labrum, are non-articulated representatives of these appendages. At any rate, they are formed at the base of the caterpillar's mandible. The maxillae consist of a cardo and stipes, imperfectly separated and immoveably united to the head. The palps are one-jointed and bear a tuft of hairs. But the bulk of the maxillae, the antliae, consists of the greatly-developed galeae. Each galea is prolonged into a long band spirally coiled when at rest; convex on its outer, concave on its inner, face, thus forming a channel. The faces are strengthened by independent systems of chitinous spots or rings. The inferior edge of each channel bears a series of processes by which one galea is strongly tied to the other; while its superior edge carries one or more series of flat processes which overlap the corresponding processes of the other side. The outer surface carries hairs and 'borers' (*opotrypes*), the latter restricted to the tip. The borers are simple in *Sphinx*. When well developed they appear to act by piercing the nectaries of flowers or even pulpy fruits (e. g. as by *Ophideres*), and it is possible that they may also be to a certain extent organs of touch. The labium is reduced to a membrane between the bases of the maxillae. Its palps are three-jointed. The terminal joint, though small, is moveable. The second is deep, compressed and grooved where it fits round the maxilla of its side, and the first joint narrows to its base which is attached to a small cone<sup>3</sup>.

<sup>1</sup> Newport (article *Insecta*) calls the first of these two spiracles, mesothoracic (p. 923), the second, metathoracic (p. 924); and Müller-Blumenau uses the same expressions, connecting the spiracles of the imago with the two closed thoracic spiracles he discovered in an aquatic caterpillar. See *ante*, p. 150, and p. 199 of paper quoted. In all the specimens I have examined they are situated as above described.

<sup>2</sup> The prominence figured by Newport (article quoted) Fig. 377, as labrum, is a process of the clypeus from which a muscle takes origin. The parts designated mandibles by him (as they are also by Savigny) are really the lateral lobes of the labrum according to Walter. The only pupa of *S. Ligustri* at my command in a fit state to decide the question appears to corroborate Walter's view.

<sup>3</sup> Walter has shown that in certain species of *Micropteryx* (*Tineinae*) there is a hinged and toothed mandible; a maxilla with moveable cardo and stipes, six-jointed palp, a thin lacinia and

Changes have taken place in the internal organs. The supra- and sub-oesophageal ganglia have coalesced round the oesophagus. The mesothoracic ganglion appears to abort<sup>1</sup>, the prothoracic persists and is approximated to the metathoracic which has coalesced with the first abdominal. The second and third abdominal ganglia abort, but the nerves which they give off persist. The abdominal ganglia of the imago correspond to the four last ganglia of the caterpillar. A remarkable structure, the chorda suprasspinalis, overlies the abdominal ganglia, extending from the spot where the nerves arise from the sixth, an aborted ganglion, to the last ganglion. It is well-developed in the imago, and has been found by Burger in a large number of *Lepidoptera*. It is triangular in section and is intimately united by one angle to the neurilemma of the nerve cord whilst lateral muscles are attached to its two other angles extending thence to the abdominal walls. It is composed either of reticular cell-tissue with intervening jelly, or of vesicular cells. The chorda forms a strong attachment for the muscles, and the latter roof in the ventral blood-sinus (see under Cockroach, p. 144). There are vesicles developed on the tracheal branches in the abdomen. In the digestive tract there is a pharyngeal sac which can be dilated and contracted by systems of muscles. The oesophagus is long, and has at its stomachal end a non-pedunculated sucking stomach. The chylic stomach of the caterpillar is much reduced. The Malpighian vessels have lost their bead-like caeca. The intestine is long and the colon, as in many *Lepidoptera*, has a large dorsal caecum.

The testis is single externally, the two embryonic testes having become enveloped in a common sheath, as is often the case in *Lepidoptera*<sup>2</sup>. But there are two vasa deferentia: they are long much contorted tubes, and each duct receives an accessory tubular gland.

Each ovary consists of four long convoluted ovarian tubules united terminally by a ligament, both *inter se* and to the dorsal wall of the abdomen. The bursa copulatrix is large and pyriform, and a slender canal starts from its neck on the ventral anterior surface, curves round the neck and enters the side of the vagina. At its entrance a slender caecum is attached to the vagina which probably represents a spermatheca. There are two accessory tubular glands which dilate each into a pyriform enlargement, then fuse, and their common duct opens dorsally into the vagina near its exit. This exit is immediately below the anus<sup>3</sup>.

enlarged galea; a labium with mentum, three-jointed palps, paraglossae and ligula. In other species of the same genus the mandible is a simple lobe, the laciniae of the two maxillae are lost, and the galeae are transformed into more or less typical antliae capable of being coiled up and closely united, and there are no paraglossae. Mandibles as more or less simple lobes articulated to the head appear to exist in most *Micro-lepidoptera*.

<sup>1</sup> So thinks (Newport Phil. Trans. 1834, p. 394), but with reference to *Vanessa Urticae* he says (p. 416) that the prothoracic and mesothoracic, his second and third, ganglia fuse. Herold states the same fact with reference to *Pieris Brassicae*.

<sup>2</sup> Cholodkowsky has shown that when the external capsule is removed, the apparently single testis consists of eight testicular follicles, four to each vas deferens. The follicles are arranged in various ways within the sheath. *Hepialus Humuli* retains the testis in the primitive condition, i. e. four free follicles on each side. In *Pygaera anachoreta*, &c., each set of follicles is contained within a separate capsule: but in most *Lepidoptera* the follicles of both sides are contained in a common capsule.

<sup>3</sup> There can be little doubt that the canal connecting the bursa copulatrix to the vagina, itself represents the primitive vagina. The aperture of the bursa is in the typical position of the vaginal aperture. The canal in question has to pass round the neck of the bursa to gain its destination. The bursa in all other insects is a dorsally-placed appendage to the vagina. These

The origin of a perfect metamorphosis, such as that of *Sphinx*, with three well-marked stages, larva, pupa, and imago, is probably due to the operation of more than one cause. The Cockroach is an example of an insect which always lives from birth to the adult state in the same manner and under the same conditions; and this is the case with all Ametabolous Insecta. At birth such insects differ from the adult only in a few points, and the differences are gradually abolished. On the other hand, the differences between a caterpillar and a butterfly are very great, and the change from one state to the other is effected in an abrupt manner. It has been pointed out by Balfour (Comp. Embryology, i. p. 353) that a pupa-stage might easily arise (1) from a change at first small, then greater, in the character of the mouth-parts which would necessitate a more or less prolonged period of quiescence, the more prolonged the greater the change; (2) from the operation of climate and other natural causes on such a period of quiescence. The question however is a very difficult and complex one, impossible to treat in a short compass, and the student must refer to the list of works given below relating to the Metamorphosis and Genealogy of Insecta. But it must be carefully borne in mind that, among the *Micro-Lepidoptera*, certain minute moths are known with mouth-parts conformed to the type of biting mouth-parts (note, p. 159); that it is possible that the period of pupation is accompanied by more than one ecdysis, and is therefore essentially a period of abbreviated development; that in some *Hymenoptera Aculeata* there is, as it were, a preparatory stage previous to the true pupa-stage (Packard, Guide to Study of Insects, 1872, p. 66); that the changes from the larval mouth-parts to those of the adult are not so very great in all *Metabola*, e. g. in the *Tenthredinidae*; and that grades may be traced among *Metabola*, e. g. the *Trichoptera* and some *Neuroptera* afford examples of a comparatively simple perfect metamorphosis, the *Lepidoptera* a more complex example; whilst in some *Hymenoptera*, and especially in the *Diptera* as a class, the metamorphic changes are of a very profound character. Nor must it be forgotten that our knowledge of many details of anatomy, embryology and of life-histories is still very imperfect.

*British Butterflies and their Transformations*, Humphreys and Westwood, London, 1841. *British Moths*, *Iid.*, 2 vols., 1843-45. *Tineina (Insecta Britannica)*, Stainton, London, 1842. *Natural History of Tineina*, *Id.*, 13 vols., London, 1855-73. *Butterflies, &c.*, Scudder, New York, 1881.

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three facts point strongly to the conclusion stated. The vaginal aperture below the anus is therefore secondary, but the mode in which it arises has not been worked out. It should be noted that in the caterpillar the somites in this posterior region are much abbreviated.

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### 32. COMMON CRAYFISH (*Astacus fluviatilis*), FEMALE.

THE body of this Crustacean, like that of all *Podophthalmata*, consists of two great divisions, an anterior, the cephalothorax, covered dorsally and at the sides by a large continuous shield, the carapace, and a posterior, the abdomen, consisting of six separate metameres or somites, and of an azygos terminal flap, the telson, the last somite of the body, upon which the anus is situated ventrally. The cephalothoracic carapace is divisible into two regions by a well-marked curved line, with its concavity looking forwards, which is known as the cervical groove. The part anterior to this line corresponds to the head, the part posterior to it to the thorax, and they are known respectively as cephalo- and omo-stegite. The omo-stegite is marked dorsally by two longitudinal and short branchio-cardiac grooves connected anteriorly by a curved transverse groove. Within the area inclosed by these three grooves lies the heart. The lateral areae of the omostegite, known as the branchiostegites, roof in the branchial chamber.



They are formed by two flaps, right and left, which are homologous with the pleura of the abdominal somites, and like those pleura have an outer and inner lamella and a free ventral edge. The cephalostegite bears a median anterior projection, the rostrum, and to either side of the base of this rostrum an eye is visible, pedunculate as in all *Podophthalmata*.

The two first antennae (antennules), each with an outer and inner division, the exopodite and endopodite, project forwards in front of the rostrum, and have to either side the long annulated second antenna (antenna) with a pointed scale or squame, the exopodite, at its base. The appendages in relation with the mouth, the two mandibles, the two pairs of maxillae, and three anterior pairs of thoracic limbs or maxillipeds, can only be clearly identified by dissection. The third pair of maxillipeds, however, is conspicuous and lies between the first and largest pair of ambulatory thoracic limbs. Of these ambulatory thoracic limbs there are five pairs. Unlike the three pairs of maxillipeds they consist of a single stem, the endopodite, the exopodite being lost in all *Decapoda*. Each limb of the first pair is very large and is often spoken of as 'Chela,' but is perhaps better termed, with Professor Huxley, 'Forceps.' It is chiefly used in prehension not in crawling, the function of the remaining limbs. These limbs are slender and consist each of seven joints, the typical number in the higher Crustacea, and known, counting from base to tip, as coxopodite, basipodite or basis, ischiopodite, meropodite, carpopodite, propodite, and dactylopodite.

One of the coxopodites bears the genital aperture in both sexes in all *Macrura*, the group to which *Astacus* and the Lobster belong, in the Hermit Crabs and the *Arthrostraca* or Sessile-eyed Crustacea. The oviducal aperture in the *Macrura* is on the third coxopodite, and in this specimen a black bristle has been inserted into it. In the male, the aperture of the vas deferens is on the fifth coxopodite. The membrane connecting the coxopodite and basipodite is the spot at which the limb separates when the animal throws it off in consequence of either fright or injury. The basi- and ischio-podite are united in the forceps, so that the joints of this pair of limbs are reduced to six. The three first pairs of ambulatory limbs are chelate. The chela or claw is produced by the enlargement of the outer angle of the propodite into a process equal in length to the dactylopodite. Foreign objects are seized between this process and the moveable terminal joint. The chela of the Scorpion is fashioned on the same plan, but the produced angle of the propodite is in this animal the internal angle. The claw in the *Squillidae* is of a different type. The two terminal joints of the limb are elongate, the propodite is more or less grooved, and the dactylopodite bends backwards and fits into the groove. Note that the space between the bases of the thoracic limbs becomes wider and wider posteriorly, and that the sternum of the last pair

is separate and moveable; whereas the anterior sterna are calcified as a continuous whole.

The six abdominal somites are all free and connected one to another by soft intersegmental membranes. Each somite bears attached a single pair of appendages, swimmerets or pleopoda. The somite forms an unbroken ring. Its ventral region between the attachments of the limbs is the sternum, while the opposite dorsal area is the tergum. The flap projecting ventrally and laterally is the pleuron, and a small space between the socket for the limbs and the base of the pleuron is known as epimeron. A typical swimmeret, e.g. that of the fourth somite, consists of a basal protopodite bearing two processes, an inner, the endopodite, and an outer, the exopodite, both fringed with setae. There are two joints in the protopodite, a small basal coxopodite and a larger basipodite. The endopodite consists of a simple unjointed basal and a terminal jointed or annulated portion. The exopodite is similar but its parts are smaller. The last pair, often termed *par excellence* the swimmerets, are somewhat modified. The protopodite consists of a single joint. The endopodite and exopodite are expanded into broad thin plates, and the latter is divided by a transverse joint. This pair of limbs together with the telson make up the caudal fin, by means of which the animal deals a powerful stroke upon the water, and darts backwards whenever the tail is suddenly flexed. The first pair of abdominal limbs is either wanting altogether in the female, or one limb is present without the other. It is rare for both to be present. When present they are reduced to slender filaments with a minute basal joint or protopodite, and a jointed terminal portion which perhaps represents an endopodite. The two first pairs of these appendages are modified in the male for sexual purposes, and are to be seen in the two following preparations.

The English and Irish Crayfish is widely spread over the Continent. It constitutes the variety of *Astacus fluviatilis* known as *A. torrentium*, the Écrevisse à pieds blancs. There is a Crayfish which is found also widely spread over the Continent and which resembles *A. torrentium* very closely. This constitutes the variety of *A. fluviatilis* known as *A. nobilis*, the Écrevisse à pieds rouges.

The body walls or integument consist of (1) cuticular structures for the most part calcified; of (2) a single layer of ectoderm or hypoderm cells (=chitinogenous cells); and of (3) connective tissue imbedding pigment cells, bloodvessels and nerves.

The cuticular structures differ somewhat in the hard calcified and the soft intersegmental regions. The former is composed of four distinct strata: (1) a cuticle, (2) a pigmented calcified layer, (3) a non-pigmented thick layer containing a very large proportion of calcareous matter, and (4) a non-calcified softish and

thin layer. The organic substratum is chitinous. The salts are Calcium carbonate and phosphate, chiefly the former.

(1) The cuticle is structureless, resistant, and of a yellowish tint. It shows areas corresponding to the outlines of the ectoderm cells, and inside these areas slight ridges. The latter are supposed by Braun to be due to the coalescence with the young cuticle during its formation of processes similar to those of the intestinal cuticle. Both areas and ridges are more distinct in the newly formed cuticle.

(2) The pigmented layer consists of a system of fine lamellae, parallel to the surface, and alternately more and less refractile, the latter being mere lines. The lamellae are perforated by minute close-set vertical pores. The pigment lies between the more refractile lamellae in the form of bluish-black granules, sometimes furnished with processes.

(3) The third layer makes up the chief substance of the hard parts. Its refractile lamellae are thick, well calcified, and perforated by pores continuous with those of the pigmented layer. The lamellae become thinner towards the inner surface, where they merge insensibly into the fourth layer.

(4) This layer is very distinct in the Lobster. It is not recognised by Braun, but according to Vitzou it is composed of delicate non-calcified lamellae, and the innermost show impressions or outlines corresponding to the ectoderm cells. It is said to possess but few vertical pores.

There are certain variations in different regions from this typical structure. The knobs on the opposing surfaces of the chelae, certain spines, e. g. those on the posterior dorsal edge of the basal joint of the exopodite in the last pair of swimmerets, are colourless. The pigmented layer is absent, and the cuticle is greatly thickened in these places. In the articular and intersegmental membranes the cuticle is present, but the remaining layers are represented by non-calcified lamellae not distinguishable into systems. The inner wall of the branchiostegite is extremely thin, and is composed of a membrane resembling the cuticle. Areas are absent here as they are on the eye-stalk, and in the oesophagus and stomach. They are very well marked in the intestine, and each area supports 3-6 pointed ridges. The cuticular structures of the alimentary canal are composed of a cuticle and underlying lamellae, which are thickened and calcified only in the gastric ossicles. Vertical pores are found also only in the same structures. There are integumental setae or hairs and glands. The setae are either hollow or solid. The hooked setae on the inner wall of the branchiostegite are solid, and certain solid setae in the oesophagus and stomach are probably simply processes of cuticle. Hollow setae are either closed or open at the base. The former are most numerous, and their stem is beset with solid barbs, i. e. they are feathered. The latter are chiefly confined to the antennae. They are short, thick-walled, and their stems are destitute of barbs. A pore-canal pierces all the layers of the integument except the cuticle, and leads to the base of each seta. The cuticle is continuous with the base of the hair, which is generally lodged in a slight depression. The pore-canal contains a process of the ectoderm, in which nuclei are present. It is prolonged internally below the integument by the *hair-tube*. This structure has nucleated walls, and expands at its inner extremity into a bulb in which cell-outlines are distinguishable. It is about half the length of a hair, and contains a hair papilla which fills its cavity. A formation of new hairs precedes the formation of a

new cuticle, &c. The barbs, when present, are first formed, then the walls of the stem, both alike from the papilla and the walls of the tube. The tip of the hair is slightly hooked, and fits into the pore-canal of its predecessor. When the old integument is cast off the new hairs are therefore evaginated mechanically. The soft substance contained in the stem atrophies and a new hair-papilla is formed, as is believed by Braun from the walls of the tube.

The glands of the integument are (1) the glands of the roof of the branchial cavity, and (2) the cement glands found only in the female. The former were discovered by Leydig. They lie in the substance of the branchiostegite and open singly on the roof of the branchial cavity. They are tubular in structure and are but slightly lobed. The gland cells are columnar and pointed. The cement glands were discovered and investigated by Braun, and have been found by him in other *Decapoda*. In the Crayfish they extend over the anterior two-thirds of the ventral surfaces of the abdominal pleura, and thence they spread along the edges of the sterna almost continuously. They also cover about a third of the base of the exo- and endo-podite of the last pair of swimmerets. These cement glands undergo a periodical development, 5-8 weeks before the eggs are laid in November or December, and then they give the parts a whitish appearance. The glands themselves are tubular with rounded or polyhedric cells supported by a basement membrane: their ducts rarely open singly, but as a rule in groups. Lereboullet, who first observed the white appearance of the abdomen, but who failed to recognise the glands, states that their secretion coagulates on exposure to water. Shortly before oviposition the female flexes the abdomen; the cavity thus formed becomes filled with a transparent viscid fluid which glues the edges of the opposing somites together. The ova pass into the chamber, are impregnated and suspended to the setae fringing the abdominal limbs, to the abdominal sterna and intersegmental membranes by a hardened layer of the cementing fluid. It is possible that the fluid may set the spermatozoa free from the coat that binds them together.

The ectoderm is composed of a single layer of cells columnar or cubical in certain places. In the inner lamella of the branchiostegite, in the abdominal pleura, and the exo- and endo-podite of the last pair of swimmerets, places where the cuticular structures of the two surfaces are near together, the ectoderm cells are enlarged at intervals, and their bases are connected from one to the other surface by bundles of nucleated fibres which appear to be, but are probably not, continuous with the ectoderm cells themselves. A layer of ectoderm cells also intervenes between the attachment of the muscle fibres to their chitinous, so-called 'tendons,' which are processes in reality of the cuticular structures, and are moulted with them, as has been proved in the case of the tendons of the adductor mandibulae and of the muscle which adducts the dactylopodite of the forceps.

Beneath the ectoderm is a layer of fibrillated connective tissue, processes of which extend inwards, accompanied by large-celled connective tissue. The pigment cells of this layer are stellate, and contain some a yellow, others a red, pigment, together also with groups of quadrate or oblong crystals of a deep blue colour. Vessels are present, and probably nerves, as irritation of the newly formed integument causes movements on the part of the animal. The moults occur in the warm part of the year (May-September). According to Chantran, they take place (in *A. nobilis*?) as follows. The young animal is hatched in May-July. It moults once

in 10 days' time; then four times at 20-25 days' interval up to September. Three more moults in May-July following complete the first year of life. There are five in the second year, two in the third, and the animal is now becoming adult. The male is sexually mature after the 15<sup>th</sup>-17<sup>th</sup> moult, and henceforward undergoes ecdysis twice yearly. The female is sexually mature in the fourth year, and only moults once a year. The process is very probably in abeyance in old Crayfish, but it is not certain at what age they cease to grow. According to Carbonnier there are 2-3 moults in the first year, and then the process becomes annual.

When the time approaches for a moult, the old integument becomes softer and thinner, and the ectoderm cells lengthen. The gastroliths and hairs are previously formed. The first step, according to Braun, is the formation of minute processes, 2-5 to each cell, which afterwards form (?) the ridges of the areae (see *supra*). Vitzou did not observe this formation in any Decapod, but states that the inner surface of the cast-off integument is covered by a soft transparent substance. A section taken through the old and new integuments shows the presence of a new and very delicate cuticle, an outer system of continuous lamellae, and an inner system traversed by vertical lines, corresponding to the contours of the subjacent ectoderm cells. Vitzou concludes from this fact, and from the subsequent shortening of the ectoderm cells, that the lamellae are developed by a specialisation, chemical and physical, of the outer ends of these cells. And his opinion is borne out by the fact that in sections taken parallel to the surface from the carapace of Crabs polygonal areae corresponding to the ectoderm cells may always be seen. The outlines are brought more distinctly into view by treatment with silver nitrate. But in most instances, e.g. Lobster, these areae are obliterated by early fusion of the cell-walls. Tullberg appears also to be of the opinion that a conversion of the outer ends of the cells takes place during the formation of the new carapace (cf. *Zoolog. Jahresbericht*, 1882, *Arthropoda*, p. 12). Vitzou has proved the presence of glycogen in the connective tissues preparatory to and during the moult. Certain tendons, the cornea of the eye and the lining membrane with the hairs of the auditory sac, are regenerated at the same time as the rest of the integument. The endophragmal skeleton is broken up previously to being cast off (Mocquard, C. R. xcvi.). The new cuticle of the alimentary canal is formed at a comparatively late period.

The pores in the lamellae are due to the development of hair-like processes from the cell-surfaces. They are very close-set, and subsequently disappear leaving the pores (Braun).

The old integument splits in all *Macrura* across the back, between the cephalothorax and the first abdominal somite. A split is said to occur also along the limbs. The animal lies upon its side and withdraws first the cephalothorax and then the abdomen with their several appendages. In the Crabs a split occurs along a circular suture between the tergal and pleural regions of the cephalothorax. The animal retains the horizontal position, and the abdomen is freed before the cephalothorax (Vitzou).

The appendages in front of the mouth, and those which are modified into mouth-parts must be disarticulated for the purpose of examination.

The eye-stalk has a short basal and a long terminal joint. It was formerly supposed that it represents a limb, and therefore a somite. It is however derived

from a process of the procephalic lobes, and the eye is not stalked at its first appearance in those forms of Crustacea in which it is stalked in the adult when they pass through a complete series of developmental forms commencing with a *Nauplius* or *Metanauplius*. The series of true appendages appears to commence with the first antennae.

The eye itself surmounts the terminal joint. It has a convex, soft and transparent cornea marked out by faint lines into square facets. The visual structures are arranged in two layers. To each corneal facet corresponds an eye-element, i. e. a crystalline cone and a retinula. The former is derived from cells of the ectoderm of the procephalic lobes, the latter from the supra-oesophageal ganglion (?). The crystalline cone is formed from four crystalline cells. The nuclei of the cells and a small quantity of protoplasm lie immediately under the corneal facet. The outer part of the crystalline cone is less refractile than the inner part, which is long and has the shape of a four-sided pyramid terminated by a long pointed piece which has four projections fitting into the rhabdome of the retinula. The retinula is composed, as in *Palaemon*, of retinal cells grouped round a rhabdome formed of four square chitinoid rods. Each rod swells out posteriorly, is red in colour, and is marked by alternate light and dark striae which do not correspond in position in adjoining rods. The retinula cells surround the rhabdome and contain black pigment granules. A basement membrane pierced by the nerve fibres, one to each retinula, separates the retinulae from the optic ganglion. Nucleated yellow brown pigment cells intervene between the retinulae, and two (or more) black pigment cells between the crystalline cones. The ectoderm cells at the margin of the eye are elongated and filled with black pigment<sup>1</sup>.

The protopodite of the first antenna is three-jointed. The basal joint is tri-hedral and lodges the auditory sac. The exo- and endo-podite are both annulated. The number of joints in the exopodite vary, but, distal to the first eight, they bear on their ventral surfaces the olfactory setae so-called. The auditory sac is curved, and possesses delicate chitinous walls. Its aperture, which is permanently open, but is protected by numerous setae springing from its outer margin, lies in the dorsal surface of the joint. The auditory setae are arranged in two rows which meet at the closed end of the sac. The largest setae are one-fiftieth of an inch long. They are hollow and are moveably attached to the wall of the sac. This attachment is by a membrane delicate on one side, stout on the other forming the 'tooth' of Hensen. A narrow plate, the 'ligula' of Hensen, is developed in the shaft of the setae, on the side opposite the tooth. The shaft with the exception of the ligula is beset with five solid barbs. The nerve fibre is furnished with a ganglion cell close to its termination, which is fine and delicate, and according to Hensen attached to the ligula. The otoliths are numerous and irregular in shape. According to Hensen's observations on *Palaemon antennarius*, these otoliths are foreign particles collected by the forceps and scattered over the base of the first antenna, whence some find their way into the sac. A specimen which moulted and was confined in a basin of

<sup>1</sup> For the terms descriptive of the structures found in the eyes of Arthropoda see the general description of that phylum. The Crayfish's eye would be described, using the terms there given, as polymeniscous, diplostichous, retinulate, furnished with vitellae, and perhaps also as exochromic. But the origin of the pigment cells has not been exactly ascertained. See Lankester and Bourne, Q. J. M. xxiii. 1883, on Eyes of *Scorpio* and *Limulus*.

filtered sea-water was supplied with crystals of uric acid. Whilst the cast-off auditory sac contained the usual otoliths, the new sac contained a large proportion of uric acid crystals. The foreign bodies thus obtained are kept *in situ* apparently by a gelatinous substance. When the auditory sac is a closed one, there are either no otoliths (*Brachyura*), or e.g. in *Mysis*, there is one otolith in the shape of a rounded laminate body, apparently a secretion.

The olfactory hairs occur 2-3 on the first two joints that possess them, the subsequent joints having an anterior and posterior row with 7-8 hairs in a row. They are about  $\frac{1}{300}$  of an inch long, 'shaped like a spatula with a rounded handle and somewhat flattened blade' (Huxley). They are two-jointed, and contain a soft granular tissue. Jourdain, who has recently investigated these structures in various Crustaceans, states that a small hyaline body projects from the free extremity and that a nerve fibre is traceable to the base of each hair, and may sometimes be seen to have a swelling (? ganglion cell). He terms the hairs 'poils à batonnet,' and divides them into 'poils à batonnet cylindriques et à batonnet stipités.' The former are long and cylindrical and usually many-jointed, the latter are usually three-jointed and somewhat fusiform. According to him the Crayfish possesses the cylindrical variety, but the hairs are short.

The protopodite of the second antenna is two-jointed. The basal joint bears a ventral tubercle, to the inner side of which is the aperture of the green gland. The second joint is divisible into two parts more or less moveable, and bears an exopodite in the shape of a scale or 'squame.' The endopodite is long and many-jointed.

The mandible or first appendage of the mouth consists of four joints. The basal (= coxopodite) is long and forms a three-sided pyramid. The base of the pyramid projects inwards over the sides of the mouth. The oral side of the base bears two stout obscurely separate teeth; the posterior side and outer angle form a sharp ridge with several teeth, but the anterior side is hollowed out, the hollow invading the centre of the base. The other three joints are small, the terminal dilated and fringed with setae. They are articulated to the anterior side of the pyramid not far from the base. They constitute the 'palp,' which is not an exopodite, a structure rarely present in the mandible of the adult, as e.g. in some *Copepoda*. In the larval form known as *Zoea*, the first *Zoea*-stage has no palp to the mandible. It sprouts out in later stages. In the *Nauplius* the mandible has the typical biramose character, but when *Penaeus*, the only Decapod with a *Nauplius* stage changes to the *Zoea*, the mandible is reduced to its basal portion, and the palp is evolved at a later period. The Phyllopod mandible is similarly reduced, and never gains a palp. But the temporary suppression of a limb or part of a limb is by no means an uncommon phenomenon in the higher Crustacea (cf. the account in Balfour's Comparative Embryology, i., of the evolution of *Sergestes*, p. 398, *Phyllosoma*, p. 396, and *Squilla*, pp. 402-3).

The other appendages of the mouth are best taken in reverse order. The most perfect is the *third maxilliped*. The protopodite is divisible into a coxopodite which bears a podobranchia and coxopoditic setae (cf. p. 182) and a basipodite. This joint, as in the forceps, is continuous with the basal joint of the endopodite which is divisible into an ischiopodite, meropodite, carpopodite, propodite and terminal dactylopodite. The exopodite or palp is short and articulates with the

basipodite. It is slender, and has a long basal joint and a many-jointed filament. The *second maxilliped* has a smaller and softer endopodite, and a larger exopodite. There is a podobranch but no coxopoditic setae. The basipodite is distinct, and the meropodite very long. The *first maxilliped* has the coxopodite and basipodite imperfectly separate and expanded into thin setose plates. The endopodite is short and two-jointed; the exopodite large, with a much elongated basal joint. The podobranch is reduced to the stem and lamina, and is known as the flagellum or epipodite of Milne-Edwards. The three pairs of maxillipeds belong to the thorax.

The *second maxilla* has a very thin lamellate coxopodite and basipodite, each partially subdivided by a fissure. The endopodite is small and simple. The exopodite forms a large plate, the *scaphognathite*, which is kept in perpetual motion and bales the water out of the branchial chamber, into which it runs posteriorly and inferiorly. For its homology see Claus, *Untersuchungen zur Erforschung der genealogischen Grundlage des Crustaceen-systems*, Wien, 1876, p. 42. The *first maxilla* has two thin simple and foliaceous expansions. The first represents the coxopodite; the second is usually termed basipodite, but the homology is doubtful. The endopodite is extremely reduced, and the exopodite absent. It is present in *Euphausia* and in the *Zoaea* of *Penaeus* up to a certain stage, and then atrophies.

The sides of the mouth are formed by a soft lip. In front it is overhung by a leaf-like projection, the labrum, attached basally to the *epistoma* or broad triangular calcified area in front of the mouth and extending forwards to the base of the antennae. The sides of the mouth are overhung by the bases of the mandibles, and behind the latter are two small soft lobes united by the posterior margin of the mouth. These lobes are the paragnatha, metastoma, or lower lip. Neither labrum nor metastoma represent appendages in development, but it is possible that the latter represents a dissociated portion of the first maxilla (Claus, p. 15, *Neue Beiträge, &c., infra*). The ventral region between the bases of the mouth parts, and again between the bases of the first and second antennae becomes calcified, forming a series of sterna. The antennary sternum constitutes the epistoma.

The rostrum in *Nebalia* is a moveable process. In *Squilla* it is jointed to the fore-edge of the carapace and moves with the somite of the first antenna. In *Nebalia* it appears to belong rather to the region of the first than to that of the second antenna, to which Professor Huxley allocates it.

The ventral and basal lateral parts of the sternal wall of the mouth-parts and thorax give origin to a number of internal cuticular folds or apodemata. These apodemata constitute the endophragmal skeleton and give attachment to muscles as well as protection to the thoracic portion of the nerve-chain and the sternal blood-sinus. Their arrangement is too complicated to be explained without the aid of figures, and the student may consult Professor Huxley on the Crayfish, p. 157, where will be found both description and figures.

There remain for examination the two first pairs of abdominal appendages in the male and the telson.

The first appendage is unjointed and cylindrical. Its apex forms a plate slightly bifid. The sides of the plate are rolled upon themselves, the anterior half surrounding the posterior, giving rise to a canal open at each end. It is not certain what parts of the typical limb are represented in this appendage.



The second appendage has a protopodite divisible into a coxopodite and long basipodite. The endopodite consists of a large basal piece and terminal jointed filament. The apex of the basal piece is prolonged upwards as a plate to the inner side of the filament, and the inner edge of the plate is rolled upon itself. The exopodite is present and has the usual structure. Both pairs of appendages are used for the transmission of sperm : see p. 186.

Both the male and female alike possess no appendages to the first abdominal segment in the *Parastacidae*—the Crayfishes of the S. Hemisphere.

The telson is a plate moveably articulated to the last somite of the abdomen. It is divided in nearly all the *Potamobiidae* or Crayfishes of the N. Hemisphere, but not in the *Parastacidae*, by a transverse suture, so that the posterior half is moveable upon the anterior half. The anus is situated on the ventral surface of the basal portion. There is some question as to what the telson represents. Hartog (British Assoc. Reports, 1882, p. 575) believes that it represents the last somite of the *Nauplius*—a post-anal plate united to the furcae anales, the latter representing paired terminal outgrowths elsewhere developed into limbs by the formation of joints. He points out that in the *Copepoda*—in his view the primitive Crustacean group—the anus is a terminal dorsal slit; that the tergum of the last somite forms a supra-anal plate, whilst the furcae project one on either side of the anus. Supposing the supra-anal plate to become adnate to the furcae, the anus becomes first terminal and ventral, and finally by growth of the plate ventral. He homologises two setose knobs projecting at the sides of the telson in *Astacus* with the furcae. It has been pointed out by Claus (Untersuchungen, &c. *supra*, p. 12) that in the *Protozoaea*-stage of *Penaeus* the anus is terminal between two furcal processes. In its youngest *Zoaea* a short transverse bridge (=supra-anal plate of *Copepoda*?) connects the furcae dorsally above the anus. During subsequent growth this bridge enlarges, the anus becomes more and more ventral, and the furcae are lost, becoming the two posterior setigerous processes of a broad bilobed terminal plate. In a young *Phyllosoma* (cf. Claus, op. cit. p. 51) the same facts may be observed, but the processes become obsolete, the setae alone persisting at the outer angles. There is much variety in the shape of the last somite of the abdomen in Crustacean larval forms. It is very frequently a broad bilobed plate, more rarely, as in the young *Astacus* itself, a simple plate. In both cases the anus is ventral. Claus concludes that the telson represents the terminal furcal somite of the abdomen in *Phyllopoda*. It is possible that it may represent a *region* rather than a *somite*. For in *Nebalia* (Claus, Z. W. Z. xxii. 1872, p. 329) there are two somites behind the sixth abdominal somite, the last bearing a pair of furcae and the anus, and in most *Phyllopoda* the abdomen contains a large number of somites.

When *Astacus* quits the egg it only differs from the adult in certain points summarised here from Professor Huxley's account. The cephalothorax is relatively large and convex in shape; the short rostrum is bent down between the eyes; the thoracic sterna are relatively wide; the chelae of the forceps are slender, and the tips of all the chelae are strongly incurved, the young Crayfish attaching itself by those of the forceps to the empty egg-case: the dactylopodites of the two last pairs of thoracic limbs are hooklike: the first pair of abdominal appendages is undeveloped: the sixth is included within the telson, which is a simple broad oval plate usually notched in the middle of its hinder margin. Setae are few in number and are mostly uncalcified prolongations of the cuticle not sunk in pits, and devoid

of barbs. It is noteworthy that at the stage of development in which the first and second antennae and mandibles are present as rudiments, and which therefore corresponds to the *Nauplius* of other Crustaceans, a cuticle is formed and then moulted. A similar phenomenon occurs in other cases, e. g. in *Nebalia*, in *Mysis* within the incubatory pouch of the mother, and has been noted in the *Isopoda*, e. g. *Asellus*. It is perhaps a general phenomenon in Crustacea with a shortened developmental history. The majority of *Decapoda* differ from *Astacus* in having a well-marked metamorphosis. The prawn *Penaeus* is hatched as a *Nauplius*, most other *Decapoda* as a *Zoea*. The Lobster (*Homarus*), placed by M. Milne Edwards but not by Faxon among the *Astacidae*, starts in the *Mysis* stage, i. e. with the thoracic feet biramose and natatory. One or two fresh water *Decapoda* have a shortened metamorphosis: one or two Land Crabs none at all.

Much has been written as to the ancestral character of the *Nauplius* and *Zoea*. The subject will be found discussed in Balfour's Comparative Embryology, i. p. 417, to which must be added some recent remarks of Claus in his Beiträge, &c., Arb. Zool. Inst. Wien. vi. 1885, p. 91. It is at present impossible to say how the *Nauplius* has been derived, and what are its affinities. It is apparently not a simple organism, for in the *Copepoda Natantia* its body is divided into three somites, but the segmentation disappears before hatching. Of its three pairs of appendages the first is uniramous and for the most part sensory in function, the second and third are biramous and natatory. The three pairs correspond to the first and second antennae and mandibles of the adult.

It is generally agreed that the second antennae are post-oral appendages. They are innervated from a post-oral ganglion in the *Nauplius*, and in the adult *Apus*, *Limnetis*, *Branchipus* among *Phyllopoda*. *Daphnia* much resembles *Branchipus*. It may be added that in the *Nauplius* they lie at the sides of the mouth, and as a rule develop a masticatory hook.

The first antennae on the contrary are generally held to be prae-oral appendages. Claus in his Beiträge (*supra*) points out (1) that they retain their uniramous character in *Entomostraca*, whilst in *Malacostraca* they become in most instances secondarily biramous; (2) that they are *sensory* in function; (3) that they arise from a region of the head morphologically unlike (as in Chaetopoda) the somites of the body. He appears to regard them (1) as limbs, and (2) at the same time to compare them with the prae-oral tentacles of Chaetopoda and the antennae of Myriapoda and Insecta. As to this second point however it may be remarked that they do not originate from the procephalic lobes as do the antennae of Myriapoda and Insecta.

Ray Lankester first drew attention to the innervation of the first and second antennae in *Apus* (Q. J. M. xxi. 1881), and Pelsener (Q. J. M. xxv. 1885) has investigated the nervous structures microscopically. He finds that the ganglia of the first antennae are contained in the supra-oesophageal ganglion, but are separate from the mass of ganglion cells supplying the eyes. They are connected by a transverse commissure. The nerve to the first antenna runs backwards accompanying the oesophageal commissure for some distance, as it does in *Limnetis*. He says that in *Branchipus* and *Daphnia* the corresponding nerve arises from a group of cells distinct from the rest of the supra-oesophageal ganglion. It may be observed that Rathke states that in the embryo Crayfish first and second antennae alike are supplied from a ganglionic rudiment distinct from an anterior rudiment apparently.

supplying the eyes. The natural conclusion is that the supra-oesophageal ganglion consists of two distinct parts in *Apus*, &c., i.e. of a true prae-oral ganglion supplying the eyes, and a second pair of ganglia shifted forwards supplying the first antennae. The shift forwards explains the backward course of the nerves. Whilst in *Apus*, &c., the second antennae have a post-orally placed ganglion, in higher Crustacea this ganglion also has shifted forwards; but there is evidence to show (embryo *Astacus*) that there is a distinct ganglion, supplying in this instance both first and second antennae, which fuses with an anterior rudiment to form the supra-oesophageal ganglion of the adult. It seems probable therefore that the first antennae, like the second, are in reality primitively post-oral appendages, or at any rate are homologous with the limbs borne by the post-oral somites of the body.

The *Arachnida* afford us an instance of a group of Arthropoda in which all the appendages are embryonically post-oral. The first pair of appendages however is invariably shifted in front of the mouth during growth. In *Scorpio* and *Limulus* at least their nerves are said not to come from the supra-oesophageal mass but from the commissures. The ganglia however have not been investigated microscopically. It is possible that these animals retain an archi-cerebrum, i.e. a supra-oesophageal ganglion not fused with other ganglia placed posteriorly to it. The Crustacea, on the contrary, evidently possess a syncerebrum, i.e. a supra-oesophageal ganglion fused with one or two posteriorly placed ganglia.

The following table shows in parallel columns the post-oral somites and their appendages in the Crustacea, Arachnida, Myriapoda, and Insecta. The antennae of the two latter classes are not included as being apparently processes of the procephalic lobes. The post-oral appendages of Crustacea and Arachnida which become prae-oral are printed in a different type, and the first antennae of the former Class are marked with a note of interrogation as being somewhat doubtfully homologous with the succeeding appendages.

See, for remarks on the descent of Arthropoda, Balfour, Comparative Embryology, i. p. 451; for a discussion on the relations of the Arachnida and Crustacea, Kingsley, Notes on the Embryology of *Limulus*, Q. J. M. xxv. 1885, p. 556.

TABLE OF POST-ORAL SOMITES AND THEIR APPENDAGES  
IN ARTHROPODA.

Number of Segment.	Crustacea.	Arachnida.	Myriapoda.	Insecta.
I.	<i>First Antenna</i> (?) uniramose in <i>Nauplius</i> and adult <i>Entomostraca</i> , secondarily biramose in <i>Decapoda</i> , &c.	<i>Chelicerae</i> .	Mandible: with a small palp in <i>Chilopoda</i> : non-palpite in <i>Diplopoda</i> .	Mandible: non-palpite.
II.	<i>Second Antenna</i> : biramose in <i>Nauplius</i> as a rule, but uniramose in many adult forms.	Chelae in <i>Scorpio</i> and <i>Thelyphonus</i> . Pedipalpi in <i>Spiders</i> .	Maxilla: palpite in <i>Chilopoda</i> : 4-lobed plate in some adult <i>Diplopoda</i> , but simple appendage in embryo.	Maxilla: palpite.

Number of Segment.	Crustacea.	Arachnida.	Myriapoda.	Insecta.
III.	Mandible : biramous in <i>Nauplius</i> : not palpate in <i>Zoea</i> , nor in <i>Phyllo-poda</i> , terrestrial <i>Isopoda</i> and <i>Amphipoda</i> , nor <i>Cumacea</i> , &c. A 3-articulate 'palp' in adult <i>Decapoda</i> .	1st pair of limbs bearing outer element of so-called 'labium' in Scorpion.	Limb-like with basal parts in contact, <i>Chilopoda</i> : short, 4-jointed with claw in <i>Iulus</i> ( <i>Diplopoda</i> ), in ♂ of some species hook-like limb.	Labium : palpate.
IV.	1st Maxilla.	2nd pair of limbs bearing inner element of 'labium' in Scorpion.	Poison claws of <i>Chilopoda</i> : 1st (single) pair of 5-jointed limbs with claw in <i>Iulus</i> ( <i>Diplopoda</i> ).	1st pair of limbs : prothorax.
V.	2nd Maxilla : aborted in adult <i>Cladocera</i> .	3rd pair of limbs.	1st pair of limbs in <i>Chilopoda</i> sometimes lost : apodous in <i>Iulus</i> : with ♂ and ♀ genital apertures.	2nd pair of limbs : mesothorax.
VI.	1st pair of thoracic limbs, <i>Phyllo-poda</i> , <i>Nebalia</i> , <i>Schizopoda</i> . Maxilliped in many forms.	4th pair of limbs.	2nd pair of limbs in <i>Chilopoda</i> : single pair in <i>Iulus</i> .	3rd pair of limbs : metathorax.
VII.	1st pair of limbs in <i>Arthrostraca</i> . 2nd pair of maxillipeds in <i>Decapoda</i> .	Genital operculum in Scorpion and <i>Limulus</i> . An embryonic limb in Scorpion and Spider : somite included in abdomen of latter.	1st double pair of limbs in <i>Iulus</i> . 'Due probably to an imperfect division of the primitive segments.' Balfour, Comp. Embryology, i. p. 324.	1st abdominal somite : rudiments of embryonic limbs on this and 9 succeeding somites in <i>Sphinx populi</i> .
VIII.	3rd pair of maxillipeds in <i>Decapoda</i> . [Last somite in <i>Ostracoda</i> .]	Pectines of Scorpion. 2nd pair of embryonic limbs in Scorpion and Spider.	Do. in <i>Iulus</i> .	2nd do. : pair of cylindrical appendages, <i>Machilis</i> ( <i>Thysanuran</i> ), and on 8 succeeding somites. 1st pair of prolegs in many Tenthredinid larvae.
IX.	1st ambulatory limb in <i>Decapoda</i> or Forceps. 4th pair of maxillipeds in <i>Squilla</i> .	1st pulmoniferous somite in Scorpion. 3rd pair of embryonic limbs in do., and do.	Copulatory organ and single pair of limbs in ♂ <i>Iulus</i> : double pair in ♀.	3rd do. : 1st pair of prolegs in many Lepidopteran larvae.

Number of Segment.	Crustacea.	Arachnida.	Myriapoda.	Insecta.
X.	2nd ambulatory limb in <i>Decapoda</i> . 5th pair of maxillipeds in <i>Squilla</i> .	2nd pulmoniferous somite in Scorpion. 4th pair of embryonic limbs in Scorpion and Spider.	Double pair of limbs in both ♂ and ♀, <i>Iulus</i> : and last somite in <i>Pauropus</i> ( <i>Diplopoda</i> ).	4th abdominal somite.
XI.	3rd ambulatory limb in <i>Decapoda</i> . 1st in <i>Squilla</i> .	3rd do., Scorpion, and 5th embryonic limb in do.: limbless somite in embryo Spider.		5th do.
XII.	4th do., in <i>Decapoda</i> . Lost in <i>Lucifer</i> .	4th do. in Scorpion, and 6th embryonic limb in do.: limbless somite in embryo Spider.		6th do.
XIII.	5th do., in <i>Decapoda</i> . Lost in <i>Lucifer</i> .	Somite without lungs in Scorpion. Limbless somite in embryo Scorpion and Spider. Embryonic somite in <i>Limulus</i> .		7th do.: no proleg in caterpillar nor in two next somites.
XIV.	1st abdominal somite with pleopod in a Malacostracan. [Last somite in <i>Daphnia</i> ( <i>Cladocera</i> ).]	1st caudal somite in Scorpion. Limbless somite in embryo Spider. Embryonic somite in <i>Limulus</i> .		8th do.: 1st pair of ♀ genital processes. ♀ genital aperture. Anal somite, some <i>Diptera</i> .
XV.	2nd do. [Last somite in a typical <i>Copepod</i> .]	2nd do., Scorpion. Limbless somite in embryo Spider. Telson in <i>Limulus</i> : Anus in front of it.	Last somite in <i>Lithobius</i> and <i>Scutigera</i> ( <i>Chilopoda</i> ).	9th do.: 2nd pair of ♀ genital processes. Anal somite, some <i>Diptera</i> .
XVI.	3rd do.	3rd do., Scorpion. Azygos terminal piece in embryo Spider.	The total number of somites may be very great in some <i>Iulidae</i> : and in the <i>Geophilidae</i> ( <i>Chilopoda</i> ) may amount to more than 200.	10th do.: anal somite in <i>Thysanura</i> , <i>Coleoptera</i> , and <i>Lepidoptera</i> . Anal proleg in caterpillar and Tenthredinid larva. 3 processes in <i>Machilis</i> .
XVII.	4th do.	4th do., Scorpion.		11th do.: anal somite in many <i>Orthoptera</i> , &c. ? Cerci anales = limbs.

Number of Segment.	Crustacea.	Arachnida.	Myriapoda.	Insecta.
XVIII.	5th abdominal somite with pleopod in a Malacostracan.	5th caudal somite in Scorpion. Anus behind it.		
XIX.	6th do.	Telson in Scorpion. A jointed filament in <i>Thelyphonus</i> .		
XX.	Telson. 7th abdominal somite, <i>Nebalia</i> .			
XXI.	8th abdominal somite in <i>Nebalia</i> , but there are only 6 abdominal ganglia in this animal. In <i>Apus numidicus</i> ( <i>Phyllopod</i> ) the total number of somites is said to reach 46.			

The following notes of the differences observable between the Lobster (*Homarus*) and the Crayfish, with which it is sometimes grouped in the family *Astacidae*, may be useful to the student.

The squame of the second antenna is relatively small ; the fifth thoracic sternum is fixed ; the first abdominal appendage in the male is two-jointed, and the terminal joint is lamellate but only curved to form a gutter, not rolled up as in *Astacus* ; the second abdominal appendage in the same sex has a small plate to represent the rolled up lamina of *Astacus* : in the female the first abdominal somite bears appendages well developed ; the telson has no transverse suture. The number of podobranchiae is as in *Astacus*, but the stem is completely split into a plume and lamina, and the branchial filaments are stiff and close set ; the single arthrobranch of the second maxilliped in *Astacus* is absent, and the total number of these organs is hence reduced to ten, but there are four pleurobranchiae. The infra-oesophageal ganglion is small relatively to the thoracic ganglia, and more distinctly constricted at the sides than in *Astacus*. The caecum of the mesenteron is small and bilobed : the caeca of the liver are short and the anterior portion of the gland large. The first part of the intestine is smooth, the terminal portion plicated, and at the junction of the two parts there is a dorsal caecum as in *Amphipoda* and most *Decapoda*. The testicular lobes are long and only joined by a commissure, and the vasa deferentia are shortened. The largest Gregarine known, *Porospora gigantea*, inhabits the alimentary canal : see Schneider, A. Z. Expt. iv. 1875 ; E. van Beneden Q. J. M. xii. 1872.

The Lobster quits the egg in the *Mysis*-stage, cf. Rathke, A. N. H., 1841 ; Sars, Vidensk. Selsk Forh. Christiana, 1874 ; Smith, Trans. Connecticut Acad. of Arts and Sciences, 1873.

The anatomy of a Crab (*Callinectes*) and its developmental forms or *Zoea* is given in W. K. Brooks's Handbook of Invertebrate Zoology, Boston, 1882, p. 168 et seqq. For the *Zoea* of the *Brachyura*, see also Balfour, Comp. Embryology, i. p. 398.

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*Organs of Special Sense. Eye*. Grenacher, Sehorgane der Arthropoden, Göttingen, 1879; Carrière, Sehorgane der Thiere, München und Leipzig, 1885. *Copepodan (azygos) eye*. Hartog, A. N. H. (5), x. 1882. *Functions of faceted eye*. Exner, Biol. Centralbl. i. 1881-2; Notthaft, Senckenberg, Abhandl. xii. 1881. *Regeneration of Eyes in Astacus*. Chantran, C. R. lxxvi. 1873. *Ear*. Hensen, Z. W. Z. xiii. 1863. *Olfactory hairs*. Jourdain, Journal de l'Anatomie, xvii. 1881; Leydig, Müller's Archiv (Archiv f. Anat. u. Phys.), 1860.

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### 33. COMMON CRAYFISH (*Astacus fluviatilis*), MALE,

Dissected so as to show the nervous, circulatory and digestive systems *in situ*, and in the relations they hold to each other and to the external body walls.

THE animal has been bisected longitudinally and the left half of the body removed together with its appendages, their muscles, the left lobes of the liver, and green gland. The series of nerve ganglia and connecting

commissures lies above the sternal elements of the various somites, the heart beneath the central area of the omostegite, whilst the reproductive and digestive organs occupy a position midway. The appendages of the right side are left *in situ*. The modified first and second pairs of abdominal limbs show that the specimen belongs to the male sex.

The supra-oesophageal and twelve post-oral ganglia, six thoracic and six abdominal, are seen in profile. The great length of the commissures between the first-named ganglion and the first of the post-oral series or infra-oesophageal ganglion, whence the six pairs of appendages connected with the mouth are innervated, may be noted as corresponding with the elongated antennary sternum. In the abdominal series a slip of blue paper has been placed beneath the commissures uniting the fifth to the sixth ganglion. A white bristle has been introduced through the mouth into the oesophagus and stomach. This latter organ is large and extends forwards behind the eyes, but its anterior wall has been displaced a little backwards. It is divisible into a larger cardiac and a smaller pyloric portion, the pyloric situate just in front of a piece of blue paper placed under the hepatic artery. The lower edges of the liver lobes of the right side may be seen below the posterior cardiac region and extending backwards below the commencement of the intestine. The aperture of the common duct of the left liver lobes lies at the apparent termination of the hepatic artery, a projection in front of it marking the so-called pylorus. The part of the digestive tract into which the liver ducts open constitutes the mesenteron, and represents the archenteron of the embryo. The oesophagus and stomach are differentiations of the stomodaeum, whilst the intestine, which runs straight to the anus on the ventral surface of the telson, and is of great relative length, is formed from the proctodaeum of the embryo. The mesenteron and its appended glands are lined by endoderm, the oesophagus, stomach and intestine by ectoderm which secretes a chitinous cuticle. This cuticle is cast by the animal whenever it moults.

The heart is a rounded body lying below the cardiac area of the omostegite. Of the arteries, to which it gives origin, the left hepatic passes obliquely downwards in front to gain the liver lobes, the sternal artery obliquely downwards behind to pass between the commissures uniting the third and fourth thoracic ganglia. Both these arteries have pieces of blue paper placed beneath them. Another piece of blue paper has been placed under the superior abdominal artery in the region of the fourth abdominal tergum. The left anterior lobe of the testis lies below and in front of the heart: the posterior azygos lobe beneath and behind it, whilst numerous coils of the right vas deferens come into view between the testis and intestine. The powerful and complex flexor muscle of the abdomen may be seen below the intestine and above the nerve chain extending into the thorax to be attached to the endophragmal skeleton (*see*



*ante*, p. 170) as far forwards as the oesophagus. It is by means of this muscle, by which the abdomen is suddenly flexed, that the animal executes its rapid backward darts through the water. The ambulatory thoracic limbs are employed for the slower movements of crawling; and the muscles that move these limbs on the right side may be seen passing through the intervals of the endophragmal skeleton from their origins upon the epimera displayed in Preparation 36.

### 34. COMMON CRAYFISH (*Astacus fluviatilis*),

Dissected to show the heart and the origins of the chief vessels *in situ*.

THE cardiac region of the omostegite and the adjoining region of the cephalostegite have been removed, as well as the tergal regions of the two first abdominal somites. The walls of an arterial pericardial sinus which surrounds the heart have also been removed, and that organ with the origins of the principal vessels has been consequently exposed. The heart is hexagonal in outline and compressed. Five arteries spring from its anterior border. One in the middle line supplies the eyes and first antennae. Two others, one on each side this median artery, pass obliquely forward to the second antennae. And finally, two hepatic arteries, not seen here, spring one from each outer and inferior angle and pass downwards between the anterior testicular lobes and the intestine to the liver. One of them is shown in Prep. 33. A single dilated trunk takes origin from the posterior border of the heart. It divides at once into two branches. One of these, the superior abdominal artery, lies immediately above the intestine in the median dorsal line. A slip of blue paper has been placed under it. The other, the sternal artery, seen in Prep. 33, passes between the commissures uniting the third and fourth thoracic ganglia. It then divides, and one division passes forwards, the other backwards beneath the nerve-cord as the inferior abdominal artery. The muscular walls of the heart are pierced by six main valved inlets, which permit blood to enter but not to pass back. Two of these inlets are on the dorsal surface and are visible in this preparation about the middle region. Two other inlets are ventral, and the remaining two are placed, one on the right, the other on the left side. In addition to these main inlets, Dezsó has described others of small size, four pairs on the dorsal and two pairs on the ventral surface. Six elastic alae cordis connect the heart to the non-muscular pericardium. Their main function is probably to antagonise the contractions of the heart itself. They may also serve to suspend it in the sinus, but the arteries are probably, in this as in other animals, the chief means by which it is kept in position.

The polygonal aspect of the Decapod heart and the presence of

arteries serve to distinguish it from the similarly unilocular and non-vasiform heart of some *Entomostraca*, while both these forms are in turn distinguished by their compressed shape from the vasiform structure found in *Squilla* and most *Arthrostraca* as well as in other classes of Arthropoda.

The tissue of the heart consists, according to Dezso, of muscle cells. The striated substance is present only on one side of the cells as in Nematoda, and the cells are so grouped that their striated sides form the axis of a cord of cells. The nuclei are numerous and nucleolated. This histological condition must be regarded as a persistent state of what is an embryological phase in the development of muscular tissue in Arthropoda. The cords formed by the cells cross in all directions, and the heart-walls are spongy in texture. The inlets 'represent blood-spaces in the walls leading into a ventricular cavity.' The pericardium is non-muscular. It lies upon the heart, and consists of elastic connective tissue with a few scattered nuclei, and an outer layer of ordinary connective tissue. Bipolar ganglion cells, each in its own capsule, are to be found in the posterior half of the dorsal surface of the heart, frequently in groups of three or more. The muscular tissue of the heart contains myohaematin, as does that of the Lobster and the Crab, according to MacMunn.

A medium-sized artery possesses three coats—a structureless intima, a middle coat composed of circular fibres, probably of connective tissue as they are not striated, and a homogeneous adventitia with numerous nuclei, regularly arranged. The intima disappears (?) in the smaller vessels. The middle coat is best marked in the large and medium-sized vessels, while the adventitia increases in thickness, and becomes both lamellate and fibrillate in the medium-sized vessels. Many of the arteries possess a sheath of cellular connective tissue, which is best seen in the superior abdominal artery.

The capillary system is well developed, and forms networks: one of the easiest to demonstrate is the one on the surface of the supra-oesophageal ganglion. The capillary has a structureless wall with an oval nucleus here and there. Its cavity is very narrow hardly admitting a blood-corpuscle.

The venous channels, according to Haeckel, have distinct walls composed of a thin plate of homogeneous nucleated connective tissue intimately united with the connective tissue coats of the various organs. They are always, according to him, well-defined channels, not irregular spaces. However this may be, they must, strictly speaking, be considered as constituting the peri-visceral cavity, rather than a system of vessels independent of that cavity. The venous space in the sternal canal is connected to the spaces which lead to the branchiae. The efferent branchial canals are distinct vessels, six in number, which ascend the walls of the thorax and open with widened apertures into the pericardial sinus.

The blood-spaces of the branchiae are inter-cellular spaces, see p. 183. It is possible that, as in *Phyllosoma*, &c., the blood circulating in the branchiostegites may return to the heart without passing through the branchiae.

The blood-corpuscles are colourless and amoeboid. The plasma contains haemocyanin (p. 112), and a red lutein, or lipochrome known as tetronerythrin, both of which are found also in the blood of other *Crustacea*, and the former in that

of many other animals as well. Tetronerythin is a pigment commonly distributed in the animal kingdom and is found in various tissues, e.g. in the integument and muscles. It has been supposed by Merejkowski to have a respiratory function, but this is doubtful. The yellowish-red granules, seen sometimes in the blood-corpuscles of Decapod *Crustacea*, are perhaps formed of it.

*Heart.* Bela Dezso, Z. A. i. 1878.

*Circulatory System.* *Astacus*, Krohn, Isis, 1834. *Stomatopoda, Schizopoda and Decapoda.* Claus, Arb. Zool. Inst. Wien, v. 1884.

*Structure of vessels, &c.* Haeckel, Müller's Archiv (Archiv f. Anat. und Phys.), 1857.

*Blood of Decapod Crustacea.* Halliburton, Journal of Physiology, vi. 1885. *Haemocyanin and Tetronerythin*, *ibid.* On the latter see also Merejkowski, Bull. Soc. Zool. France, viii. *Haemoglobin in Crustacea*, see lists in Halliburton, *op. cit.*; also van Beneden on *Lernanthropus, Clavella, and Congericola*. Bull. Acad. Roy. Sc. Belgique (2), 49, 1880; Id. Z. A. iii. 1880. *Myohaematin*. MacMunn, P. R. S. xxxix. 1885.

### 35. COMMON CRAYFISH (*Astacus fluviatilis*),

Dissected so as to show its digestive, reproductive, and respiratory systems *in situ*.

THE greater part of the tergal region of all the segments of the body has been removed, together with the heart and its vessels and in the abdomen the thin stratum of extensor muscles. The stomach occupies a central position anteriorly, and is clearly divisible into a wider cardiac portion in front and a narrower pyloric portion behind. An arcuate plate, the 'cardiac ossicle,' crosses the cardiac portion at the point of greatest width, and receives the insertion of the major part of the anterior gastric muscles which spring from the base of the rostrum. A pyloric ossicle crosses the pyloric portion of the stomach in a similar manner, and gives attachment to the posterior gastric muscles which take origin posteriorly from the carapace. The other stomachal ossicles can only be studied when the stomach is properly opened. To the right side of the pyloric portion of the stomach is seen the end of the *adductor mandibulae* muscle separated from its attachment to the carapace; and behind it, as well as to either side, are the two lobes of the liver. On the left side, in front of the liver, is to be seen a small portion of the sac of the green gland. The paired anterior lobes of the testis lie in the middle line between the liver lobes. The azygos posterior lobe overlies the intestine. At the spot where these three lobes unite the right and left vas deferens take origin as slender tubes, the calibre of which rapidly widens. They are disposed in many convolutions which intrude some way into the abdominal cavity before they turn downwards, to open on the coxopodites of the last pair of thoracic limbs. The intestine takes a

straight course, as in all Crustacea, to the anus. The branchial cavity is just exposed on the left side, but largely on the right by the removal of a great part of the branchiostegite and of the united thoracic epimera which separate the viscera from the branchial cavity on the inner side. The branchiae are seen lying in the cavity thus exposed. They may be distinguished as podo-, arthro-, and pleuro-branchiae. Podobranchiae are attached one to each coxopodite from the second maxilliped to the fourth thoracic limb inclusive. The arthro-branchiae are divisible into an anterior and posterior, or external and internal set, and they are attached to the membranes uniting the coxopodites to the body. The second maxilliped bears an anterior arthrobranch only, the third maxilliped and the thoracic limbs to the fourth inclusive possess both sets. The fifth thoracic limb bears no branchiae, but a pleuro-branch is attached to the epimeron of its somite. There are also two rudimentary pleuro-branches, one on the third, another on the fourth, epimeral regions. The number and arrangement of the branchiae varies much among the *Decapoda*.

A podobranchia consists of a broad *basal* portion convex posteriorly and inferiorly, beset with setae and articulated to a coxopodite. The *stem* of the branchia bends at right angles to this base and divides into an *apical plume* and a *lamina*. The free extremity of the plume is simple and filiform. At its base it gives origin to a number of cylindrical branchial filaments. Similar filaments spring also from the outer and anterior surfaces of the stem itself. The lamina originates about the middle of the stem. It is folded upon itself. The edge of the fold looks forwards, and the leaves of the fold are one external, the other internal, the latter extending downwards towards the base of the stem to a distance greater than the former. The folded edge of one podobranchia fits into the space between the leaves of the foregoing podobranchia. The surface of each leaf is plaited longitudinally ten or twelve times. The edges and surfaces of the leaves, especially of the plaits, are beset with small elevations each bearing a single minute hooked seta. The epipodite (so-called) of the first maxilliped represents the base, stem and lamina of a podobranch. It is slightly folded, but the edge of the fold is posterior, whilst the internal edge of the lamina and its posterior surface bear hooked setae. The structures known as coxopoditic setae are long and slender filaments arising close to the bases of the podobranchiae, with acute apices and their terminal portions beset with foliaceous scales. They ascend vertically, lying among the branchiae, and it is suggested by Professor Huxley that they exclude parasites. The Crayfishes (*Parastacidae*) of the S. Hemisphere differ from those (*Potamobüidae*) of the N. Hemisphere in having (1) the laminae of the podobranchs rudimentary; (2) some at least of the branchial filaments, the setae of the stem, and the coxopoditic setae terminally hooked; and (3) a few branchial filaments upon the epipodite of the first maxilliped. An arthro- and pleuro-branch have a structure similar to the base, stem and apical plume of a podobranch. The anterior of the two rudimentary pleurobranchiae is often a mere papilla, but the posterior resembles in structure a branchial filament. Of the two varieties (? species) of *A. fluviatilis*, the *A. nobilis* differs from *A. torren-*

*tium* in possessing three instead of two rudimentary pleurobranchiae. The Crayfishes of the S. Hemisphere, with the exception of *Astacoides* from Madagascar, have four functional pleurobranchiae. It is remarkable that these organs are entirely absent in *Cambarus* (the only other genus besides *Astacus* of *Potamobiidae*), which is distributed East of the Rocky Mountains from the Great Lakes to Guatemala, and is found also in Cuba.

Inasmuch as the branchial filaments are all cylindrical in the Crayfishes, the branchial plumes are *tricho-branchiae*. The Crayfishes in this respect agree with all *Decapoda Macrura* except the genera *Gebia* and *Callinissa*, the Prawns, Shrimps, and *Mysidae*. The branchiae of the last-named are either absent or rudimentary. In the other Macrurans mentioned, as in the Hermit Crabs and *Brachyura*, the filaments are replaced by lamellae, and the branchiae are *phyllo-branchiae*.

Claus has pointed out (Arb. Zool. Inst. Wien, vi. 1885, pp. 39-47) (1) that the relation of the coxopodite to the body-walls is by no means a constant one in Crustacea, and the arthro-dial membrane has limits often ill-defined; (2) that in the branchiferous *Schizopoda* (*Euphausia*, &c.) the branchiae, which are all trifold, form a row of podobranchiae; (3) that in the larva of *Penaeus* there are three rows of branchial rudiments, which he terms distal, middle and proximal. The last is a double row, but one of the elements appears at a later period than the other. The distal rudiment on each limb represents the podobranch + epipodite (=lamina): the middle and the first proximal, the anterior and posterior arthrobranchs, and the second proximal the pleurobranch, in *Astacus*. It may be noted that the primitive distal rudiment from the second maxilliped to the third thoracic foot inclusive pushes out a basal bud. The bud becomes a branchia, afterwards lost on all the feet save the second maxilliped, while the primitive rudiment forms an epipodite. The three sets of rudiments which first appear belong distinctly to the original basal joint of the limb, but the arthro-dial membrane develops in such a manner that they come to lie subsequently on the coxopodite, the arthro-dial membrane, and the epimera.

The cavity of the branchial stem is divided by a septum into an outer and inner channel communicating at the apex. The latter is continuous with one of the six blood passages or 'branchial veins' which open into the pericardial sinus with widened mouths. The former is continuous with bloodvessels coming from the sternal sinus lodged in the sternal canal. Each branchial filament is similarly divided by a septum incomplete at the apex. According to Haeckel the blood-spaces are intercellular spaces, or lacunae, and not true vessels. The tissue is spongy. The cells are pyriform, one end pointed and united to the cuticula, the other swollen and nucleated, and attached to other cells (cf. Haeckel, Arch. Anat. u. Phys. 1857, p. 554).

The oesophagus and stomach (=stomodaeum), and the intestine (=proctodaeum) are lined by a chitinous coat. This coat consists of a superficial delicate cuticle similar to that of the carapace, and a deeper lamellate layer, sometimes penetrated by pores, especially where it is much thickened. There are numerous setae in the stomach, principally in its pyloric portion, and in the intestine. They are of two kinds, hollow hairs, similar to those of the carapace, very plentiful in the pyloric portion, and solid continuous processes. Minute ridges secreted by the chitinous cells, and corresponding three or more to a single cell, occur in the intestine

where the chitinous coat is divided into areas corresponding, as on the carapace, to the individual cells. The cuticular coat of the stomach ends at the pylorus with five projecting processes; that of the intestine commences with six elevations prolonged into ridges which traverse the tube in a spiral fashion. Beneath the chitinous coat is the single layer of chitinogenous, or ectoderm cells, large in size, and then a fibrous membrane followed by a layer of cellular connective tissue which incloses muscle fibres, both longitudinal and circular, in the stomach and intestine.

The chitinous layer of the stomach is thickened in the dorsal and lateral walls to form certain ossicles which, according to Vitzou, have the same structure as the carapace. Some of these ossicles have simply a supporting function, others constitute the 'gastric mill.' The latter are named and arranged as follows. There is a *cardiac* ossicle crossing the cardiac region transversely, articulating laterally with a *ptero-cardiac* piece, and extending forwards into a softer disc upon which the anterior gastric muscles are principally inserted, and backwards into a narrow *uro-cardiac* piece which is produced inferiorly into two *accessory* or *cardiac* teeth, rudimentary in the Lobster. A *pyloric* ossicle crosses the pyloric region transversely and dorsally, and gives insertion to the posterior gastric muscles. It articulates in front with a *prepyloric* ossicle which is bent downwards so as to form with it an acute angle backwards way, and articulates in turn with the *urocardiac* piece (*supra*). Close to this articulation the *prepyloric* ossicle is produced into a *bifid median* tooth, single in the Lobster. The *pyloric* ossicle articulates laterally on each side with a *zygocardiac* ossicle lying in the walls of the cardiac region. This ossicle articulates at its outer extremity with the corresponding extremity of the *ptero-cardiac* ossicle (*supra*) of its own side. Its inner extremity bears the great serrated *lateral* tooth. Just below the anterior end of this tooth projects an *infero-lateral* tooth borne by the 'lateral cardiac piece' of Milne-Edwards, one of the supporting bars of the stomachal walls. The stomach possesses extrinsic and intrinsic muscles. The former set includes the gastric muscles above mentioned, as well as the anterior lateral, the posterior, superior and inferior dilators. The latter set includes various muscles. One system of fibres unites the *ptero-* and *zygo-cardiac* ossicles. The remainder, according to Mr. T. J. Parker, act as constrictors, especially a layer which embraces the pyloric region. This region has its cavity, more particularly in the posterior part, narrowed by the bulging inward of its side-walls and the development of a median ventral ridge. The surfaces of these parts are beset with setae and form a most efficient 'filter.'

There is on either side of the stomach, at the entrance of the oesophagus, a round white spot caused by the presence of a flattish papilla having the same structure as the rest of the wall of the stomach. Forty days before a moult in the adult, or for a shorter period in the young according to age, the chitinogenous cells of this papilla develop a number of minute knobbed processes which raise the overlying chitinous cuticle and eventually break up into corpuscle-like bodies. Beneath the cuticle, and between the ends of the chitinogenous cells and their processes, lamellae of calcified organic matter are laid down forming the *gastrolith*. The lamellae are pierced by pores. Their substance consists of Calcium carbonate, with a small admixture of phosphate, and of organic substances partly soluble in water, partly insoluble, and perhaps chitinous in nature. During the development of the *gastrolith* the papilla becomes more prominent and changes its shape. The fully

formed stone is slightly concave and smooth on its stomachal or inner face, convex and marked by ridges on its external face. The lamellae of this face are the last formed and the hardest. The stone is eventually cast off into the stomach, previous to the moult, and ground down. It is to be regarded as a cuticular structure forming a storehouse of calcareous matter preliminary to the moult, which is not effected healthily unless the gastroliths are previously and well developed. If they fail to be developed properly, the animal, so it is said, usually dies.

The cuticular linings of the stomach and intestine are thrown off and regenerated at each moult. The parts of the gastric mill are said to be first of all broken up in all *Decapoda*. The remaining parts are moulted entire.

Tubular glands occur in *Astacus*, as in all *Decapoda*, in the walls of the oesophagus and the terminal dilated portion of the intestine. Glands have also been found by Braun on certain of the mouth-appendages, e. g. in *Astacus*, to the number of twenty on the 'median flattened' joint of the first maxilla, 'opening on its outer surface,' and on the 'lingula' (=metastoma). They resemble the glands of the branchial cavity (see *ante*, p. 166) rather than those of the digestive tract.

The mesenteron (=archenteron), or median portion of the digestive canal, is extremely short as in all higher Crustacea. It has a dorsal caecum, and receives on each side the common liver duct. Its cells form no cuticle. The liver, or hepatopancreas, derived as an outgrowth from the mesenteron, consists of a right and left gland, each consisting of an anterior, a median, and a posterior lobe. The secretory portion consists of innumerable tubular caeca lined by cells. These cells in all Crustacea possess a fringe of fine hairs affixed to a membrane, which is probably porous. The protoplasm is distinctly striated, especially in *Isopoda*. In *Decapoda* there are two kinds of cells, one that secretés coloured drops of fat and contains masses of small globules; the other, fine and coloured granules (=ferment-cells). In the *Isopoda* there is one kind of cell only forming both fat and fine granules, whilst the globules are absent (Frenzel). There are cells in reserve destined to replace those which are destroyed. The secretion is acid in reaction and contains, in many instances, cholesterin, in the Crayfish haematin, as well as a diastatic, peptic, tryptic, and possibly a fat-destroying ferment. Glycogen has been found in the gland (cf. Vitzou, A. Z. Expt. x. p. 554).

The 'green gland,' or renal organ, opens on the inner side of a ventrally-placed papilla upon the basal joint of the second antenna (p. 169). The duct, lined at its commencement by chitinous cuticle, widens out into a thin walled sac which, together with the gland itself, lies in the thorax at the base of the antenna, the sac dorsally to the gland. The latter forms a disc-like body composed of a tube coiled upon itself and divisible into three sections: (1) a long whitish tube which opens into the sac; (2) a green-coloured tube opening into (3) a triangular yellow-brown lobe. The coils are so disposed that the third section of the tube lies centrally and dorsally; the green section forms the outer circumference, and the white section lies between the two others. The bloodvessels are derived from the antennary and sternal arteries, and are especially numerous on the terminal lobe. Nerves derived from the supra- and the infra-oesophageal ganglia are distributed to the excretory sac. This sac and the tube are lined throughout by a single layer of epithelium supported by a fine structureless tunica propria. In the green section the cells have a striated cuticle, and the protoplasm is striated as in the tubuli

contorti of the Mammalian kidney. Guanin and uric acid have been stated to occur in the gland. Grobben compares the terminal lobe with its rich vascular supply to the Malpighian capsule; the remaining sections to the tubuli uriniferi of the Vertebrate kidney. The shell gland of the *Phyllopoda* and *Copepoda* consists of a similar terminal lobe and tube, but it opens on or close to the second maxilla.

The ovary is a trilobed gland like the testis, but the fissures between the lobes are not so deep. The oviducts originate as do the vasa deferentia, but they are wide, short, and straight. The ovary is lined by a delicate cuticle. The ovum is developed by the growth of a single cell out of a small mass of cells. It has a vitelline membrane, and when ripe, is set free into the cavity of the ovary. It is fecundated externally to the body, and is suspended to the feet, sterna, &c., of the abdomen during the development of the embryo. For the mode of suspension and the cement glands, see *ante*, p. 166.

The testis is a tubular gland. The tubes branch, and the ultimate branches end in a number of short stalked vesicles varying in size according to the state of their contents. The lining cells multiply and are differentiated into spermatozoa. These bodies are disc-like structures with a number of slender curved rays attached to the circumference of the disc. The structure of the disc is still somewhat obscure. The spermatic fluid is milky, and contains a viscid substance which agglutinates the spermatozoa into thread-like spermatophores. The sperm is shed through the channels of the first pair of abdominal limbs. The second pair are worked to and fro in these channels as if to keep them clear. The male throws the female on her back and deposits the sperm on the ventral surface of the last pair of swimmerets and on the thoracic sterna round the oviducal apertures, parts which are approximated during oviposition.

*Branchiae.* Huxley, P. Z. S. 1878; Claus, Arb. Zool. Inst. Wien, vi. 1885.

*Digestive tract; structure of walls, glands, and epithelium.* Vitzou, A. Z. Expt. x. 1882; Braun, Arb. Zool. Zoot. Inst. Wurzburg, ii. 1875, iii. 1876-7; Frenzel, A. M. A. xxv. 1885. *Ossicles of stomach and muscles.* Mocquard, A. Sc. N. (6) xvi. 1883; T. J. Parker, Journal Anat. Phys. 1877; Albert, Z. W. Z. xxxix. 1883. *Working model of gastric mill.* Roth, Nature, xxi. 1879-80. *Pyloric filter.* Huxley, The Crayfish, p. 58. *Gastrolith.* Braun, Arb. Zool. Zoot. Inst. Wurzburg, ii. 1875; Chantran, C. R. lxxviii. and lxxix. 1874; *its chemical composition*, Dulk, Müller's Archiv (Arch. f. Anat. und Phys.), 1835.

*Structure of liver.* Frenzel, Mitth. Zool. Stat. Naples, v. 1884. *Its Chemical action.* Krukenberg, Untersuch. Phys. Inst. Heidelberg, ii. 1882. *Its Colouring matter.* MacMunn, P. R. S. xxxv. 1883.

*Green gland.* Wassiliew, Z. A. i. 1878; Grobben, Arb. Zool. Inst. Wien, iii. 1881. *For guanin and uric acid in it*, cf. Griffiths, P. R. S. xxxviii. 1885.

*Testis.* Lemoine, A. Sc. N. (5) x. 1868; Rougemont, Organes génitaux, &c., *Astacus*, Bull. Soc. Sc. Nat. Neuchatel, ii. 1880 (not seen). *Spermatozoa.* Grobben, Arb. Zool. Inst. Wien, i. 1878; cf. note in Huxley, The Crayfish, p. 354. *Spermatogenesis.* Sabatier, C. R. c. 1885; Hermann, C. R. xcvi. 1883.

*Fecundation.* Chantran, C. R. lxxi. 1870; lxxiv. 1872.

*Structure of ovum.* Waldeyer, Eierstock und Ei, Leipzig, 1870, p. 85; cf. *general account* by Ludwig, Arb. Zool. Zoot. Inst. Wurzburg, i. 1874.

*Cement glands.* Braun, Arb. Zool. Zoot. Inst. Wurzburg, ii. 1875; iii. 1876-7. *Their secretion and fixation of ova.* Lereboullet, A. Sc. N. (4), xiv. 1860.



36. COMMON CRAYFISH (*Astacus fluviatilis*), MALE,

Dissected so as to show its nervous system.

THE supra-oesophageal ganglion and the twelve post-oral ganglia of the adult Crayfish, of which six belong to the thorax and six to the abdomen, have been displayed by the removal of the whole tergal region of the body, of the viscera of organic life, and the endophragmal skeleton in the thorax. The oesophagus, through which a black bristle has been passed, and a small terminal portion of the intestine remain *in situ*.

The supra-oesophageal ganglion was seen by Rathke to be made up of two rudiments in the embryo; of which the posterior, or the one placed nearest to the mouth, was the larger and supplied the first and second antennae. The ganglion itself in the adult gives off nerves to the eye, the eye-muscles, to the integument of the head, and the first and second antennae, besides furnishing two azygos nerves, one anterior, the other posterior, to the stomato-gastric nerve. The superior and inferior roots of this nerve (*infra*), together with the two commissures to the sub-oesophageal or first post-oral ganglion, are seen passing over a piece of blue paper placed under them in front of the oesophagus. The left end of this blue paper rests on the secreting portion of the left antennary or green gland. The infra-oesophageal ganglion is the largest of the post-oral series and innervates no less than six pairs of appendages, viz. the mandibles, the two pairs of maxillae, and the three pairs of maxillipeds or foot-jaws. In the developing Crayfish, as shown by Rathke, this mass is represented by six pairs of white specks. It is followed by five thoracic ganglia, which remain distinct and correspond in the adult as well as in the embryo of Macrurous Decapods to the five pairs of thoracic feet. Each ganglion is connected to its successor by two longitudinal commissures, showing the primitive bilateral composition of the chain. The commissures between the third and fourth ganglia are widely separate for the passage of the sternal artery seen in Preparation 33. The fourth and fifth ganglia are approximated. The first abdominal ganglion is some distance behind the last thoracic, and all the six abdominal ganglia are equidistant one from the other. A slip of blue paper has been placed under the third and fourth, and another under the commissure to the last of the series. The commissural cords are clearly double. The third ganglion is seen to give off a pair of nerves on each side, while another pair springs from the commissures immediately behind the ganglion. The anterior nerve on each side goes to the swimmerets; the posterior and the commissural pair to the muscles of the same, i.e. the third somite. All the abdominal ganglia resemble the third pair in these points with the

exception of the terminal ganglion, which may be seen to give off a large number of nerves. Accurate investigations have shown that of these there are five pairs and one posterior, median and azygos nerve. This azygos nerve supplies the termination of the intestine; and the nerves to either side of it, i. e. the fifth or innermost pair, are destined for the telson. The two outermost pairs of nerves, i. e. the first and second, go to the exopodite, and the third pair to the endopodite of the last enlarged pair of swimmerets. The fourth pair, according to Krieger, supplies muscles in the same manner as do the commissural pairs of nerves corresponding to the five foregoing ganglia.

The infra-oesophageal and the thoracic ganglia lie in the sternal canal formed by processes of the apodemata. The roof of this canal has been cut away to expose the nerve chain, but parts of the apodemata may be seen on either side of it in the shape of vertical tubular processes.

The two eyes with their stalks, the bases of the first and second antennae, are shown by the removal of the overhanging rostrum. The surface of the basal joint of each first antenna thus exposed is the one that contains the aperture into the auditory sac. The aperture itself is concealed by setae.

The summits of the branchial plumes are well seen in this specimen between the branchiostegite and the epimera of the thoracic somites. From the internal aspect of the epimera, the muscles which move the limbs upon the thorax are seen trending downwards and bifurcating as they pass between the sections of the endophragmal skeleton to their insertions.

The sub-oesophageal ganglion gives off six inferior and four superior or dorsal nerves. The six inferior are destined for the mouth-parts. The mandibular nerve accompanies the commissures round the oesophagus for a certain distance. The last nerve, which goes to the third maxilliped, arises at some distance behind that for the second maxilliped, and the part of the ganglion from which it springs has a certain amount of distinctness or individuality. Of the four superior nerves the first is of considerable size and innervates the scapho-gnathite. The three remaining nerves are fine, and their destination unknown.

Each of the five thoracic ganglia gives off two pairs of nerves: an anterior large pair destined for the limb and the gills belonging to the somite, and a posterior fine pair destined for the corresponding thoracic muscles.

The median azygos nerve given off by the last abdominal ganglion divides, according to Lemoine, into two branches, a posterior anal branch and an anterior intestinal branch. The latter subdivides into (1) a branch to the anal end of the intestine; (2) a branch which courses along the ventral surface of the intestine, to which it gives twigs from spot to spot; and (3) a branch which turns round the intestine and runs upon its dorsal aspect. Lemoine traced these two last-mentioned branches as far forwards as the genitalia.

The nerve-factors which make up the stomatogastric system are derived from two sources, from the supra-oesophageal ganglion itself, and from the commissures connecting it to the infra-oesophageal ganglion at the spot where these commissures come into contact with the walls of the oesophagus. The nerves derived from the first-named source are two, a superior azygos nerve and an inferior azygos nerve. The former has a small ganglion close to its origin; it is short and runs upwards, i.e. dorsally. The latter is long and runs backwards and downwards. Two small ganglia, the mandibular or oesophageal ganglia, recently investigated by Krieger, give origin to the second set of factors named above. They are semi-oval and lie on the ventral side of the commissures, and from each of them spring at least three nerves. One is external and bends down, branching on the oesophagus; the two others, the superior and inferior roots, are internal and pass forwards between the commissures. The inferior roots unite together to form a single trunk, to which the superior roots then unite. The single nerve thus formed is joined by the inferior azygos nerve from the supra-oesophageal ganglion, and constitutes a median nerve which runs upwards in front of the stomach, giving off one after another three branches to that organ (Lemoine). It then unites with the superior azygos-nerve<sup>1</sup> from the supra-oesophageal ganglion. The single trunk formed by this union bends round the stomach on to its dorsal aspect. Close to the point of union it gives a nerve to the stomach and twigs to the anterior gastric muscles through which it passes. It then forms the stomatogastric ganglion, from which spring two nerves, an upper, the cardiac nerve of Lemoine, lodged in the integument and going to the heart, and an inferior or gastro-hepatic which lies on the dorsal wall of the stomach. The latter passes backwards and divides posteriorly into the *terminal* branches. Between these and the stomatogastric ganglion is a slight swelling from which rise the two *lateral* branches. Both lateral and terminal branches pass downwards. The latter supply the posterior gastric muscles. They eventually distribute themselves to the liver so-called and various stomachal muscles, and anastomose both with the lateral branches and the *postero-lateral* nerve which arises from each oesophageal commissure dorsally to the oesophageal ganglion, and passes upwards on the oesophagus. These various nerves give off numerous branches which have recently been investigated in detail by Mocquard in various Decapoda.

The ganglia consist of central masses of Leydig's 'punkt-substanz' formed by dense networks of fine nerve-fibrils, and external masses of ganglion cells, varying in size. The ganglion cells themselves differ in the same respect: the smallest possess but little protoplasm. Each cell is contained in a connective tissue capsule. Their processes, though numerous, originate in most instances from one surface or pole. The nerves are tubular, and, according to Krieger, consist of an external sheath and homogeneous fluid contents, but Freud states that there are delicate fibrillae imbedded in this homogeneous substance; and he traces the same distinction, viz. a homogeneous matrix and imbedded fibrillar network, in the bodies of the ganglion cells. The nerves branch repeatedly. There is a tough elastic perineurium or common investment, composed of decussating fibres and covered within and without by cellular connective tissue.

*Histology of nerve-cord, nerves, &c. In Astacus, Krieger, Z. W. Z. xxxiii. 1880;*

<sup>1</sup> This root is not mentioned by Mocquard, but is figured by both Krieger and Lemoine, and I have found it myself more than once.

Freud, SB. Akad. Wien, lxxxv. Abth. 3, 1882. *In Decapoda*, Yung, A. Z. Expt. vii. 1878.

*Stomatogastric system with figures, and posterior intestinal nerves.* Lemoine, A. Sc. N. (5), ix. 1868; Mocquard, A. Sc. N. (6), xvi. 1883.

### 37. COMMON STARFISH (*Asterias* or *Asteracanthion rubens*),

Dried.

THE animal consists of a central disc, which is prolonged into five lobes, the so-called *arms, rays, or radii*. The interval or part between each radius is known as an *interradius*. Two surfaces may be distinguished:—one flat or somewhat concave, the ventral, oral, *actinal*, or *ambulacral* surface; the other convex, and termed the dorsal, aboral, *abactinal*, or *anti-ambulacral* surface. In the centre of the ventral aspect of the disc is the membranous peristome with the mouth. Five sets of spines, the mouth-papillae, project over this area interradially, giving it a pentagonal appearance: and there radiate from it the five *avenues* or *ambulacral grooves*, one to each ray, which lodge the locomotor feet and hence give this aspect of the animal the name of ambulacral. The feet in question have been removed from two of the grooves for a short space, but are left *in situ* and in a dried condition elsewhere. Examining the exposed part of each groove attentively, it is seen to be formed by two series of narrow parallel ossicles—the so-called *ambulacral* or *vertebral* ossicles, the long axes of which are at right angles to the axis of the ray. The ossicles of one side of the groove are inclined at an obtuse angle, open ventrally, to the corresponding ossicles of the other side; and their dorsal ends are articulated moveably together. The summit of the angle is median. The groove lodges the radial water-vascular vessel, the inferior transverse vertebral muscles, the radial periaemal spaces and bloodvessels, and the radial nerve-cord, with the feet. Between the ossicles are a series of pores, one pore between each pair, formed by the apposition of two grooves in adjoining ossicles. The ampullae of the feet which lie on the dorsal side of the ossicles communicate through these pores with the ventrally placed feet. The two first pores lie in the same straight line, while the succeeding, to very near the tips of the arms, are arranged in a zig-zag fashion, being alternately near to, and remote from, the axis of the ray. Hence there *appear* to be four rows of pores and four rows of feet to correspond. In the majority of Asteroidea, however, the pores retain a straight linear arrangement for the whole extent of the grooves.

The edges of a groove are bordered immediately by a series of fine moveable spines, borne by the adambulacral ossicles (*infra*). In this

specimen there are three rows of such spines, but in many instances there are only two. At the oral end of each groove they form the mouth-papillae above-mentioned, the spines of one side in one groove meeting the spines of the adjoining side of the contiguous groove interradially. Externally to this series of spines comes another series in triple row of stout spines, fixed like all the other spines of the body. They are borne by the median set of interambulacral ossicles (*infra*). This series of spines, and the series of moveable spines, both extend to the tip of the ray, ceasing at a spot where a circling of spines denotes the position of the eye-speck and terminal feeler or tentacle in the living animal. A third series of stout spines in a single row, borne by the inferior marginal ossicles (*infra*), borders the ventral aspect of the ray on either side.

Turning to the dorsal or aboral surface the *perisoma* or integument with its network of calcareous ossicles and membranous soft intervals may be first noticed. The spine-bearing ossicles form more or less regular lines parallel to the axes of the rays. One line in the middle must be noted particularly. Attached to the soft intervals and at the bases or tips of the spines may be seen scattered pedicellariae. Other pedicellariae are grouped round and on the series of moveable spines of the ventral surface. These two sets of pedicellariae differ remarkably from one another. Both however are to be regarded as modified spines, not zooids, like the polymorphic aviculariae and vibracula of Polyzoa. (See *Flustra*, Preparation 48, *post.*) In one of the interradii is a circular calcareous plate, the madreporic tubercle or *madreporite*, the surface of which is marked by grooves radiating from the centre. By the removal of the perisoma from the disc, it may be seen that a canal with calcareous walls—the *stone-canal*,—curved like the letter S, leads from this plate to the ventral surface, where it opens into the circum-oral water vascular vessel. The two rays, one on either side the madreporic plate, constitute the *bivium* as ordinarily defined; the three remaining rays the *trivium*. The central one of the three lies opposite the madreporic interradius and is often spoken of as the anterior ray.

The perisoma has been removed from the dorsal surface of three rays, and the ambulacral ossicles can be seen from their dorsal aspect. Their median ends form a prominent *vertebral* ridge with median furrow.

Each first ambulacral ossicle is large, broad, and pointed medianly, and projects over the peristome radially. It appears to be formed by the fusion of two ossicles. The pore is large. At the outer end of this ossicle and to the outer side of the pore is an enlarged first adambulacral ossicle, which is, however, smaller than the ambulacral. This adambulacral with its fellow adjoining the same interradius carries the oral papillae or spines which project over the peristome interradially. In the majority of Starfish the first adambulacral itself projects interradially over the peristome beyond

the corresponding ambulacral ossicle and with its fellow in the adjoining ray forms two *teeth*. The ambulacral is in this case a *support* for the teeth. The first type of mouth is termed ambulacral, the second adambulacral. The former appears to be characteristic of those Starfish in which the ambulacral pores are arranged in zig-zag; the latter of those in which they maintain a linear arrangement. A small plate, somewhat indistinct in this specimen, overlies interradially each set of first adambulacrals. It is known as the *odontophore*, and appears to be homologous with the *oral* plate of many other Echinoderms. See the general account of the Phylum. A single row of minute adambulacral ossicles articulating immediately with the outer ends of adjoining ambulacrals can be made out in nearly the whole length of the arm; as well as the transverse rows of five *intermediate* ossicles, which unite them with a longitudinal row of *inferior marginal* ossicles bordering the ventral aspect of each arm. The median intermediate ossicle of the five is enlarged and spine-bearing, and is connected to the intermediate ossicle in front and behind. In some Starfish, e. g. *Astrogonium*, there is a series of well-developed dorsal *superior marginal* ossicles.

The perisoma or integument consists of two layers, an outer and an inner, between which exists a system of irregular channels which are ultimately continuous with the system of perihæmal spaces. The calcareous ossicles, spines and pedicellariæ, belong to the outer layer with the single exception of the ambulacral ossicles which belong to the inner one. The outer layer passes across the ambulacral groove from side to side, inclosing a space between itself and the ossicles. In this space are lodged (proceeding from the dorsal to the ventral wall) the water-vascular radial canal, the transverse ambulacral muscles, the right and left perihæmal space with the bloodvessels, and the nerve-forming ectoderm.

The outer surface of the perisoma is covered by a ciliated epithelium (ectoderm) which possesses a distinct cuticle pierced by pores for the cilia. The constituent cells are (1) supporting cells, (2) gland cells, (3) sense-cells. At the base of the epithelium is a network of nerve-fibrils with ganglion cells. In the ambulacral nerve and circum-oral nerve-ring the supporting and sense-cells are of great length, and the nerve-fibre layer much thicker, and the fibres parallel to one another. These structures are continued on to the terminal feeler or tentacle, the first formed tubefoot of the arm, as well as on to the paired feet; but in the latter the nerve-fibres are arranged in longitudinal bundles, and gland-cells occur plentifully on the terminal sucking disc. The eye-speck is placed on the ventral surface of the feeler and is composed of several eyes, the number increasing with age. Each eye consists of a conical depression in the epithelium over which the cuticle passes uninterruptedly. The walls of the depression are formed of sense-cells, some of which contain pigment, and its central cavity is filled with a clear liquid. If the radial nerves are divided close to the ring, the animal loses the power of coordinating the movements of the several arms: and if the eye-specks are removed, it ceases to react to light.

The pedicellariæ in the Asteroidea possess only two blades with the exception

of *Luidia*, where they possess three as in Echinoidea. But the stalk of the Asteroid, unlike that of the Echinoid pedicellaria, is formed entirely of soft structures. There are in the Asteroidea, which possess four rows of ambulacral feet, two kinds of pedicellariae. Both agree in having three calcareous pieces, a basilar piece bearing two blades opened and shut by muscles. But in one kind which occurs chiefly isolated the blades are articulated opposite to one another, in the other the blades cross one another at a certain point like the blades of a pair of scissors. The latter are termed *crossed* pedicellariae. They occur in rings or semi-rings upon the spines. In other Asteroidea there is a form of pedicellaria termed 'valvulate,' in which the blades are broader than they are long. The pedicellariae are used to take hold of objects such as algae until the feet can be applied.

The apical system of plates is not traceable in this nor in the majority of adult Starfish. It is disguised by the formation of new plates and ossicles during growth. See the general account of the Echinodermata and Asteroidea. The ossicles are developed from a calcareous network as is usual in Echinodermata, and the calcareous matter is chiefly Calcium carbonate.

The series of ambulacral ossicles end at the tip of each arm with a *terminal* plate which supports the tentacle on its ventral surface, and is formed in the young Starfish at an early period. All new ossicles and plates are added between it and already existing ossicles and plates. A series of plates on the dorsal surface connects it to a *radial* plate of the apical system in the young Starfish and some adults. And when the radial becomes indistinguishable, this median row of plates may remain conspicuous. In *Asterias* it is often well marked, but the ossicles are similar to the other ossicles of the general perisoma which are arranged in linear series.

According to Viguier, ten muscles correspond to each pair of ambulacral ossicles: four vertical muscles (two on each side) uniting the ambulacral and adambulacral ossicles: four longitudinal (two on each side, one superior and one inferior), and two transverse muscles. One of the transverse muscles is ventral and deepens the groove when it contracts: the other dorsal and antagonistic to the ventral.

The dermal branchiae of the dorsal surface are delicate contractile tubular processes of the perisoma.

The madreporite contains tubular ciliated canals radiating conformably with its superficial furrows. These canals send up minute vertical non-ciliated tubes which open in the furrows by ciliated funnels. Of these openings *A. rubens* has about two hundred. The radiating canals join the stone-canal. This canal has at its dorsal end an ampulla, which is seven-lobed. Its cavity is partially divided by a septum, but in many Asteroidea it is completely broken up into many tubes. To the circumoral water-vascular ring are attached in pairs nine racemose vesicles or Tiedemann's bodies. A tenth is missing, and the stone canal opens where it should be. The bodies consist of branched canals lined by cubical cells. The radial vessels spring from the circumoral. They give off laterally, corresponding to the interval between two ambulacral ossicles, the branches for the feet. These open into the bases of the feet in such a manner that water cannot regurgitate. A branch from the base of every foot passes through a corresponding ambulacral pore and swells into an ampulla on the dorsal aspect of the series of ossicles. Longitudinal muscles exist in the walls of the ampullae and feet, circular in other parts of the water-vascular system.

The so-called heart or plexiform organ (gland) is composed of a plexus of vessels lying to the inner, i.e. adcentral, side of the stone canal inclosed in a perihæmal space. At its ventral end it is connected to a circumoral plexus which lies in an incomplete septum dividing the circumoral perihæmal space into an outer and an inner space. The radial vessels are similarly lodged between a right and left space. At its dorsal end the plexiform organ is connected with a peri-anal ring which gives off the ten vessels to the genitalia and two vessels, one on either side of its dorsal end, to the intestine. These vessels are also lodged in spaces. The vascular system contains brown cells, which also occur, but more sparingly, in the water-vascular system. The perihæmal spaces are probably a part of the coelome. They are lined by an epithelium which in the *radial* spaces forms an interrupted ventral band of columnar cells which were supposed by Lange to be nervous. They are said to communicate both with the coelome and the channels in the perisoma.

The water-vascular oral ring lies to the dorsal and outer side of the two perihæmal spaces, and below or ventral to them is the thickened nerve-ring just as in the arms.

The coelome is lined by ciliated epithelium.

*Echinodermata*, Encyclopaedia Britannica (ed. ix.), vii. *System der Asteriden*, Müller und Troschel, Brunswick, 1842. *Stellérides du Musée*, Perrier, A. Z. Expt. iv. 1875; v. 1876.

*Species of genus Asterias*, Bell, P. Z. S. 1881.

*Skeleton*. Gaudry, A. Sc. N. (3), xvi. 1851 (for figure of *Asterias rubens*, Pl. 18, Fig. 1); Agassiz, Memoirs Harvard Museum, v. 1877; Viguier, A. Z. Expt. vii. 1878.

*Names of ossicles belonging to ambulacral series*. J. Müller, Abhandl. Akad. Berlin (Classis Physica), 1853-54, p. 162; p. 210.

*Oral and apical system of Asteroids*. Sladen, Q. J. M. xxiv. 1884 (contains general references).

*Oral ossicles*. Viguier, A. Z. Expt. vii. 1878; Ludwig, Z. W. Z. xxxii. 1879; cf. remarks in Carpenter on 'oral and apical system of Echinoderms,' Q. J. M. xxii. 1882.

*Pedicellariae*. Perrier, A. Sc. N. (5) xii. 1869. *In Echinoids*, Id. A. Sc. N. (5), xiii. 1870; Geddes and Beddard, Trans. Roy. Soc. Edinburgh, xxx.; Foettinger, Archives de Biologie, ii. 1881; Sladen, A. N. H. (5) vi. 1880. *In Euryalidae*, Ludwig, Z. W. Z. xxxi. 1878.

*General Minute Anatomy*. Beiträge zur Histologie der Echinodermen, Hamann, pt. ii. Die Asteriden, Jena, 1885.

*Nervous system, eye, perisoma, feet, &c.* Hamann, Z. W. Z. xxxix. 1883, p. 170.

*Mode of locomotion*. Romanes and Ewart, Ph. Tr. 172, 1881, p. 836. *Function of eye and pedicellariae*. Iid. J. L. S. xvii. 1884, p. 131; cf. Romanes, Jelly-fish, Starfish, and Sea-urchins, Internat. Series, 1. 1885.

*Fission in Asteroidea and Ophiuroidea*. Kowalewsky, Z. W. Z. xxii. 1872; Simroth, Ibid. xxviii. 1877; Haeckel, Ibid. xxx. (suppl.) 1878; E. von Martens, A. N. 32, 1866, p. 68.



38. COMMON STARFISH (*Asterias*, or *Asteracanthion rubens*),

Dissected so as to show its digestive and motor systems.

ONE of the rays, the central ray of the trivium, has been cut short, and more or less of the dorsal or anti-ambulacral integument removed from each of the other four, and from the central disc. In the interradial space which is opposite to the ray cut short, is seen the madreporite; and a little to the left of a line drawn along the axis of the central ray to the madreporic tubercle, and near the centre of the disc is seen the small piece of dorsal integument in which the anus opens. It lies on this aspect in the interradius, to the left of the madreporite (see note, Plate xi.). From the intestine, and close to the anus, arise two diverticula. They bear several irregular caecal ampullae and reach a short way into two interradia, the interradius between the central and left ray of the trivium and the interradius between the left rays of the bivium and trivium respectively. The internal surface of these diverticula is longitudinally plicated and they are probably highly extensile. They are generally considered to be the homologues of the respiratory trees of the Holothuroidea. The intestine itself cannot be seen. It is short and arises from the pyloric division of the stomach. This pyloric division is pentagonal in outline, and a single trunk may be seen to arise above each angle of the pentagon. Each trunk enters the corresponding ray, and divides into two branches which, with their foliaceous glandular ampullae, fill up the greater part of the cavity of the ray. The saccular dilatations of the anterior or cardiac division of the stomach are to be seen lying below the trunks of origin of the complex caeca, and bulging for a short distance into the cavities of the rays. These sacculi can be evaginated so as to enclose the animals on which the Starfish feeds, e.g. young oysters, cockles, &c., too large to be drawn into the disc. Each sacculus is retracted after protrusion by a pair of muscles attached to the sides of the vertebral ridge of the ambulacral groove. The Asteroidea are the only group of Echinodermata which possess a radial development of caeca to the digestive tract as seen here. The two divisions of the arborescent caeca have been separated in two of the rays to show the ampullae of the feet. These are arranged in two symmetrical rows on either side of the vertebral ridge of the ambulacral ossicles, thus corresponding to the arrangement of the pores seen in the preceding preparation.

On the ventral surface the mouth is to be seen placed centrally. The ambulacral feet are variously contracted, some more, some less. They have sucker-like ends, which are not supported by calcareous plates as they are in Echinoidea and most Holothuroidea. In the left ray of the trivium the feet are completely retracted, and in the left ray of the bivium the series of

*adambulacral* moveable spines has closed completely over the groove, thus protecting the soft parts which it lodges.

The pedicellariae may be seen strewn among the spines of the perisoma, and upon the moveable *adambulacral* spines. It is possible that some of the minute elevations among the spines are the incompletely retracted tubular respiratory processes of the integument.

The oesophagus is short and longitudinally plicated: the cardiac and pyloric divisions of the stomach are partially separated by a circular fold, and the intestine has a narrow plicated aperture into the stomach. The epithelium of the stomach is stated by Hoffmann to be ciliated.

The arborescent caeca in the arms with their ducts are suspended to the dorsal perisoma by a couple of mesenteric bands. The cells in the caeca form enterochlorophyll, and tryptic, peptic, and diastatic ferments. They pour their secretion into the stomach.

The development of the genital glands is periodical: when sexually mature they reach far down into the arms. They are branched glands alike in both sexes, and are surrounded by a blood sinus. Each gland has a single duct in *A. rubens*, but this duct opens by a sieve plate, i.e. a plate pierced by many pores. There are ten plates corresponding to the number of the glands. They are placed interradially and dorsally close to the bases of the arms. In most instances the genital plate has only one aperture. These calcareous genital plates have been supposed to be the homologues of the genital, i.e. basal plates of the apical system in Echinoidea. It is certain however that this is not the case: and in Starfish in which the apical system is retained in its typical form, no relation is observable between the genital apertures and the basals. Moreover in certain Starfish there is a more or less numerous series of genital glands, each with its own aperture, extending up the sides of the arms to a greater or less degree. In *Asterina gibbosa* the genital apertures are ventral. The duct in *Asterina pentagona* has unicellular glands by which the coat of the ovum is formed. These are probably present in other Starfish as well. Impregnation is external.

*General Anatomy of soft parts.* Ludwig, Z. W. Z. xxx. 1878; cf. Carpenter, Q. J. M. xxi. 1881. *Add on generative organs.* Ludwig, on *Asterina gibbosa*, Z. W. Z. xxxi. 1878.

*General minute Anatomy.* Beiträge zur Histologie der Echinodermen, Hamann, pt. ii. Die Asteriden, Jena, 1885.

*Digestive ferments.* Krukenberg, Vergleich. Physiol. Vorträge, ii. 1882, and lit. cited, p. 78. *On colouring matters.* Id. op. cit. iii. 1884, and lit. cited, p. 179. *Enterochlorophyll.* MacMunn, P. R. S. xxxv. 1883; Id. P. R. S. xxxviii. 1885.

### 39. COMMON EARTHWORM (*Lumbricus terrestris*, s. *Agricola*),

; Suspended by the anterior extremity to show its external characters.

THE anterior region of the body tapers to a conical point: the posterior is flattened dorso-ventrally and tapers abruptly. The first somite so-

called or prostomium (*infra*) lies entirely in front of the mouth and corresponds to the praeoral somite in other Chaetopoda. The mouth is ventrally placed in the second segment and is therefore subterminal. The anus on the other hand is posterior and terminal. The whole body is distinctly divided into a series of somites or segments, separated by well-marked intersegmental furrows. Vertical transverse septa or dissepiments which divide the body into compartments, correspond internally to these furrows with the exception of the first five or six. The compartments communicate with one another round the supra-nervian blood-vessel. The chitinous cuticle has been loosened by maceration in the spirit and may be seen lying in folds in the posterior region of the body. In life it is iridescent owing to the presence of two sets of fine parallel superficial lines crossing each other at angles of  $75^{\circ}$  to  $80^{\circ}$ . On the ventral surface of the fifteenth somite counting the praeoral as the first, are two white tumid elevations. These correspond to the apertures of the vasa deferentia. If the worm be held so that the light falls upon it obliquely, two somewhat raised lines may be seen running down the body on each side parallel to one another. The more ventral of these lines corresponds very nearly in position with the apertures of the vasa deferentia. Both lines indicate the position of the setae which constitute the locomotor apparatus of the Chaetopoda. There are in each somite of the common Earthworm two setae in each line, implanted a small distance apart, but they are often lost by accidents. The outer row is wanting in some instances as far back as the clitellum (*infra*). The inner row usually commences on the fourth or fifth somite. Both rows may be absent in the posterior somites. The spot corresponding to the inner or ventral row on the twenty-sixth somite of this specimen is somewhat swollen. The setae are here, as in the region of the clitellum, peculiarly long and delicate in a sexually mature worm, and are generally retracted. They are supposed to act as accessory copulatory organs.

The dorsal and lateral parts of somites thirty-one to thirty-eight, and especially of somites thirty-three to thirty-six, are white and swollen, and the swollen region is bordered by a prominent well-marked edge on either side of the median ventral line. These swollen somites constitute the clitellum, an organ especially characteristic by its great development of the terrestrial *Oligochaeta*. It is glandular and secretes a plentiful mucus from which the cocoon is formed. The prominent ventral edge acts as a copulatory organ. The development of the clitellum depends on the age and the state of sexual activity of the individual.

Vejdovsky believes, from his observations on the growth of the prostomium or praeoral somite in the individual produced by fission of *Aeolosoma tenebrarum* as well as in embryos of *Rynchelmis*, that it is really an outgrowth of the buccal somite and not a separate somite. In *Aeolosoma* the buccal somite develops the

supra-oesophageal ganglion, the two cephalic provisional nephridia, and the pharynx, the prostomium growing forwards by degrees. \* It is not separated by a furrow from the buccal somite as it is in all other Chaetopoda except *Chaetogastridae* (see Vejdovsky, op. cit. *infra*, p. 162). In *Typhaeus* from India it is apparently absent, and the mouth therefore terminal.

In *Microchaeta Rappi* the somites are secondarily annulated, as in the Leeches. The number of annuli in the first and in each somite from the ninth onwards is three: but in the second to the seventh somite inclusive it is either six or seven.

The cuticle is thin, transparent, and variable in thickness in different regions of the body. It is said to consist of two layers, an outer longitudinal and a thicker inner circular fibrillar layer. It is pierced by minute pores, the orifices of unicellular hypodermic glands.

The hypodermis or epidermis consists of a single layer of cells. In the intersegmental furrows they are shorter than elsewhere, and are non-glandular: whereas in other regions glandular and non-glandular cells occur intermixed. The non-glandular cells are either cylindrical with several basal processes, or more or less globular with a slender external process and one or more basal processes. The latter kind of cell lies at a deeper level than the former. The glandular cells vary somewhat in shape and in the nature of their contents, probably in accordance with their state of activity. According to Professor Ray Lankester, processes of pigment cells belonging to the subjacent connective tissue pass up, especially in *L. olidus*, between the hypodermis cells, as in the Leech. In the clitellum non-glandular cells are not to be found in the common Earthworm and some of its allies; in others they are present in reduced numbers. Its glandular cells are divisible into a more superficial layer with coarsely granular contents which stain readily with carmine, and a deeper layer with finely granular contents which do not stain with the same reagent. In *Allolobophora (Dendrobaena) rubida*, Vejdovsky traced nerve-filaments into apparent continuity with the glands. Capillaries penetrate between the clitellar glands, and are very numerous in the common Earthworm: in some species they are few in number. In *Perionyx* and *Megascolex* the general hypodermis is vascularised as in the Leech. An elastic basement membrane separates the hypodermis from the muscular layers of the body-wall. It is highly developed in *Perionyx* and *Perichaeta*.

The muscles are disposed in an outer circular and an inner longitudinal layer. Each muscle-fibre corresponds to a single cell with a well-developed cortical fibrillar substance and a central medulla or protoplasm which is scanty, and in which a nucleus has been found in *L. olidus* and *Phreorcytes*, two worms in which the fibrillar cortex is sometimes deficient at one spot, so that the muscle-cell becomes coelomyarian. In *L. terrestris* and some other *Lumbrici* and a few other Earthworms, as well as in *Serpula* and *Protula* among *Polychaeta*, the simple layer of longitudinal cells found in the lower *Oligochaeta* is disposed in parallel folds, the bipinnate bundles of Claparède, which are held together by intervening connective tissue. The muscle-cells of the longitudinal coat in other Chaetopoda are arranged in more or less regular groups or bundles. The longitudinal coat is divided in *Oligochaeta* into distinct tracts by the projection internally of the sacs of the setae. The bundles of protrusor or parieto-vaginal muscles attached to the bases of the sacs in question are derived however from the circular coat. Bundles of muscular or inter-follicular fibres pass from the bases of the sacs in the dorsal row to the bases

of the sacs in the ventral row. They appear to be special formations. Branched pigment cells are found most plentifully in the connective tissue of the circular layer of muscles. They are more numerous on the dorsal and lateral aspects of the body than on the ventral; more numerous in its anterior than in its posterior half. The body-cavity is lined by a peritoneal epithelium which varies in character in different regions and where it coats different organs.

The septa dividing the body into compartments are composed of connective tissue, of radial muscular fibres continuous with the fibres of the circular coat, and of circular fibres surrounding the digestive tract, the supra-neural blood vessel and nerve cord. *Aeolosoma* has only one septum separating the head from the rest of the body. The most anterior septa in the common Earthworm are replaced by the muscular bundles which pass to the pharynx from the body-wall. The perforations in the septa, by which one division of the body-cavity communicates with another, are in some instances near the body-wall.

The divisions of the body-cavity communicate with the exterior in most Earthworms by dorsal pores, situated quite close to the anterior intersegmental furrow of each somite. In the genus *Lumbricus* these pores commence in the sixth, seventh, or eighth somite. They become occluded in the clitellum by the pressure of the gland cells. They are simple perforations of the body-wall. Their aperture is surrounded by a circular sphincter muscle, and is opened by an anterior and posterior band of longitudinal fibres. The peritoneal cells at the margin covering the longitudinal divaricators are massed in a small heap. The function of the pores appears to be that of expelling coelomic fluid, or lymph. A cephalic pore is found in the lower *Oligochaeta* except *Aeolosoma*, either on the ventral or dorsal aspects of the prostomium, or else anteriorly and terminally. Dorsal pores are found in *Enchytraeus*, *Nais*, &c. They are absent in *Polychaeta*.

The setae are S-shaped, with the outer end more pointed than the inner. They are implanted in sacs or trichophores, which are simple invaginations of the hypodermis, composed of three (?) cells, one basal and two lateral. New setae are produced in the same sac as the old, and each seta is the product of a single cell. The genital setae of the tenth to the fifteenth somites, of the twenty-sixth somite and of the clitellum, are produced in the sacs of the ordinary setae present before the worm becomes sexually mature. The sacs enlarge as soon as the ordinary setae drop out, and from the enlarged cells are produced the long delicate genital setae. The corresponding setae in the aquatic *Oligochaeta* are produced in new sacs, the setae and sacs previously present undergoing atrophy (Vejdovsky). The setae of *Urochaeta* are bifid at their apex: the genital setae of *Acanthodrilus* (? all species) and of *Urochaeta*, and the setae in general of *Rhinodrilus*, are variously ornamented. Consequently the setae of terrestrial *Oligochaeta* are not invariably simple as Claparède supposed. The form of the setae in aquatic *Oligochaeta* is generally either simple and hair-like, or else slightly curved with a bifid apex. In the genus *Anachaeta* the trichophores are present but form no setae. The same thing occurs in *Urochaeta* with certain setae. In *Branchiobdella* (if it is an *Oligochaete*) all traces of the sacs are lost. Genital setae are always developed on the clitellum, and their form is variable, but different as a rule to those of other parts of the body.

The arrangement of the setae in two rows, an outer and inner or dorsal and ventral, is the common one in *Oligochaeta*, but it is sometimes departed from. The

number of setae in each somite is also not constant. Among Earthworms *Lumbricus* has a pair in each of the four longitudinal rows (i. e. eight) in each somite. In some species of *Acanthodrilus*, in *Titanus*, the eight setae are sometimes separated by equal intervals, and there are consequently eight rows, i. e. four on each side. The eight setae when thus separated may not remain in line from somite to somite, but alternate in position, as in the posterior somites of *Urochaeta*. *Megascolex* has very numerous setae, interrupted only in the median dorsal and ventral lines, whereas in *Perichaeta* and *Perionyx* single setae are implanted at intervals round the circumference of each somite. It is difficult to say whether the concentrated or scattered mode of distribution is the more primitive (see under nephridia, p. 205). The genus *Acanthodrilus* affords an instance of variations in this particular in different species.

The clitellum of Earthworms appears to fulfil two functions. It is a copulatory organ, and in *L. foetidus* Perrier observed the formation of a resistant membrane from its surface during sexual congress. It also secretes the cocoon in which the ova are contained together with spermatozoa and albumen. The cocoon is stripped off *forwards* by contractions of the body: and is charged with its contents in transit (?). The two ends of the cocoon close of their own accord as soon as it is freed from the body. In some Earthworms the clitellum surrounds the body, and there is no ventral furrow, as occasionally happens in *L. terrestris*. Its position and extent are variable not only in different groups of terri-colous *Oligochaeta*, but within certain limits in the same genus and even the same species. In the aquatic *Oligochaeta* it includes only the somite in which the vas deferens opens, and it does not secrete during congress. It is apparently absent in *Moniligaster* among terrestrial *Oligochaeta*.

Phosphorescence has been noticed in various *Lumbrici*, and appears to be due to a fluid excreted from the hypodermis (see Vejdovsky, p. 67).

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*Lumbricus terrestris*. Claparède, Z. W. Z. xix. 1879; Horst, Tijdskr. Nederland. Dierk. Vereen, iii. 1876; cf. A. N. 43, (ii), 1877, p. 481; Brooks, Handbook of Invertebrate Zoology, Boston, 1882, p. 140; Howes, Atlas of Practical Elementary Biology, London, 1885.

*Plutellus*, Perrier, A. Z. Expt. ii. 1873. *Urochaeta*, Id. op. cit. iii. 1874. *Pontodrilus*, Id. op. cit. ix. 1881. *Megascolex* (= *Pleurochaeta*) *Moseleyi*, Beddard, Trans. Roy. Soc. Edinburgh, xxx. pt. 2. *Megascolex*, *Perichaeta*, Id. A. N. H. (5), xiii. 1884. Do. with *Perionyx* and *Typhaeus*, 'Earthworms from India,' Id. op. cit. xii. 1883. *Perichaeta*, *Moniligaster*, 'Earthworms from Ceylon,' Id. op. cit. xvii. 1886. *Acanthodrilus capensis*, Id. Proc. Roy. Soc. Edinburgh, 1885. *Microchaeta Rappi*, Id. Tr. Z. S. (to appear); and Benham, op. cit. *supra*.

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*Cocoon and congress*. Perrier, A. Z. Expt. iv. 1875, notes, p. xiii.; cf. Ratzel, and Warschawsky, Z. W. Z. xviii. 1867-69, p. 547.

*Phosphorescence in Earthworms.* Vejdovsky, op. cit. *supra*, p. 67; Cohn, Z. W. Z. xxiii. 1873. *In Polychaeta.* Panceri, Atti Acad. fis. mat. Naples, vii. 1878 (cf. Journal de Zool. v. 1876, p. 94); Robin, Bull. Soc. Philomath. (7), vii. *In Polynoe.* Jourdan, Z. A. viii. 1885. *General account.* McIntosh, Nature, xxxii. 1885, p. 476; cf. Panceri, A. Sc. N. (5), xvi. 1872, and Secchi, *on Spectrum*, *ibid.* *In decaying organisms.* Pflüger, in his Archiv f. Physiol. xi. 1875.

*Vegetable mould and Earthworms.* Darwin, London, 1881; Hensen, Z. W. Z. xxviii. 1877. *Turriform heaps.* Trouessart, C. R. 95, 1882. *Absence from N. W. Prairies of N. America.* Nature, xxix. 1883-84. *Habits.* *Ibid.* xxx. 1884.

#### 40. COMMON EARTHWORM (*Lumbricus terrestris*, s. *Agricola*),

The first forty-one somites of the body including the clitellum, dissected to display so far as possible the reproductive system as well as the portions of the digestive, and circulatory systems contained in this part of the body.

THE integument has been divided down the middle dorsal line and fastened out on either side. The digestive tract occupies the centre of the preparation. It consists of a buccal cavity, not seen here; of a pharynx, oesophagus, crop, gizzard, and intestine or stomach, and a short rectum. The pharynx occupies the first five somites of the body. It has a rough exterior owing to the number of muscular bundles which pass between it and the body walls and have been severed in dissection. The oesophagus is narrow and extends through ten somites. About a quarter of an inch from its posterior end there is very visible on the right side, one of the three calcigerous or oesophageal glands,—the glands of Morren. The crop occupies a large space in the sixteenth and seventeenth somites. It has thin walls and dark-coloured contents. The gizzard comes next and lies in the seventeenth and eighteenth somites. It is smaller than the crop and has light-coloured muscular walls; and is followed by the intestine or stomach. The first portion of this tube is distinctly sacculated laterally, a feature which becomes less and less marked posteriorly. Its walls have a darkish appearance due to the modified and pigmented 'chloragogen' cells of the peritoneum which coat it and form the tissue, often miscalled hepatic.

The dorsal blood-vessel is clearly seen on the dorsal surface of the crop and intestine in the middle line. It has a distinctly moniliform appearance which is more marked in some other terrestrial *Oligochaeta*. On either side of the anterior part of the oesophagus may be seen four of the five or six pairs of 'hearts' which connect the dorsal vessel with the supra-neural vessel, in the somites behind the pharynx. The large pendulous vesiculae seminales lie anteriorly to the crop and to the outer side of the oesophagus. The two pairs of spermathecae may be seen, especially on the left side, in the line of the outer row of setae. Remnants of the septa may also be discerned on the internal surface of the body-walls, and in most of the posterior

somites the nephridia or excretory organs are left *in situ* on either side of the intestine.

The stomodaeum in *Aeolosoma* is restricted to the first somite of the body; in other *Oligochaeta* it extends backwards through a variable number of somites, and is differentiated into a buccal cavity and a musculo-glandular pharynx. The muscular tissue is most developed on the dorsal aspect of the pharynx, and is irregular in arrangement. The pharyngeal glands appear to correspond to the septal glands of the *Enchytraeidae*: they are large in *Megascolex Moseleyi* and *Pontodrilus*.

The oesophagus and stomach-intestine jointly represent the archenteron. The oesophagus of *Perichaeta* has three sets of glands attached to it. The gizzard is absent in *Pontodrilus* and all aquatic *Oligochaeta* except some *Naidomorpha*. It is in some instances placed more anteriorly in the body, e. g. in *Urochaeta*, *Antaeus*, &c., than it is in *Lumbricus*. *Digaster* possesses two, *Moniligaster* five, gizzards. The second gizzard in the former is separated by a whole somite from the first: the last four gizzards of *Moniligaster* follow one another closely, but are six somites behind the first. In these cases a longer or shorter tube intervenes between the gizzards, as is the case also between the gizzard and the sacculated region of the intestine. It is difficult to say whether the last-named tubular region should be considered as intestine or oesophagus. Glands are attached to it, e. g. three pairs in *Urochaeta*, one pair in *Microchaeta*, which appear to bear a lime-secreting function. They may be regarded as either homologues or analogues of the glands of Morren, according to the view which is taken as to the oesophageal or intestinal nature of the tube from which they originate. Calcigerous glands are entirely absent in some instances, e. g. in *Megascolex*, *Typhaeus*, *Pontodrilus*, &c. A pair of ventrally placed caeca open into the commencement of the sacculated intestine of *Perichaeta*, whilst *Typhaeus* and *Megascolex* possess a series of dorsal paired glands, five in the former, fifteen to sixteen in the latter, opening into it more posteriorly.

The walls of the digestive tract consist of the following layers from without inwards: (1) an epithelial peritoneum; (2) a longitudinal, (3) a circular, layer of muscle-cells; (4) a layer of capillary bloodvessels, and (5) the epithelium. The peritoneal cells in the region of the stomach and the stomachal vessels are pyriform and branched at their attached ends. They are coloured in all instances—green, black, or in the Earthworm brownish-yellow: hence chloragogen cells. They have usually a well-defined membrane, and contain concretions. They appear to be set free into the coelome, and then degenerate; and their products, soluble and insoluble, are probably excreted through the nephridia. The longitudinal layer of muscle-cells is thin, but is better developed in the gizzard where the circular layer attains an extraordinary development. The capillaries are well developed everywhere, but more especially in the pharynx and oesophagus. The lining epithelium is columnar. In the Earthworm it secretes a cuticle in the pharynx, oesophagus, crop and gizzard, but in the stomach is ciliated. In many of the lower *Oligochaeta* it is ciliated throughout the whole tract. The cells in the oesophagus from the 11<sup>th</sup> to the 13<sup>th</sup> somite are glandular. To this region belong the calcigerous glands. The first pair of these glands in the Earthworm is a pair of hollow diverticula, whilst the second and third pair consist solely of enlarged gland-cells (Claparède). They secrete a milky fluid which owes its milkiness to the presence



of Calcium carbonate in the form of rhombohedra (especially in the first pair), or of minute spherules. The Calcium carbonate has a chemical action, not a mechanical, as supposed by Claparède, and partly neutralises the acids of the humus swallowed by the worm, partly acts on the humus itself.

The dorsal wall of the stomach-intestine is invaginated in nearly all terrestrial *Oligochaeta* to form a ridge or typhlosole. This structure is absent in *Megascolex*, and in the aquatic *Criodrilus* and semi-marine *Pontodrilus*, which in many respects resemble the terrestrial forms. The ridge is complicated anteriorly, simple posteriorly, and consists of all the layers entering into the wall of the intestine. In some cases (*Urochaeta*, *Allolobophora cyanea*, &c.) a longitudinal supra-intestinal vessel runs along the cavity of the typhlosole, but in *Lumbricus* its walls are supplied by vessels derived from the dorsal longitudinal vessel. It is kept invaginated, according to Claparède, by muscles passing across from one to the other side in each somite. The epithelium covering it internally is often found enlarged with smaller cells between the bases of the large cells. The large cells are probably thrown off into the cavity of the tract and there resolved. The same changes have been noted in the intestinal epithelium of *Rhynchelmis*.

The digestive tract ends with a short thin-walled rectum, which is lined by cuticle and extends only through a single somite. The anus is dorsal in *Criodrilus*, and there are in this worm at least seven somites with an embryonal nerve-cord traceable behind it.

A longitudinal dorsal and ventral mesentery are present in *Criodrilus*. The dorsal is aborted in other instances, but the ventral usually persists.

The contents of the oesophagus are acid; of the stomach-intestine alkaline. There is a diastatic and tryptic ferment, and a peptic as well, but the latter must be inactive in the living animal owing to the alkalinity of the stomach (Krukenberg).

The vascular system of the Earthworm consists of a median dorsal vessel, of a supra-neural (=ventral) vessel, and three neural vessels, two lateral and one sub-neural<sup>1</sup>. The dorsal, supra-neural, and sub-neural vessels branch anteriorly and anastomose on the pharynx. In the region of the oesophagus six pairs of dilated and pulsatile vessels or 'hearts' pass from the dorsal to the supra-neural vessel. A small seventh pair gives origin to a lateral oesophageal vessel on each side which runs forward to the pharynx. The supra-neural vessel is connected from place to place with the capillary network in the walls of the intestine, and by this means indirectly to the dorsal vessel. A vascular loop unites the dorsal to the sub-neural vessel in each somite of at least the intestinal region. The integument and nephridia are provided with a rich supply of capillaries. The blood supply of the latter is said to be connected with the supra- and lateral, neural vessels; of the former, with the dorsal and sub-neural vessel. But there is some uncertainty about

<sup>1</sup> Howes figures in his *Atlas of Practical Elementary Biology* (Pl. xii. fig. 2) a sub- or infra-intestinal vessel applied to the inferior aspect of the intestine. Such a vessel exists in some *Polychaeta* and *Oligochaeta*, but not in the common Earthworm, so far as I can find from actual observation, by dissection of fresh specimens and of mounted sections. Benham also appears to have failed to find it (Q. J. M. xxvi. p. 253). It seems to me that the dark streak on the inferior aspect of the intestine which looks like a vessel is due to the attachment of the ventral mesentery in which the supra-neural or ventral vessel is suspended, and the consequent absence of chloragogen cells. Dark lines due to the same cause mark the attachments of the septa to the intestine. If the chloragogen cells are removed by a scratch, the scratched spot has a similar dark appearance.

these points. In *Urochaeta* and *Criodrilus* the dorsal and supra-neural vessels give origin to the integumentary capillaries. Dilatations occur in the nephridial capillaries, especially in the middle and posterior regions of the body. Similar dilatations occur elsewhere.

The most remarkable variations in the circulatory system of *Oligochaeta* are the following. The dorsal vessel, in two sp. of *Acanthodrilus* from New Zealand is double from the pharynx backwards, an embryonic feature seen also in some *Polychaeta*: in *Megascolex* and *Microchaeta* the sections of the dorsal vessel in the anterior somites are double between the septa, single where they perforate them (Beddard, Proc. Roy. Phys. Soc. Edinburgh, 1885). In some Earthworms, e. g. certain sp. of *Acanthodrilus*, *Urochaeta*, the posterior hearts connect a supra-intestinal vessel to the supra-neural or ventral vessel; and in some instances, e. g. *Urochaeta*, *Enchytraeidae*, &c., the dorsal vessel has moniliform pulsatile dilatations, and in the *Lumbriculidae* blind lateral and sometimes branched processes. Integumental capillaries are wanting in aquatic *Oligochaeta*, except at the posterior extremity of the body in some *Naidomorpha*, the *Tubificidae*, and *Criodrilus*.

The blood-vessels of *Lumbricus* are lined by an endothelium, the cells of which vary in character in different regions, suggesting a distinction into arteries and veins. The contained liquid is coloured with haemoglobin, as in most *Oligochaeta*, except *Aeolosoma*, *Chaetogastridae*, and most *Enchytraeidae*. It contains floating corpuscles, flattened, fusiform, sometimes nearly circular, which, according to Ray Lankester, are 'the nuclei of the endothelial cells set free from the walls of the vessels.' Vejdovsky, however, points out that the *Lumbricidae*, like the Leeches, have minute valve-like or irregular masses of cells connected to the walls of the vessels by fine processes. They are also present but confined to the dorsal vessel in aquatic *Oligochaeta*. Some of these cells are set free, according to him, and form the corpuscles which are absent only in *Enchytraeidae* and *Naidomorpha*.

The coelomic fluid contains amoeboid cells, 'large colourless vacuolated corpuscles, with a ragged outline often produced into filaments and provided with a large nucleus.'

The excretory nephridia, or segmental organs as they used to be called, are found one pair to each somite throughout the whole extent of the body from the fourth somite onwards. Each organ consists of a ciliated funnel or nephrostome, a convoluted tube, and a terminal muscular duct. The funnel is bilobed, but one of its lips is very small: its free margin is formed by a single row of ciliated cells. It opens into the cavity of the somite anterior to that in which the duct opens externally<sup>1</sup>, an arrangement common to all *Oligochaeta*, but by no means so in *Polychaeta*. The tube, therefore, to which it is connected passes backwards through a septum. The convoluted tube forms typically three loops. The first portion of it is clear-walled and ciliated; the second rather wider, its cells granular, and their cilia peculiarly long; the third part is wider still, its cells coarsely granular and not ciliated. The tube appears to perforate the cells, i. e. is intra-cellular as in the corresponding region of the Leech's nephridium. The duct is long, with muscular walls, and is dilated. It corresponds to the more or less pyriform vesicle into which the glandular part of the nephridium opens in some

<sup>1</sup> The *Oligochaete Plutellus* is an exception to this rule. Its nephridia (and oviducts) open both externally and internally in the same somite, as in many *Polychaeta*.

terrestrial and most of the aquatic *Oligochaeta* and the Leeches, and is probably therefore derived from an invagination of the hypodermis, as is the vesicle of the aquatic forms, the rest of the nephridium being mesoblastic. The pore by which the duct opens is generally placed slightly in front of the setae in the ventral row, but it may be placed in a similar position relative to the dorsal row. There seems to be much variability in the position of the aperture in the same individual, and the apertures of the right and left organs in the same somite may not correspond (cf. Claparède, Z. W. Z. xix. 1869, p. 620; Hering, Z. W. Z. viii. 1856-57, note, p. 401). The variation is perhaps due to the loss of nephridia originally present in each somite, and opening in different positions relatively to the setae. Perrier observed in *Plutellus* an alternation in the position of the nephridial apertures between the upper and lower rows of setae. Beddard has noted a similar but irregular alternation in a species of *Acanthodrilus* in which the dorsally placed nephridia have the duct represented by a large thin-walled muscular sac, with a small diverticulum; whereas those ventrally placed open laterally into a long muscular sac, much as do the nephridia of aquatic *Oligochaeta*. There is therefore an anatomical difference between the two sets of nephridia opening dorsally and ventrally. The last-named anatomist has also described the nephridia of a New Zealand *Acanthodrilus* (*A. multiporus*), in which there are four nephridia on each side in each somite of the body, corresponding to the setae. The two ventral nephridia on each side are intertwined and anastomose (?). In the posterior region of the body the organs open externally, each by a single aperture placed dorsally to each of the eight separate setae; in the anterior region, however, there are innumerable minute orifices in a single circular row, and in the same line with the setae, due to the branching of the ducts which appear to form a circular canal round the somites in this region. It is quite possible therefore that in other Earthworms certain of the nephridia in each somite are aborted, but that it is sometimes one, sometimes another pair which is missing. Benham states (Q. J. M. xxvi. p. 256) that numerous small nephridia occur in each of the somites of a small *Perichaeta* from the Philippine Islands. Details are wanting at present.

The aquatic *Oligochaeta* have a single pair of nephridia in each somite opening near the ventral set of setae, and composed of the same parts as in *Lumbricus*. The duct, which is sometimes glandular, is usually vesicular, and the gland-tube opens into it laterally. The funnel is absent in *Chaetogastridae*. Vejdovsky finds that both funnel and gland-tube are produced by the growth of peritoneal cells covering the septa: the duct by an invagination of the hypodermis.

Nephridia of the ordinary shape appear to be absent in *Megascolex* and *Typhaeus*, and their place is taken by tufted bunches of tubes, the structure of which has not been investigated. But they appear to be closely similar to the first pair of nephridia of *Urochaeta*, and the nephridia in general of *Microchaeta*. Each organ in the last named consists of a muscular vesicle opening externally to which are attached (1) a series of U-shaped loops, each loop containing intra-cellular tubes, and (2) a single simple tube which perforates a septum in the usual manner and opens into the coelome by a small contracted funnel. The mode of connection of the tubes to the vesicle has not been ascertained as yet.

The Earthworm is hermaphrodite like most of its congeners. The organs are figured in Pl. xii. The male apparatus consists of two pairs of testes, three

pairs of vesiculæ seminales, and a paired vas deferens. The testes are situated near the nerve cord on the posterior faces of the anterior septa dividing the tenth and eleventh somites. Each testis is described by Blomfield as 'a white translucent body of irregularly quadrangular form, rarely more than one-tenth of an inch in diameter, much flattened, and attached by one side to the coelomic epithelium of which it appears to be a local modification.' In the *Chaetogastridae* the spermatozoa begin to develop in the coelome and complete their growth in the spermathecae, but in most *Oligochaeta*, as in the Earthworm, they develop in vesiculæ seminales which are caecal outgrowths of the septa. This is their probable origin in *Lumbricus*. The immature vesiculæ in this worm are, according to Blomfield, 'six small light-coloured vascular growths on the three septa 9-10, 10-11, 11-12, arranged in three pairs.' The first and second pairs are anterior outgrowths of the septa to which they belong: the third is a posterior outgrowth of the septum 11-12 (Benham, note, p. 259, Q. J. M. xxvi. 1886). The cavities of the vesiculæ are traversed by connective tissue trabeculae and capillary bloodvessels. The spermoplasts and fully formed spermatozoa are lodged in the interstices of the trabeculae, in which may also be found the Gregarine *Monocystis Lumbrici* in all stages of its life-history. When the Earthworm is sexually mature the first four vesiculæ 'form a central body covering in the rosettes and testes of the tenth segment.' A similar coalescence occurs in the eleventh somite between the two last vesiculæ. Each vas deferens consists of two ciliated funnels or rosettes, one situated in the tenth, the other in the eleventh somite, which join a common duct. The latter opens near the ventral set of setae in the fifteenth somite. It therefore traverses three somites.

The two ovaries occupy a similar position to the testes but are lodged in the thirteenth somite. Each is invested by a layer of flat peritoneal cells. When mature it has the form of a pear with a long stalk—the latter being formed of a single string of ripe ova. It consists, when immature, like a testis, of a finely granular protoplasm with scattered nuclei, in other words, of a syncytium. The ova of the aquatic *Oligochaeta*, e.g. *Tubificidae*, break away from the ovary and ripen in the coelome or in an 'egg-sac' similar to the vesiculæ seminales. Each oviduct commences with a wide ciliated aperture vis à vis to the ovary. The duct perforates the septum between somites thirteen and fourteen, and opens in the fourteenth somite near the ventral row of setae. A receptaculum ovarum, or 'egg-sac,' is attached to the oviducal funnel and receives the ripe ova. It contains 1-5 ova, and like a vesicula seminalis, it is a diverticulum of a septum,—that which separates somite thirteen from somite fourteen. It projects into the latter (Bergh). The female apparatus is completed by two pairs of vesicular spermathecae which open in the intersegmental furrows between somites nine and ten, and ten and eleven, and are derived as in aquatic *Oligochaeta* from invaginations of the hypodermis (Bergh). They receive the spermatozoa in congress and secrete a clear fluid, which, according to Vejdovsky (op. cit. pp. 154-5), forms the spermato-phores. The clitellar glands are usually supposed to form these structures. The spermato-phores are  $1\frac{1}{2}$ -2 mm. long and 0.5-0.7 mm. wide, somewhat spirally coiled, and with an open hollow at one end in which the spermatozoa lie parallel to one another. In some worms they are closed. They are usually attached on or about the clitellum.

The testes of *Microchaeta* are four in number as in *Lumbricus*, and are contained in the vesiculae. The organs in Earthworms usually described as testes appear to be the vesiculae. Of these there are generally two pairs; in certain forms, however, only a single pair, which extends through three somites in *Urochaeta* and *Typhaeus*, through twelve to fifteen in *Titanus*, and thirty or more in *Urobenus* (Benham). There is always a single pair of ovaries, which in *Plutellus* are situated in front of the testes. The ovaries may be lobed, e. g. in some species of *Perichaeta*. There are four separate vasa deferentia in *Moniligaster* and *Acanthodrilus*, each with its own aperture: and they each appear to possess, as does the vas deferens of the aquatic *Oligochaeta*, a terminal vesicle homologous with a nephridial vesicle. The ciliated funnels are in front of the vesiculae in *Pontodrilus Marionis*, while *Anteus* is stated to possess no sperm-ducts at all. The genital apertures are sometimes approximated ventrally and the oviducal aperture is single, and median in *Perichaeta*, *Perionyx*, and sometimes in *Megascolex*. The position of the male apertures with reference to the clitellum varies, and has been used by Perrier as a means of classifying Earthworms. The apertures in question are situated (1) in front of the clitellum,—*Ante-clitelliani*, e. g. *Lumbricus*: (2) within it,—*Intra-clitelliani*, e. g. *Anteus*, *Titanus*, *Urochaeta*: (3) behind it,—*Post-clitelliani*, e. g. *Perichaeta*, *Megascolex*, *Plutellus*, *Pontodrilus*, *Acanthodrilus*, *Perionyx*: (4) or there is no clitellum even in sexually mature specimens,—*Aclitelliani*, e. g. *Moniligaster*. *Megascolex* has been termed by Beddard *Infra-clitellian*, for though the vasa deferentia open within the clitellum, yet they occupy a non-glandular ventral area. As to the other accessory organs of generation, the setae of the male somites are sometimes much enlarged, especially in the genera *Acanthodrilus* and *Eudrilus*; copulatory papillae are present in some species of *Perichaeta*; and prostatic glands opening into the sperm-ducts are found in the worms just named. The spermathecae are always in front of the vesiculae except in *Microchaeta* and *Eudrilus*. They vary in number and size even in the same genus, and are sometimes complicated as in *Perichaeta Houletti* by the addition of glands. There may be more than two spermathecae in each somite: in this case they are arranged in transverse rows. See Beddard, A. N. H. (5), xvii. 1886, pp. 91–92 and 93–94: Benham, Q. J. M. xxvi. pp. 263, 280.

In the aquatic *Oligochaeta* the nephridia atrophy away in the somites in which the sexual glands and ducts are undergoing evolution. In *Lumbricus* and many other Earthworms the two sets of structures co-exist. Vejdovsky is inclined to suppose that the larger size of the coelome is the cause of this persistence. The evolution of the genital ducts in the Earthworms remains to be worked out<sup>1</sup>. In many aquatic *Oligochaeta* it is accurately known. The vas deferens has in them a funnel, and a ciliated tube derived from peritoneal epithelium, and an atrium which is invaginated from the hypodermis like the nephridial vesicle, but is not represented in most Earthworms. The spermathecae are invaginations of the same kind. The oviducts are either simple slits (*Aeolosoma*, *Chaetogastridae*, &c.) or a pair of funnels (*Lumbriculidae*), and are obviously degenerate. Vejdovsky is inclined to conclude (op. cit. p. 161) that the sexual ducts either correspond to all the parts of an ordinary nephridium (vasa deferentia of aquatic *Oligochaeta*, of *Acanthodrilus* and *Moniligaster*) or to some of them (spermatheca to the nephridial

<sup>1</sup> Bergh states that he intends to publish on the subject.

vesicle: the oviduct of all, and vasa deferentia of *Lumbricus*, &c. to the nephridial tube): and that they are excretory organs developed only at the time of sexual maturity. In the lower *Oligochaeta* the sexual apparatus atrophies after the sexual products are discharged, but the worms appear to live on and may propagate themselves asexually. It is probable that the development of the sexual apparatus of the Earthworms will be found to be similar to that of the aquatic *Oligochaeta*. The only thing that must be regarded as certain at present is the fact that the sexual ducts of *Oligochaeta* are not, as in many *Polychaeta*, ordinary nephridia, which take on a sexual function at the reproductive season. It is possible that the resemblances traceable between them and the nephridia are merely homoplastic<sup>1</sup> and not homogeneous: i. e. the structures may not be identical. And the fact that the vasa deferentia of the Earthworms extend through several somites before they open externally may be held to support this view. It is true that the nephridia of the aquatic *Phreatothrix* extend through several somites. They form, however, U-shaped tubes and their external and internal apertures are always in two contiguous somites as in other *Oligochaeta* (Vejdovsky, op. cit. p. 124).

The terrestrial *Oligochaeta* do not multiply by fission and gemmation as do many of the aquatic forms. They appear, however, to have considerable powers of regeneration: and can form new anterior and posterior somites, supra- and sub-oesophageal ganglia, and pharynx in the place of parts removed by excision. They have been occasionally found with a bifid posterior extremity.

*Digestive tract.* Claparède, op. cit. ante, p. 600; in general, Vejdovsky, op. cit. pp. 100-112. *Chloragogen cells*, Vejdovsky, op. cit. pp. 110-112. *Secretion of calcigerous glands*, Robinet, C. R. 97, 1883. *Digestive ferments*. Krukenberg, Untersuch. Physiol. Inst., Heidelberg, ii. 1882, p. 37; Frédéricque, Bull. Acad. Belg., (2) 47, p. 217. *Colouring matter from intestine*. MacMunn, Proc. Philos. Soc., Birmingham, iii. 1881-3, p. 389.

*Vascular system.* Jaquet, Mitth. Zool. Stat. Naples, vi. 1885; Vejdovsky, op. cit. pp. 112-120. *Double dorsal vessel*. Beddard, Proc. Roy. Phys. Soc., Edinburgh, 1885. *Blood and blood corpuscles*. Vejdovsky, op. cit. p. 118; Ray Lankester, Q. J. M. xviii. 1878, p. 72; Blomfield and Bourne, Q. J. M. xxi. 1881. *Endothelium of vessels*. D'Arcy Power, Q. J. M. xviii. 1878. *Coelomic, i. e. amoeboid cells*. Kükenthal, J. Z. xviii. 1885.

*Nephridia.* Claparède, op. cit. ante, p. 615; Gegenbaur, Z. W. Z. iv. 1853. *In general and development*. Vejdovsky, op. cit. pp. 120-129. *Of Acanthodrilus multiporus*. Beddard, A. Sc. N. (6) xix. 1885. *Of a N. Z. Acanthodrilus*. Id. Z. A. viii. 1885.

*Sexual organs.* Hering, Z. W. Z. viii. 1856-57; Bergh, Z. A. ix. 1886. *In general and development*. Vejdovsky, op. cit. pp. 125-151. *Development of spermatozoa, vesiculæ seminales*. Blomfield, Q. J. M. xx. 1880; cf. Jensen, Archives de Biol. iv. 1883. *Spermatophores*. Fraisse, Arb. Zool. Zoot. Inst., Wurzburg, v. 1882; Vejdovsky, op. cit. p. 154. *Accessory organs*. Vejdovsky, op. cit. p. 135. *Homologies*. Id., op. cit. pp. 157-161.

*Regeneration of excised parts*. Miss Fielde, Proc. Acad. Nat. Sc. Philadelphia, pt. 1, 1885; cf. on *Lumbriculus*, Bülow, Z. W. Z. xxxix. 1883. *Bifid Earthworms*.

<sup>1</sup> For 'homoplasmy,' see Ray Lankester, 'Use of the Term Homology,' &c., A. N. H. (4) vi. 1870.

Bell, A. N. H. (5) xvi. 1885. *Regeneration in marine Chaetopoda*. De Quatrefages, A. Sc. N. (3) ii. 1844, p. 100; Claparède, Annélides du Golfe de Naples, 1868, p. 30. For lit. of subject in general, see Milne Edwards, Leçons sur la Physiologie et l'Anatomie comparée, Paris, viii. 1863, p. 301 et seqq.; or Fraisse, Die Regeneration von Geweben und Organen bei der Wirbelthieren, Cassel und Berlin, 1885; cf. Horst, Z. A. ix. 1886.

#### 41. COMMON EARTHWORM (*Lumbricus terrestris*, s. *Agricola*),

Dissected so as to show its nervous system.

THE integument has been divided down the middle dorsal line and fastened out on either side. The entire digestive tract with the exception of the buccal cavity, most of the nephridia or excretory organs, and the septa dividing the body into compartments, have been removed. Of the reproductive organs only the spermathecae or receptacula seminis, two globular white sacs, have been left *in situ* on the right side. They open respectively between the ninth to tenth and tenth to eleventh somites, on a level with the dorsal row of setae. The two lobes, making up the supra-oesophageal or cerebral ganglia, are pyriform, and have their broader ends apposed to each other in the middle line. A thick nerve passes off from each of their outer or narrower ends. It bifurcates, and ends in a plexus in the prostomium, on which are situate numerous sense-bodies. A right and left oesophageal commissure surround the passage from the buccal cavity to the pharynx and connect the supra-oesophageal to the first ganglion of the ventral nerve-cord. This cord extends to the posterior extremity of the body. It takes the shape of a thick band in which ganglionic enlargements are recognizable with difficulty for a space corresponding with that occupied by the pharynx, oesophagus and reproductive organs. Posteriorly to the fifteenth somite it becomes more slender, and the ganglia more distinct. Finally, for a length nearly equal to the posterior half of the animal, it becomes thicker and moniliform, the ganglia being plainly marked but closely apposed. The terminal ganglion is, contrary to what is seen in some Vermes and many Arthropoda, smaller than those which precede it.

The two rows of paired setae are well seen on each side in most of the somites. The enlarged inner copulatory setae of the two somites, fifth and sixth in order anteriorly to the clitellum, as well as of the clitellum itself, can be readily distinguished. In the interval between each inner row of setae and the nerve-cord in the fifteen anterior somites, a longitudinal muscular fascicle is seen passing forwards. It is inserted on the outer ends of the supra-oesophageal ganglia and on the commissures, and acts as a retractor muscle to these parts. Between the two rows of setae of the eighth

to the thirteenth somite inclusive, may be seen, on the right side, the capsulogenous glands of D'Udekem. These structures appear to be merely enlarged setiparous sacs, and not glands. They have been supposed to secrete the albumen surrounding the ova in the cocoon. The nephridia are left *in situ* on either side of the nerve-cord in some of the posterior somites.

The supra-oesophageal or cerebral ganglia belong developmentally to the stomial region of the first somite of the body, but generally shift in the adult backwards even as far in some instances as the 3<sup>rd</sup> or 4<sup>th</sup> somite. They retain a position in *Microchaeta Rappi*, &c., in the first (buccal) somite. The oesophageal commissures are composed of one or two fibrous cords. The ventral nerve-cord lies internally to the longitudinal muscular coat, except in the *Lumbriculidae*, where it lies next to the circular coat. The cerebral ganglia of *Aeolosoma* are, however, in continuity with the hypodermis, but a ventral cord is absent in this genus. In a few Chaetopoda, in *Protodrilus*, *Polygordius*, and *Histriodrilus* (= *Histriobdella*), the ventral cord as well as the cerebral ganglia are similarly continuous, and the three genera in question have been made into a separate group of Archi-annelidae (Hatschek). *Saccocirrus*, in which the nervous system is also hypodermic in position, is in other respects not so archaic a type, and has been classed by Foettinger apart from other Chaetopoda as Archi-chaetopoda.

The nerve-cord is composed of (1) an external layer of polygonal epithelial cells belonging to the peritoneum; (2) a coat of longitudinal muscle fibres, which does not extend up the commissures to the supra-oesophageal ganglia; (3) of a neurilemma, formed by the cord itself; and (4) the nervous matter proper, with a neuroglia or supporting connective tissue. The ganglion cells are found on the anterior surface of the supra-oesophageal ganglia, and as a layer on the ventral surface of the ventral cord, but not in the oesophageal commissures. They have no sheaths. In the first part of the cord they form a perfectly continuous layer (a fact denied by Vignal), with a right and left and two median aggregations, while in the posterior region these aggregations are separated from one another. This continuous arrangement is found only in *Lumbricidae* and *Lumbriculidae* among *Oligochaeta*. The number of cells does not appear to be much increased in the ganglionic enlargements, which are due chiefly to the greater amount of fibrous matter present at the origin of the chief nerves. According to Claparède the cord is divided into a right and left half by a median connective tissue septum.

The nerve-cord has in *Lumbricidae* three special blood-vessels running longitudinally within the muscular sheath, one subneural and two lateral, one on either side. The three are connected by ventral loops just behind each ganglionic enlargement. The lateral vessels give off a branch which accompanies the paired nerves (*infra*), the median a branch which accompanies each septal nerve (*infra*), and all three are connected to a capillary plexus ramifying in the substance of the cord and round the ganglion cells. The presence of these vessels was supposed to be a distinctive feature of the *Oligochaeta terricola*, as opposed to *Oligochaeta limicola*, but the subneural vessel is absent in the terrestrial *Megascolex*, *Perichaeta Houletti*, and *Microchaeta Rappi*, in the semi-marine *Pontodrilus*, but present in the aquatic *Criodrilus*.



The nerves originating from the cerebral ganglia usually break up into a plexus, in which ganglion cells are interpolated. The network is especially well-developed and visible in *Tubifex*, and in *Limnodrilus* and *Anachaeta* its ganglion cells are aggregated into special ganglia.

The first ganglion of the ventral chain generally gives off many nerves; the following ganglia a pair of nerves on either side. A single septal nerve arises also on each side, between successive ganglionic enlargements, and is distributed to a septum.

A pharyngeal plexus or 'Vagus' system is derived in most, probably in all, *Oligochaeta* from the oesophageal commissures. In some of the lower *Oligochaeta* there are distinct pharyngeal ganglia. In the Earthworm the system consists usually of a more or less elongated mass lying on either side of the pharynx, continuous with a rich plexus, the fibres of which are ultimately lost among the muscular structures. Leydig and Vignal state that ganglion cells are found in all parts of this plexus; Claparède, on the contrary, that none occur in the plexus so far as it is visible to the naked eye, but that they are present on the finer branches among the muscular bundles.

A cord of ganglion cells in continuity anteriorly with the cerebral ganglia runs down each side of the body in most *Oligochaeta*. It is especially easy to see in *Nais*, and is contained in the hypodermis. It is said to supply the muscles of the head, sacs of the setae, and the nephridial apertures; and is, perhaps, in connection with the ganglion cells, which have been found in the walls of the digestive tract in some instances. A zone of ganglion cells encircles each somite in the Naid *Slavina appendiculata*, is connected to the lateral cords, and supplies the tactile eminences (*infra*). In *Lumbricidae* the lateral cords are to be detected clearly in the young posterior somites, but they are resolved in the older anterior somites into scattered cells.

As to organs of special sense. *Oligochaeta* never possess otocysts. Eyes are found only in some *Naidomorpha*; supposed gustatory organs in the pharynx of *Enchytraeidae* and *Limnodrilus*; and olfactory (?) organs as a couple of ciliated pits on the head in *Aeolosoma*, *Ctenodrilus*, *Parthenope*. The last-named structures occur also in some *Polychaeta*. Tactile organs, however, are commonly distributed, and in various forms; as (1) a hypodermis cell furnished with an external tactile seta, and continued basally into a nerve fibril, in its turn often connected to a ganglion cell,—found in numbers on the prostomium of *Aeolosoma*, *Chaetogastridae*, and *Naidomorpha*; (2) tactile papillae, in which the hypodermis cell is protrusible, and furnished with short setae (*Chaetogastridae*); (3) tactile eminences, apparently composed of aggregations of tactile hypodermis cells, arranged fifteen to twenty in number in a zone on each somite of *Slavina appendiculata*; and (4) goblet bodies, or aggregations of very delicate hypodermis cells provided with sense-hairs, found most plentifully on the prostomium and buccal somite of *Lumbricidae*, more sparingly on the anterior somites of the body, but especially round the setae. A single goblet body is found also on each side of the somites of the *Lumbriculidae*, seated on the lateral cord of ganglion cells. They become enlarged on the clitellum of the Lumbricid *Rhynchelmis*, where gland cells occur among the sense cells. See on the subject Vejdovsky, op. cit. pp. 96–100.

On the dorsal aspect of the nerve-cord there are to be found three remarkable

*giant tubular fibres.* They are found in all *Oligochaeta* except in *Aeolosoma*, *Phraeoryctes*, and *Branchiobdella*, and the number given is usually that found in the Earthworm. They occur also in many *Polychaeta*, where their number varies from one as in *Eunice*, to six as in *Glycera*. These fibres do not extend into the oesophageal commissures, and they taper anteriorly and posteriorly. Each fibre is composed of a doubly contoured sheath with clear contents. No connection between the giant fibres and nerve fibres has ever been demonstrated. On the contrary the giant fibres are separated from the nerve-cord by the inner neurilemma, and they are imbedded in a connective tissue sheath containing reticulate cells. They appear to have a purely supporting function, and the apparatus is hence termed 'Neurochord' by Vejdovsky (op. cit. pp. 86-87), who compares it physiologically with the notochord of Chordata.

*Nervous system.* Claparède, op. cit. ante, p. 585. Leydig, Vom Bau des Thierischen Körpers, i. Tübingen, 1864, pp. 139, 168. Id. Tafeln zur Vergleich. Anatomie, Tübingen, 1864, Taf. i. fig. 5; Taf. iii. fig. 8; Taf. iv. figs. 7 and 8; Taf. v. figs. 1 and 2. Vignal, A. Z. Expt. (2), i. 1883, p. 373. *Of Oligochaeta in general.* Vejdovsky, op. cit. pp. 79-96; and *on Neurochord*, p. 87.

*Organs of special sense in Oligochaeta.* Vejdovsky, op. cit. pp. 96-100.

#### 42. MEDICINAL LEECH (*Hirudo medicinalis*),

Suspended to show the external form of the body and the coloured bands which differentiate the variety *H. medicinalis* from the variety *H. officinalis*.

THE animal is suspended by the anterior extremity which is formed by the funnel-shaped buccal cavity or anterior sucker which leads to the mouth, and is not separated from the rest of the body by a constriction in Leeches with jaws (*Gnathobdellidae*) as it is in Leeches with a protrusible proboscis (*Rhynchobdellidae*). The body itself has a flat or slightly concave ventral surface and a convex dorsal surface: and it is terminated by a disc-like solid posterior sucker which is formed by the fusion of posterior embryonic somites, according to Leuckart seven in number.

The body is annulated, and, according to Whitman, *H. medicinalis* has in all one hundred and two rings, representing twenty-six somites. Consequently the annuli do not represent somites: they are, on the contrary, due to a secondary and imperfect division of them. It has been pointed out by Whitman that certain of the annuli or rings bear what he terms segmental papillae. These organs resemble in histological structure the eyes, but reduced in size and deprived of pigment, and they may be regarded as the metameric or serial homologues of those organs. In *Hirudo* and some other Leeches there are normally fourteen segmental papillae, eight on the dorsal and six on the ventral aspects of the annuli upon which they occur. The eight dorsal papillae are arranged as a median pair, with three organs to either side of it, an inner, outer, and marginal organ. The

first pair of eyes replaces the median pair of papillae, the remaining four pairs a papilla of the inner series. The first and second annuli of the body carry a pair of eyes; the third annulus does the same, but it is followed by an annulus with neither eyes nor segmental papillae: and the two therefore go together. The fifth annulus bears eyes; the eighth and eleventh only segmental papillae, and these three annuli (fifth, eighth, and eleventh) are each followed by two annuli which have neither eyes nor papillae. Whitman therefore concludes that the first and second somites are represented by a single annulus, the third by two annuli, the fourth to the sixth inclusive by three apiece. The seventh and succeeding somites, up to the twenty-second inclusive, are each composed of five annuli, the first of them bearing the segmental papillae. The twenty-third somite has three, the twenty-fourth to the twenty-sixth two annuli apiece.

The buccal annuli are the fifth and sixth, the post-buccals the seventh and eighth, and these two pairs of annuli are fused ventrally. A pair of nephridial pores opens on the ventral surface of the last annulus of the sixth to the twenty-second somite inclusive. This annulus can be readily recognised in *H. medicinalis* by the fact that it is the one that carries a large black spot in the middle of the three light lines which traverse the body lengthwise on each side of its dorsal aspect. The male orifice lies between the second and third rings of the tenth somite, i.e. the thirtieth and thirty-first annuli of the body. The female orifice occupies a corresponding position in the eleventh somite. The ninth, tenth, and eleventh somites constitute the clitellum or region which secretes the cocoon. The anus lies either *in* the last annulus or *in front of* it. It may be added that papillae occur also on the sucker, but they do not afford any clue to its composition.

The grouping of the annuli, as above detailed, is characteristic of the genus *Hirudo*. Slight differences are observable in allied genera.

The medicinal Leech varies much in its colouration: and no less than sixty-four varieties have been enumerated. The variety *H. medicinalis* has in the natural state the dorsal surface greenish grey, with three rust-red longitudinal streaks on either side. The middle one of these three streaks has a black spot more or less distinct on each annulus, and it may be readily seen that one of these spots at regular intervals is much enlarged. It marks the last annulus of a somite. There is also a small black spot in the same annulus interrupting the inner light line. The ventral surface is greenish yellow spotted with black, or else black. The action of the spirit soon destroys these bright colours, as it has done here. *H. officinalis* has a median dorsal green band bordered by a red or brown line. The lateral dorsal regions are green with black and reddish-brown spots, sometimes grouped in two longitudinal lines. The amount of black pigment is very variable, and sometimes the red prevails. The ventral aspect is green, and as a rule not spotted. There are many intermediate forms between these two

varieties, but however much the colouration may change, the form of the teeth distinctive of the medicinal Leech remains constant (Leuckart).

The somite is not always composed typically of five annuli in Leeches. In *Branchellion* it has three, in *Pontobdella* four. The *Gnathobdellidae* appear to agree with *Hirudo*.

The ten-eyed Leeches of Japan possess six segmental papillae on the dorsal, and six on the ventral surface of the annulus that bears them.

The clitellar somites form the cocoon which contains the ova, a certain number of spermatozoa with albumen, the latter absent in *Piscicola*. The substance of the cocoon is secreted by the clitellar glands (*infra*). When it is fully formed, the animal withdraws its head, and the two ends of the cocoon close up. The openings are plugged by hardened albumen, through which the young Leeches eat their way when ready to escape. *Hirudo*, like *Aulostoma*, lays its cocoon in damp earth. The cocoon is usually attached to some foreign object in the water. Its shape is variable among Leeches.

The surface of the body is covered by a delicate cuticle perforated by pores, which are the apertures of unicellular glands. This cuticle is continually undergoing regeneration, the old one being peeled off, as may be readily seen in a *Hirudo* kept in confinement.

The epidermis or hypodermis of the medicinal Leech consists of mallet-shaped cells about  $\frac{1}{1500}$  of an inch long. The heads of the mallets are placed superficially beneath the cuticle. The handles are consequently separated by spaces, into which processes of pigmented connective tissue cells with capillaries make their way. The nucleus lies in the handle of the mallet. The hypodermis cells vary much in character in different Leeches, and in *Rhynchobdellidae* the pigment cells and capillaries do not always intrude between them.

From the hypodermis cells are produced numerous unicellular glands. In *Hirudo* these glands pass into the dermis, and their ducts are consequently long. Those of the general body-surface appear to be simply mucous glands. The more deeply situated glands are (1) clitellar glands, which occur in the clitellar region in groups of four to five, the glandular part lying in the longitudinal muscle layer; (2) prostomial glands of doubtful function, but probably found only in *Gnathobdellidae*, with ducts opening round the edges of the buccal cavity, and their contents not staining with borax carmine; (3) salivary glands, which belong to the buccal cavity itself, with ducts opening on the ridges which bear the teeth, and with contents which stain with borax carmine.

The hypodermis cells are also modified to form sensory cells, with which nerves are continuous. In the head region are found the goblet-like bodies and the eyes, the visual nature of which is doubted by Carrière. Of the latter there are ten, two on the first and second annulus, and two on the first annulus of the three following somites. Each eye consists of a projecting cap of short non-pigmented hypodermis cells, covered by cuticle and containing at their outer ends small refractile bodies: of an external layer of pigmented cells, separated by a lamina (?) from a layer of nucleated clear cells with well-defined walls and protoplasm largely replaced by a vacuole, and lodging a corpuscle of unknown significance: and of a

slender core of hypodermic cells as they appear to be from a comparison with the segmental papillae and from their histo-chemical properties (Whitman). The nerve enters at the side but near the base, and at its point of entrance there appear to be ganglion cells. The goblet-bodies and segmental papillae have a bulb-like thickening of the hypodermis cells, no pigmented coat, and relatively few clear cells. The former are exceedingly numerous (about sixty in number), especially on the anterior margin of the prostomium. They are situated on branches of the same nerves as the eyes. The Leech is sensitive to light, but the prostomial region appears to be equally if not more sensitive to other impressions (touch, taste?). The eyes of *Clepsine* differ from the eyes of *Hirudo*, and consist, according to Carrière, of a semi-globular cup of large pigmented retinal cells, containing a number of transparent and smaller cells. They are situated in the muscular coat. The eyes of *Nephelis* appear to be similar; those of *Piscicola*, a Leech in which they occur on the posterior as well as the anterior sucker, appear to be more simple, judging from Leuckart's figures. The visual nature of these eyes seems certain.

The sub-hypodermic tissues consist of a connective jelly-like matrix imbedding nucleated corpuscles with very fine branches, and more or less pigmented, as well as 'vaso-fibrous' tissue. The latter consists of nucleated branched cells, containing a plentiful supply of pigment granules. Their branches sometimes become tubular, and the nuclei project into the lumen, and even drop into it. These cells occur in all parts of the body, and their processes pass out between the hypodermic cells. According to Professor Lankester, the tubular cells may become continuous with the thin-walled capillaries, in the cavities of which free nuclei may sometimes be detected. The botryoidal or so-called 'hepatic' tissue, which surrounds, but not in immediate contact, the walls of the alimentary tract appears to be merely a modification of the same tissue. It consists of largish vessels with cellular walls. The individual cells are swollen up, nucleated, and pigmented. The vessels thus formed partly end caecally, partly form a plexus continuous with the ordinary thin-walled capillaries. The corresponding pigmented cells of *Rhynchobdellidae* never become tubular, and usually remain more or less rounded. In the same group, vacuolated cells and fat cells are found in the connective tissue matrix. They do not occur in *Gnathobdellidae*.

The muscles of the body are imbedded in the connective tissue matrix, leaving a sub-hypodermic layer free. They are arranged in an outer circular and a deep longitudinal series. Between the two are diagonal fibres. In *Hirudo* connective tissue with longitudinal fibres intervenes between the circular and diagonal layers. A set of dorso-ventral and radial fibres takes the place of the septa of Chaetopoda. The fibres of this series near the centre of the body pass between the caeca of the first portion of the alimentary canal. The outer ends of the radial fibres are branched, and end close under the hypodermis in the sub-hypodermic connective tissue. The muscle fibres themselves possess an outer fibrillate layer and an inner granular medulla with a nucleus. Their ends are often much branched, especially on the walls of the alimentary canal.

The amount of connective tissue matrix present, as compared with muscular fibres, is very variable in Hirudinea. Where there is little of it, as in *Clepsine* and *Nephelis*, the worm is perfectly firm and rigid to the touch when living. In *Aulo-*

*stoma* and *Haemopsis*, where it is plentiful, the animal is always limp. *Hirudo* occupies a middle position between these two extremes.

*Anatomy of the Hirudinea.* A. Gibbs Bourne, Q. J. M. xxiv. 1884. Remy Saint-Loup, A. Sc. N. (6) xviii. 1884. Leuckart, Die Parasiten, i. 1863, Leipzig. Moquin-Tandon, Monographie de la famille des Hirudinées, with Atlas (ed. 2), 1846, Paris. *Leeches of Japan*, Whitman, Q. J. M. xxvi. 1886. *Leech*, McIntosh, Encyclopaedia Brit. (ed. ix.), xiv. *Genera, &c.* Diesing, SB. Akad. Wien, xxxiii. 1858; Id. Systema Helminthum, 1850, i. p. 433, and Leuckart, op. cit.

*Somites*, Whitman, op. cit. *supra*; Proc. Amer. Academy, xx. (n.s. xii.) 1885, or American Naturalist, xviii. 1884.

*Cuticle, hypodermis, vasifactive and botryoidal tissue.* Ray Lankester, Q. J. M. xx. 1880. *Dark-green pigmented network of Hirudo.* Joseph, Z. A. vi. 1883. *Muscle.* Shore, Nature, xxvi. 1882, p. 493. *Nerve endings in ditto.* Hansen, Archives de Biol. ii. 1881.

*Eyes and Segmental papillae.* Whitman, Q. J. M. xxvi. 1886. *Eyes.* Carrière, Sehorgane der Thiere, München und Leipzig, 1885; Ranke, Z. W. Z. xxv. 1875. *Ditto and goblet-bodies.* Leydig, Arch. f. Anat. und Physiol. 1861; Id. Tafeln zur Vergleich. Anatomie, Tübingen, 1864, Taf. ii. figs. 5, 7; Taf. iii. figs. 1, 2, 3.

*Sense-cells of hypodermis.* See Gibbs Bourne, op. cit. p. 434, Pl. 27, fig. 15.

*Pigment of skin.* MacMunn, Proc. Birmingham Phil. Soc. iii. 1881-3, p. 389.

#### 43. MEDICINAL LEECH (*Hirudo medicinalis*),

Prepared to show its laterally sacculated stomach and the intestine. A stiffening injection of gelatine was thrown into the digestive tube, the specimen hardened in spirit and then dissected.

THE integument has been divided down the middle dorsal line and reflected to either side: the portions of the vascular system interposed between the digestive tract and the body-walls cut away, and the entire cavity of the 'crop' and its diverticula exposed by the removal of their dorsal wall. Anteriorly to the crop is the pharynx with a villous exterior. This appearance is due to the presence of numerous unicellular salivary glands and to the cut ends of radial muscular fibres. The pharynx is succeeded by the crop which has thin walls. Lateral diverticula or caeca which occupy five-sixths of the entire body are appended to it on either side. These caeca are really segmental dilatations of a central tube. There are eleven of them in all. The first is small. The second appears to be double. The third has much the same appearance but not so well marked. It is due to the great development of a partial septum which may be seen in the succeeding seven caeca projecting backwards from the anterior wall. In some species of *Clepsine* the caeca are very distinctly bifid at their outer ends. The last pair of caeca, the only pair in *Aulostoma*, are of very great length and bending sharply almost immediately at their commencement so as to become apposed to each other along the middle line, are prolonged back-

wards to a point on a level with the commencement of the rectum, and nearly as far as the end of the body. The form of the caeca, it should be noted, depends very much on their state of distension. This region of the digestive tract serves, first, as a crop or reservoir for the blood which forms the sole food of the animal, and, secondly, as a place where slow changes go on in the various constituents of that fluid. The oxy-haemoglobin is extracted by degrees from the corpuscles: it is reduced to haemoglobin and crystallised, and changes gradually take place in the corpuscles.

Between the two last caeca lies the stomach or 'gastro-ileal' (Gratiolet) section of the alimentary canal. A black bristle has been passed into it. It communicates by a narrow aperture with the crop, and at its commencement there is a pair of small caeca, one on the right, the other on the left, directed forwards. These caeca and the stomach are much larger in the Horse-leech (*Aulostoma gulo*). The stomach is very vascular, and it has a villous interior with a spirally arranged valve. The contents of the crop enter into it very slowly, and the red colour of the blood then changes from dark-red to green. The posterior end, colon or intestine, of this section of the alimentary canal is little vascular and contains no valve. It is followed by a short rectum of small calibre which terminates in a dorsally-placed anus, as in all Leeches except *Acanthobdella* where it opens in the centre of the posterior sucker. From a developmental point of view the pharynx and rectum must be regarded as invaginations from the exterior, i. e. as stomodaeum and proctodaeum, while the rest of the canal is archenteron, i. e. lined by endoderm or hypoblast.

The ventral nerve chain may be seen in part through the walls of the stomach. The spot where the walls of the caeca meet centrally (i. e. in the median tube) corresponds very nearly in most instances with a ganglion.

On either side of the crop and adherent to the inner surface of the reflected body-walls may be seen remains of the botryoidal tissue. It is arranged chiefly in four bands, two dorsal, two ventral, close to the walls of the digestive tract but separated from it by a layer of vaso-fibrous tissue and capillaries.

A section taken through the pharyngeal region shows, according to Gibbs Bourne, the following structures passing from within outwards: (1) Pharyngeal epithelium composed of minute cells; (2) three ridges, one dorsal, two lateral, composed of salivary ducts and radiating muscles, the branched ends of which abut upon the hypodermis; (3) a circular layer of muscles very dense and compact; (4) the longitudinal muscle layer of the body wall, in which occur blood sinuses, vessels, and salivary glands; (5) the diagonal and circular muscle layers of the body; and (6) the hypodermis and cuticle. To the three pharyngeal ridges correspond the three muscular jaws. They bear at their edges in the medicinal Leech about 80-90 fine chitinous teeth. These teeth contain lime carbonate both in *Hirudo* and

*Aulostoma*. Haycraft (P. R. S. xxxvi. 1883-84, p. 478) has proved that the secretion of the pharyngeal glands has the power of arresting coagulation in blood apparently by destroying the coagulation ferment. The muscle cells of the 'crop' are for the most part disposed in a transverse direction, and their ends are branched. Its epithelium is low, columnar, and the cells, according to Gibbs Bourne, may be seen giving off clear droplets into the blood. In *Aulostoma* the alimentary epithelium is ciliated. Its food consists of worms, &c. Moquin-Tandon states that when young this Leech possesses distinct lateral caeca to the crop in addition to the posterior pair. The region of the crop is not sacculated in *Nepheleis*, *Trocheta*, or *Pontobdella*. In the last two it is constricted at intervals, and the last-named possesses a posterior azygos caecum underlying the stomach. *Trocheta* is carnivorous like *Aulostoma*.

The body-cavity or coelome is in all adult Leeches almost obliterated by connective tissue growths. This process of obliteration of the coelome is termed by Gibbs Bourne *diacoelosis*. The remains of the coelome are much more conspicuous in the *Rhyncho-* than in the *Gnathobdellidae*. In the medicinal Leech its chief remains are in the form of the dorsal and ventral sinus, the latter lodging the nerve-cord. They are in *direct* connection only by means of the dorsal sinus of the gastro-ileal section of the alimentary canal. Other remains of the coelome are found in the network of vessels surrounding the testes, &c. The blood-vessels, which with their branches have *muscular* walls, are represented by a right and left longitudinal trunk which anastomose at the anterior and posterior extremities of the body. These trunks give off in each somite *latero-abdominal* vessels which anastomose ventrally, and two sets of dorsal vessels, short *latero-lateral* and long *latero-dorsal* branches. In the gastro-ileal region the latter anastomose *inter se* dorsally by means of their posterior branches. Anteriorly to this region they are connected only through the capillary system of thin-walled vessels. There is a superficial network of fine capillaries which penetrate the hypodermis, and more deeply pass into an intermediate layer connected with the lateral vessels and with the botryoidal tissue. The latter forms the deepest layer, connected on the one hand with the vessels given off from the lateral vessels, on the other hand with the sinuses. It tends to form a secondary coelome (= *metacoelosis*, Gibbs Bourne). The dorsal and ventral sinuses, according to Gibbs Bourne, communicate with (1) the cutaneous network, (2) the capillaries of the crop, and (3) of the stomach, and (4) the sinuses (moniliform hearts of Brandt) which surround the nephridial funnels and lie upon the testes.

The thin-walled capillaries of the Leech possess no endothelium and no nuclei. The walls of the vessels in the botryoidal tissue are formed solely by the pigmented cells themselves. The blood-plasma in the *Gnathobdellidae*, but not in *Rhyncho-*  
*bdellidae*, is coloured red by haemoglobin. It contains amoeboid corpuscles, and here and there Prof. Ray Lankester detected nuclei set free from the walls of the developing capillaries, as in the Earthworm. But they appear to be very scanty in number in the Leech.

*Bite of Leech*, Carlet, C. R. 96, 1883. *Lime in teeth*, Schneider Zool. Beiträge, i. 1885.

*Alimentary canal*. Gratiolet, A. Sc. N. (4), xvii. 1862, p. 182; Gibbs Bourne, op. cit. p. 492.



*Digestion of blood by the common Leech.* Stirling, Journal Anat. and Physiol. xvi. 1882.

*Vascular system and coelome.* Gibbs Bourne, op. cit. p. 453; Jaquet, Mittheil. Zool. Stat. Naples, vi. 3, 1885.

#### 44. MEDICINAL LEECH (*Hirudo medicinalis*),

Dissected so as to show its nervous system.

A PART of the pharynx with the jaws has been left *in situ*, and a black bristle also passed down it through the oesophageal or nerve-collar. The supra-oesophageal ganglion is seen above the pharynx, part of the glandular and muscular walls of which have been removed to show it *in situ*. It lies immediately behind the dorsally placed jaw, which is very visible in this preparation. It is connected by commissures forming an extremely narrow ring to the ventral chain of ganglia. This chain, counting the infra-oesophageal ganglion as the first of the series, numbers twenty-three ganglia in all. The infra-oesophageal ganglion and the second ganglion, which is closely apposed to it, are to be seen with difficulty here. The first ganglion, easily seen, is the third of the series. The longitudinal commissures between the third and fourth, the fourth and fifth ganglia increase in length, though they are shorter than those connecting the ganglia belonging to the middle region of the body. The sixth ganglion is concealed by the prostate gland at the base of the muscular penis. It is close to the seventh ganglion. The ganglia at the posterior extremity of the body, beginning with the nineteenth ganglion, are again closely aggregated together. The last ganglion is much larger than any of the series except the first.

It can be readily seen with the naked eye that nerves are given off laterally from each ganglion. They are in reality paired, but one branch is dorsal, the other ventral. There are no nerves given off between the ganglia in the Leech, as there appear to be in the Earthworm. But in the Leech the ganglion cells are really aggregated in the ganglia, not scattered along the whole cord as in the last-named worm.

In front of the supra-oesophageal ganglion lie three minute ganglia closely connected to it, one median and two lateral. The nerves given off by these ganglia supply the three jaws. The nerves originating from the supra-oesophageal ganglia supply the eyes and the goblet-shaped organs of Leydig.

The infra-oesophageal ganglion, according to Leuckart, is composed of three ganglia in the embryo which fuse in the adult. As figured by Leydig, it is composed of two halves, right and left, connected by five transverse fibrous commissures.

Through the four interspaces between these commissures and in front of the first one of the series small bundles of muscle fibres pass vertically. According to Leydig each ventral ganglion is pierced by a central hole which transmits a similar muscular bundle. The terminal ganglion of the chain is composed of seven embryonic ganglia. According to Vignal the distinction between these ganglia can be traced in the adult. There appears to be a larger number of fused embryonic ganglia in some other Leeches.

The infra-oesophageal ganglion gives off five nerves on each side. The two nerves given off by the other ganglia of the chain on each side are dorsal and ventral respectively. The ventral nerve of the third ganglion in the chain and its successors has a minute ganglion at the spot where it first bifurcates.

The ganglion cells in the Leeches tend to accumulate in masses on the outer surface of the ganglia. This follicular appearance is much more marked in some other instances than it is in *Hirudo*, e.g. in *Haemopsis* and *Nephelis*. At the point of origin between the two nerves of each ganglion on either side lies a large ganglion cell, the connections of which are not known. The fibrous commissures between the ganglia of the ventral chain are three in number, two large and lateral, one small, median and dorsal. The latter is the intermediary nerve of Faivre, its discoverer. Each of these commissures has its own sheath, and all three have in addition a common sheath, the outer surface of which is pigmented. The three commissures, according to Vignal, fuse centrally in each ganglion.

Brandt discovered in connection with the ventral surface of the crop a median nerve which bifurcates posteriorly in correspondence with the last pair of caeca. This nerve forms a rich plexus on the walls of the crop, and the filaments of the plexus are in connection with numerous ganglion cells. The exact mode of connection of this sympathetic system, which appears to be chiefly in relation with the muscles of the crop, to the ventral chain is not known. It takes place probably through branches of the nerves given off by the ganglia.

The ventral chain of ganglia is contained within a ventral blood sinus in all Hirudinea.

*Nervous system.* Leydig, *Bau des Thierischen Körpers*, Tübingen, 1864; Remy Saint-Loup, *A. Sc. N.* (6), xviii. 1884. *For figures*, see also Leydig, *Tafeln zur Vergleich. Anatomie*, Tübingen, 1864, Taf. i. figs. 4, 6, 7; Taf. ii. figs. 1, 3, and 5. Cp. figures of other genera on same plates and on Taf. iii. figs. 4 and 5.

*Histology only.* Vignal, *A. Z. Expt.* (2), i. 1883, p. 343.

*Lateral ganglion cell*, Leydig, *Tafeln, &c.*, Taf. ii. fig. 3, 1.

*Sympathetic nerve.* *Id. op. cit.* Taf. i. fig. 4; Taf. ii. fig. 5.

Hermann, *Centralnervensystem von H. medicinalis*, München, 1875; Hoffmann, *Untersuchungen über den Bau, &c. der Hirudeen*, Verh. Ak. Amsterdam, 1880; Köhler, *Système nerveux de Nephelis*, Nancy, 1883, have not been accessible to me.

45. MEDICINAL LEECH (*Hirudo medicinalis*),

Dissected so as to show its reproductive and segmental organs or nephridia *in situ*.

A BLACK bristle has been passed into the pharynx through the nerve-ring, and the ventral chain of ganglia is visible throughout the greater part of its extent. In the middle line, covering the sixth ganglion of the ventral chain, is seen a globular body, projecting chiefly to the left side of the nerve-cord and connected posteriorly with a median siphon-shaped muscular tube. The globular organ has walls partly muscular, partly glandular, and is called consequently the prostatic part of the male intromittent apparatus. The glands appear to secrete the material which forms the spermatophores. The median siphon-shaped tube is the copulatory organ or penis, and its walls contain both circular and longitudinal muscle fibres. From the base of the prostatic body passes to right and left a ductus ejaculatorius. These are each connected respectively to what is easily seen with attention to be a mass of coiled tube of a yellowish colour. The coiled tubes, according to Leuckart, contain at the height of the reproductive season numberless minute globules. The masses in question may be regarded provisionally as vesiculae seminales. Each coiled tube is continuous with a duct, the vas deferens, which passes backwards parallel to the nerve-cord. It is slightly tortuous. From its inner or median side nine branches arise, each passing to a testis. The nine pairs of testes are globular bodies lying close to the ventral nerve-cord, one behind each ganglion from the eighth to the sixteenth inclusive. They are therefore segmentally arranged. The prostatic apparatus, copulatory organ, and vesiculae lie in the tenth somite (Whitman), the male aperture being median and ventral in the second annulus of that somite. It is difficult to see unless the penis is protruded, as it sometimes is in this Leech and in the common Horse-leech, *Aulostoma gulo*, when the animal is killed by chloroform. The female organs lie in the eleventh somite (Whitman), therefore in the somite interposed between the first pair of testes and the male intromittent apparatus. Close behind the seventh ventral ganglion may be seen two roundish bodies, the capsules which contain the true ovaries, lying one on either side of the longitudinal nervous commissures. The oviduct is continuous with or rather perforates these capsules. Its anterior part is forked, one branch of the fork passing under the nerve-commissure to the left ovarian sac. The posterior part is single and may be distinguished by its yellow colour. It enters the base of an oval sac, the vagina, which has muscular walls and a cuticular lining and opens by a median ventral aperture in the second annulus of the eleventh somite.

Externally to each vas deferens and alternating in position with each testis, is a row of globular sacs only a very little less in size than the testes themselves. These are the vesicles of the segmental organs or nephridia. Each vesicle opens by a pore on the last annulus of its somite. In front of it, and in part externally to it, is a loop-shaped body. This is the chief part of the nephridium, representing the main and apical lobes of that organ. A narrow caecal process passes inwards from it and lies upon a testis. This is the testis-lobe which ends in the nephridial funnel or nephrostome. The funnel lies in a vascular sinus, the perinephrostomial sinus, or the moniliform heart of Brandt. The two pair of nephridia lying behind the last pair of testes in the twenty-first and twenty-second somites (Whitman), possess these sinuses as well as funnels, but this is not the case with the five first pair of nephridia which correspond to the somites six to ten (Whitman). There are in all seventeen pairs of these organs.

The azygos and median position of the generative pores is a noteworthy feature, as is also the development of a muscular intromittent organ. It is doubtful however whether they are of any importance in determining the affinities of Hirudinea.

The ductus ejaculatorius, according to Leuckart, has a stratum of circular muscle fibres in its walls. The vas deferens is surrounded by a space or sinus packed with cells, 'which possess a rather degenerate appearance' (Bourne). The sacs in which the true ovaries are lodged contain similar amoeboid corpuscles. It has been suggested by Gibbs Bourne that these spaces represent a portion of the original coelome, and the cells original blood corpuscles, and that they have been closed in by the growth of the connective tissue before haemoglobin appeared in the blood-plasma.

The true ovary is a filamentous body, 10 mm. long in some instances. It is coiled within the ovarian capsule. The oviduct opens into the capsule, but it is not simply continuous with the walls of that space. On the contrary, its anterior end is disposed in coils within it. These facts support the view quoted above from Gibbs Bourne as to the nature of the capsule. The median or single portion of the oviduct is surrounded by glands, by which the albumen mixed with the ova in the cocoon is secreted in all probability. The vagina has muscular walls, is lined by cuticle, and receives the spermatophores in congress. These bodies are stated to contain not only spermatozoa, but corpuscles similar to those found in the coils of the vesiculae seminales. They are resolved in the vagina, and the spermatozoa, now free, are said to penetrate into the ovarian capsules.

The ovarian capsules are sometimes of great length, as in *Nephelis* and *Clepsine*. In these genera 'egg-strings,' produced by the continuous division of a cell, lie free in the capsular cavity. The formation of the string from a ridge of the epithelium lining the capsule has been observed in *Nephelis*. The ova sometimes degenerate, and Schneider states that they are destroyed by amoeboid cells in the ovarian capsule. The same thing occurs with the spermatozoa. But the full

account of his observations on these points, and on the origin of the ova in various Leeches, has not been accessible to me. Joseph has recently discovered in *Clepsine* that the vasa deferentia and oviducts arise independently of the sexual glands. In *Branchiobdella*, (which is probably an Oligochaete), both ovaries and testes are proliferations of cells lining the coelome, and the generative products are carried away by ducts with open mouths, which are, perhaps, modified nephridia. It is quite possible that the glands and ducts have the same origin in the Hirudinea. The extension of the vas deferens through several somites, and the presence of nephridia in the same somites, creates a difficulty for this view,—the same difficulty, however, that recurs in the Earthworm.

The *Rhynchobdellidae* possess neither the tubular intromittent organ nor the muscular vagina.

The nephridial funnel of *Hirudo* appears to be degenerate. It is imperforate and multilobed. The lobed ciliated cells which compose it are set upon a vesicular dilatation containing a débris of cells. The various lobes of the nephridium are made up of nucleated cells, varying in size and character. These cells are perforated by intracellular ductules with independent walls. The ductules pass from one cell into another, and are branched, especially in the cells of the main lobe, some of the branches remaining caecal. The main duct has cellular walls, its lumen perforating the cell, as in part, at least, of the Earthworm's nephridium. The vesicle has thin walls with muscular fibres, and is contractile. It is lined by a ciliated epithelium. The cells of the gland are surrounded by a rich network of capillary vessels connected with the lateral blood-vessel, and through the testicular sinus with the main ventral blood sinus. The whole gland is invested with vaso-fibrous tissue.

Nephridial funnels appear to be present in all Leeches. They vary in complexity. Among the *Gnathobdellidae*, they are perforate in *Nepheleis* and *Trochaeta*, and in these genera they open into special spaces developed in the botryoidal tissue, termed by Gibbs Bourne 'metacoelome.' They are present and usually perforate in *Rhynchobdellidae*. In *Clepsine* they open into the ventral blood sinus, and in *Pontobdella* into a dorso-ventral sinus. In all Leeches the dilatation following the funnel appears to be present. As to the gland, in *Pontobdella*, *Branchellion*, and *Piscicola*, the tubules form a network continuous on both sides of the body and across the ventral median line. The funnels and external openings, however, of *Pontobdella* are metamericly arranged. *Branchellion* and *Piscicola* require further examination. There is no terminal vesicle in *Rhynchobdellidae*. The *Gnathobdellidae* in general appear to agree more or less closely with *Hirudo*.

Gibbs Bourne has found in the ductules of the nephridium in the medicinal Leech minute clear structureless bodies; in the liquid of the vesicle, and sometimes in the main duct, bunches of needle-shaped crystals, soluble in nitric acid.

According to Leuckart, the embryo of *Hirudo* has four pairs of nephridia in front of the first persistent pair of the adult, and three pairs behind the last persistent (or seventeenth) pair.

*Genitalia.* Leuckart, Die Parasiten, (ed. 1.) i. p. 672. *Ovary and ova of Nepheleis Aulostoma, Piscicola, Pontobdella.* Schneider, Das Ei und seine Befruchtung, Breslau, 1883. *Egg-strings of Clepsine*, Whitman, Q. J. M. xviii. 1878; *of Nepheleis*, Jijima, Q. J. M. xxii. 1882.

*Sinus of vas deferens and the ovarian capsule.* Gibbs Bourne, op. cit. p. 473.

*Spermatophores.* Cf. Robin, A. Sc. N. (4) xvii. 1862.

*Nephridia: of Hirudo,* Gibbs Bourne, Q. J. M. xx. 1880; xxii. 1882, p. 337;  
*of other Leeches,* Id. Q. J. M. xxiv. 1884, p. 478; Schultze, A. M. A. xxii. 1883.

#### 46. TAPEWORM (*Taenia serrata*),

With the cysts of *Cysticercus pisiformis*, s. *C. Taeniae serratae*.

IN the upper part of this preparation is suspended a portion of the great omentum of a Rabbit (*Lepus cuniculus*). Seven pyriform sacs may be observed attached to it, a group of three on the left-hand side and a fourth at the right-hand corner being especially conspicuous. These sacs are connective tissue cysts which lodge each a single individual and rarely more of the cystic stage (*Cysticercus pisiformis*) of *T. serrata*. See next preparation. The presence of the parasite, like the presence of any other foreign body, has had an irritating effect on the tissues of the omentum, and the consequence is the formation of a protective capsule. The brain and the eye are the only two parts of the body in which this capsule is never formed.

In the lower part of the preparation is suspended a Tapeworm, *Taenia serrata*, which inhabits the intestines of the dog. When a dog devours a rabbit, and swallows an encapsuled *Cysticercus pisiformis*, the head and neck of the latter develop into the Tapeworm, as it is seen here. The head and neck are displayed in the middle line, bent forwards and downwards. With the aid of a simple lens the head may be seen to possess a slight median projection, the rostellum, at the base of which is a circlet of chitinous hooks. The possession of these hooks constitutes the difference between an 'armed' and an 'unarmed' Tapeworm. 'Unarmed' Tapeworms are not found in the Carnivora. The head expands below the hooks, and bears four rounded pit-like suckers, one of which is turned towards the observer. It then contracts into a short unjointed neck. The neck begins to broaden out into the body of the worm, and it is at the same time divided by transverse lines into a series of joints. The first joints are almost linear: they then become broader and deeper, and finally their depth becomes greater than their breadth. Their posterior margin becomes at the same time remarkably prominent. The two last joints are of considerable length and comparative narrowness. They are ripe and ready to be detached.

If the lateral margins of the joints are attentively examined, one or other is seen to present near its centre a prominent papilla. This papilla is the projecting edge of the porus genitalis. It alternates generally, but not invariably, in succeeding joints from the right to the left side.

The head and neck are often termed 'scolex,' the joints, 'proglottides,' and the whole Tapeworm, 'strobila.'

There are five Tapeworms ordinarily found in the intestines of the dog. Of these, *Taenia Echinococcus*, derived from the cystic form *Echinococcus veterinorum*, which occurs in a variety of Mammals, consists as a rule only of a head and neck with three or, at the utmost, four joints. It is not much longer than an intestinal villus. *Taenia elliptica*, derived from the *Cysticercus T. ellipticae*, which inhabits the dog-louse (*Trichodectes Canis*), is recognisable at once by the elliptic shape of its ripe joints and the two pori genitales, one right and the other left. It also possesses a peculiar round rostellum beset with four irregular rows of sixty small hooks. The other three Tapeworms are not so easy to distinguish. They are *T. serrata*, derived from the *C. pisiformis* of the Rabbit; *T. marginata*, from the *C. tenuicollis* of the Sheep, &c.; and *T. coenurus*, from *Coenurus cerebralis* of the Sheep, and perhaps of the Rabbit.

*T. serrata* has the largest head (1.3 mm.), and a circle of 38-48 hooks, alternately large and small, the large hooks being 25 mm. long, and the length of the anterior branch of their forked roots very great; the proglottis, when ripe, is 8 mm. long and 3 mm. broad; the uterus, when full of ova, has 8-10 main lateral branches beset with numerous short ampullae. There are about 325 joints between the neck and the first ripe joint.

*T. marginata* has scarcely any constriction behind the head: the number of hooks is 22-42, the hooks being smaller than those of *T. serrata*: the proglottis is larger and longer; the uterus has about eight side branches which are much branched laterally. There are about 510 joints in front of the first ripe joint.

*T. coenurus* has a pyriform head; 24-32 hooks, which are small; the proglottis is smaller than that of *T. serrata*; the uterus has 20-25 simple branches. There are about 200 joints before the first ripe joint.

The egg-shell of all three is about .027 mm. in diameter, but in *T. serrata* it rarely bears processes as it does in *T. marginata*.

The rostellum of *Taeniae* often attains a greater size than it does in *T. serrata*. It has a special system of muscles. The same is true of the suckers which are composed of radial and equatorial fibres almost exclusively. The former deepen the cup, the latter contract its margin.

The surface of a Tapeworm is bounded by a vertically striated cuticula which, according to Griesbach, is a product of the gelatinous connective tissue of the body. The striae are due to pores<sup>1</sup>. Beneath the cuticle is a system of transverse or circular fibres which Leuckart considers to be muscular; Griesbach as elastic. The substance of the body in *Solenophorus* consists of a gelatinous matrix which forms a system of trabeculae with lacunar spaces representing the coelome. The matrix contains elastic fibres and nuclei, small rounded, as well as stellate cells, and therefore closely resembles the connective tissue of Mollusca (Griesbach). A fine granular protoplasm with nuclei (? cellular: see *infra* under *T. lineata*) covers the trabecula immediately below the cuticula, but does not appear to extend

<sup>1</sup> It has been said that protoplasmic processes extend into these pores from the granular protoplasm covering the subjacent connective tissue trabeculae.

continuously into deeper strata. There is a thin superficial layer of longitudinal muscles and two deeper layers, an outer of longitudinal and an inner of circular fibres, as well as a system of dorso-ventral fibres. The deep longitudinal and circular layers surround a nucleus or core of connective tissue which lodges the generative organs, the longitudinal excretory canals, and longitudinal nerves.

In *Taenia lineata* the cuticula has the same structure as in *Solenophorus*. There is a similar matrix which is finely granular. It contains large granular, oval, round or amoeboid cells, small fusiform or stellate cells, and scattered nuclei with or without traces of surrounding protoplasm. Tubular or vasiform spaces filled by a granular material lie immediately beneath the cuticula: they sometimes occur empty. There is also a layer of vertically spindle-shaped sub-cuticular cells which give origin to (?) the cuticula. They lose their individuality if the specimen is preserved only in alcohol. The deep longitudinal muscle-fibres are grouped in bundles and retain no trace of their formative cells, as do the dorso-ventral and circular muscle-fibres (Hamann). *T. serrata* has not been investigated by modern methods with reference to these points. The term 'parenchyma' is often used in speaking of the connective tissue substance of Cestoda. It is better discarded as the tissue in question is not cellular in structure.

The nervous system of *T. serrata* has been carefully investigated by Niemiec. It consists, as in some other *Taeniae*, of the following parts. A nerve-ring lies a little below the base of the rostellum. It gives off nerves to the muscles of the hooks, and contains eight slight ganglionic enlargements from each of which originates a stoutish nerve passing backwards. Two pairs of these nerves (*A, A*: *A, A*), situated at opposite extremities of the same diameter of the ring, unite each with one of the two lateral principal ganglia. The other two pairs (*B, B*: *B, B*) unite with the secondary transverse commissure and the polygonal commissures (*infra*). The two lateral principal ganglia are connected by a primary transverse commissure in the middle of which is a voluminous central ganglion. This ganglion gives origin to a slender secondary transverse commissure which lies at right angles to the primary transverse commissure and forks at either end. Each branch of the two forks unites with one of the nerves *B, B*, &c. *supra*, and with the superior polygonal commissure. The lateral principal ganglia and the nerves *B, B*, &c., are united by two ring-like polygonal commissures, one superior, the other inferior. The points of union of the nerves *B, B*, &c., with the secondary transverse and the polygonal commissures are swollen and form secondary ganglia, from which, as well as from the lateral principal ganglia, nerves are given off to the suckers

The nerves *B, B*, &c., are continued backwards through all the joints as slender filaments, two on each surface. Three longitudinal lateral nerves, a median stout nerve with a slender nerve on either side, extend backwards in a similar manner, and lie to the outer side of the longitudinal excretory trunks. They are said to degenerate in the ripe joints by Hamann. It is possible that branches may originate in some instances from the lateral nerves. Riehm states that they possess a swelling close to the posterior margin of each joint in *Dipylidium pectinatum* (= *T. pectinata* in part) of the Rabbit from which nerves pass both inwards and outwards. Similar swellings exist in *Ligula* and *Schistocephalus* (Kiesling). Their ganglionic nature is by no means certain.



The nervous system of *Bothriocephalus* and *Ligula* is said to be simpler than that of the *Taeniae*.

The excretory system of *T. serrata* appears to correspond in its main features with that of most *Taeniae*, a general description of which is given in the account of the Class Cestoda. Ciliated funnels have been detected by Fraipont in this Tapeworm and in its *Cysticercus* (Archives de Biol. i. 1880, p. 439). Leuckart figures the anterior anastomosis between the longitudinal vessels as consisting of a ring-like vessel with branches in connection with it (Parasiten (ed. 2), i. p. 379, fig. 153). Two longitudinal vessels are certainly present, perhaps four. P. J. Van Beneden does not figure a cross anastomosis at the posterior margin of each joint, nor does he mention the presence of valves; points which lack of material has prevented me from determining. He mentions, however, that treatment of the scolex with acetic acid causes an evolution of Carbon dioxide in the excretory canals which escapes by the foramen caudale or aperture of the pulsatile vesicle.

Peculiar rounded or elliptical bodies of a bright refractile appearance are found in the head and neck, and in the joints, especially the young joints, of all Cestoda. These bodies are very numerous in *T. serrata*. They are found principally in the superficial part of the connective tissue, but may occur also in the more central part where they are absorbed on the evolution of the sexual organs. They often show concentric lines like those of starch granules, and under the action of an acid they give off a gas, Carbon dioxide, which exists in combination with lime. Hence the name Calcareous bodies given to them. They contain a small amount of organic matrix, and are believed to be either calcified cells or portions of calcified cells. They lie, according to Griesbach, in the lacunae of the connective tissue, and he appears to think that they may enter the excretory system through direct communications between its cross anastomoses and the coelomic lacunae. It is certain that the excretory canals contain calcareous particles, and in certain Trematoda their branches have appended ampullae, in which lie calcareous bodies similar to the calcareous bodies of the coelomic lacunae in the Cestoda. The function of these structures is unknown; it may be partly excretory, partly skeletal.

For the generative organs of a *Taenia*, see Pl. xiv. (*post*), figs. 2 and 3.

The structure and development of the ovum in *T. serrata* have been carefully studied by E. Van Beneden. It consists of a delicate shell containing a germ or ovum-cell together with a quantity of a hyaline, homogeneous and colourless albumen or deutoplasm (=secondary yolk). The germ segments into two cells, one transparent, the 'embryogenic globe,' the other a 'granular cell,' which segments no further. The former of the two divides, and the result of its division is a number of cells of which (1) three are larger and constitute the 'albuminogenous layer;' (2) the remainder are smaller and constitute the 'embryonic mass.' The three cells (1 *supra*) enlarge and surround together with the 'granular cell,' the 'embryonic mass,' and secrete a delicate superficial cuticle, the cell-limits becoming indistinct. In the 'embryonic mass' there are three, four, or sometimes five flattened cells placed laterally and containing, unlike the remaining cells, nucleolated nuclei. These cells constitute a 'chitinogenous layer.' They give origin to (1) a superficial homogeneous coat; (2) a coat or shell of radially placed juxtaposed chitinous cylinders which increase in length at the expense of

(3) an internal faintly striated coat in which lie the degenerating nuclei of the chitinogenous cells. The remaining cells of the 'embryonic mass' become the hexacanth embryo or proscoplex, as it is called, and are arranged in an incomplete superficial set of more granular cells, and a contained set of clearer cells which protrude at one pole, but are probably grown over subsequently. The three pairs of hooks belong to the superficial set of cells. When the proscoplex is mature the original egg-shell and the albuminogenous layer of cells disappear, and it remains invested solely by its chitinous coat. The ova of some other *Taeniae*, e. g. *T. medioacancellata* s. *saginata*, appear to have a similar development. The ovum sometimes undergoes regular and equal segmentation, e. g. in *T. bacillararis*, and then the albuminogenous layer is formed by a layer of numerous cells raised from the surface of the embryonic mass. For figure of proscoplex, see Pl. xiv. fig. 4.

Van Beneden regards the albuminogenous layer of cells as the homologue of the ciliated coat of cells or 'embryophore' of some species of *Bothriocephalus*, of *Schistocephalus*, and *Ligula*. Moniez, on the other hand, considers the chitinogenous set of cells as the homologue of the same structure; but he missed the albuminogenous coat in *T. serrata*, &c., though he appears to have detected it in other Tapeworms. Leuckart's account agrees essentially with Van Beneden's. The latter thinks the successive coats of cells, formed as above, are to be considered as layers of ectoderm cells thrown off one after the other.

The last joints of a *Taenia* contain the uterus alone of all the genitalia, laden with the proscoplices contained within their chitinous coats. They are detached either singly or in small numbers. For their subsequent fate, see next Preparation. Some Cestoda possess a uterine aperture, and the ova are consequently discharged at an earlier stage, e. g. *Bothriocephalus*.

*Parasites of Man and diseases resulting from them*, Leuckart, transl. by W. E. Hoyle, Edinburgh, i. 1886; the German original 'Parasiten des Menschen,' i. (ed. 2), 1881; ii. 1876. *Parasites*, Cobbold, London, 1879. *Vers Intestinaux*, P. J. Van Beneden, Paris, 1858 (or Supplément aux Comptes Rendus de l'Acad. des Sci., ii. 1861); *Vers Cestoides*, Id. Mém. de l'Acad. Roy. Belg. xxv. 1850. *Les Cysticerques*, Moniez, Travaux Inst. Zool. Lille, iii. 1, 1880; *Les Cestodes*, Id. pt. 1, ibid. iii. 2, 1881.

*Lists of Parasites and Hosts*, von Linstow, Compendium der Helminthologie, Hannover, 1878.

*Cestodes of Hares and Rabbits*, Riehm, Inaug. diss. Halle, 1881 (Zeitschr. f. d. ges. Naturw. Giebel, 54, 1881). *Taenia lineata*, Hamann, Z. W. Z. xlii. 1885. *T. perfoliata*, Kahane, Z. W. Z. xxxiv. 1880. *Solenophorus*, von Roboz (Beiträge, &c.), Z. W. Z. xxxvii. 1882; Griesbach (Beiträge), A. M. A. xxii. 1883. *Triaenophorus*, Megnin, Journal de l'Anat. et Physiol., 1881. *Ligula* and *Schistocephalus*, Kiessling, A. N. 48, 1882.

*Suckers*, Niemiec, Recueil Zool. Suisse, ii. 1885. *Connective tissue, &c.*, Griesbach, on *Solenophorus* (*supra*). *Ditto, and muscular tissue*, Hamann on *T. lineata* (*supra*).

*Nervous system*, Niemiec, Recueil Zool. Suisse, ii. 1885; cf. Lang, Mitth. Zool. Stat. Naples, ii. 1881.

*Excretory system*, Fraipont, Archives de Biol. i. 1880; ii. 1881. Pintner (Untersuchungen, &c.), Arb. Zool. Inst. Wien, iii. 1881.

*Coelome*, Fraipont, op. cit.; cf. Van Beneden and Ray Lankester, Z. A. iv. 1881; v. 1882. Griesbach on *Solenophorus* (*supra*).

*Sexual organs of T. mediocanellata* (= *saginata*) and *T. solium*, Sommer, Z. W. Z. xxiv. 1874; of *Bothriocephalus*, Id. and Landois, Z. W. Z. xxii. 1872.

*Development of proscoplex from ovum in T. serrata*, E. Van Beneden, Archives de Biol. ii. 1881. For general account, see Moniez, Travaux Zool. Inst. Lille, iii. 2, and Leuckart (*supra*).

#### 47. TAPEWORM IN CYSTIC STAGE (*Cysticercus pisiformis*, s. *C. Taeniae serratae*),

Mounted as a preparation for the microscope.

THE worm has been removed from its connective tissue sac or capsule, and the head with a small portion of the neck has been evaginated by gentle pressure from the vesicle, or proscoplex, within which it is generally retracted. The vesicle has delicate walls, and in life is distended by a liquid which contains only a trace of albumen and is little more than a solution of salts, chiefly of sodium.

Under the microscope, using a  $\frac{1}{2}$ -inch objective, the principal features of the head may be readily made out: the slightly projecting rostellum: the circlet of hooks and the suckers. The hooks are arranged in alternation, one large with one small. The free part of a large hook is longer and somewhat straight as compared with the corresponding part of a small hook. The imbedded portion or root is in both cases forked, but the anterior (or rostellar) branch of the fork is of remarkable length in the large hooks.

In the neck, especially in the part not completely evaginated, may be noticed numerous clear rounded bodies. These are the calcareous bodies, or concretions: see *ante*, preceding preparation, p. 227. They do not exist in the walls of the vesicle.

The life-history of *Taenia serrata* is briefly as follows. The ripe proglottides are scattered among the grass by the way-side, &c., and are swallowed by a Rabbit, the soft tissues being digested in the stomach, and the chitinous shells containing the hexacanth embryos or proscoplices set free (cf. p. 228): or the proglottides decay naturally and set free the contents of their uteri, which are then eaten with herbage. The chitinous shell of the proscoplex, under the combined influence of warmth and the gastric juice, becomes brittle, and either break up spontaneously or is broken by the movements of the embryonic hooks. The embryo, now free appears to bore its way into the tissues: and it has been found in the portal blood by Leuckart. The embryos of *T. marginata* have been similarly found by Leisner in the portal capillaries of the Lamb. The parasite sojourns for about four

weeks in the liver, in which it creeps about. It then escapes into the abdominal cavity, and becomes encapsuled either on the omentum or mesentery. The *Cysticercus* of some Tapeworms, e.g. of *T. solium*, is generally found in the connective tissue of muscles, &c. In these instances the hexacanth embryo probably migrates through the tissues, not through the blood-current.

The changes undergone by the embryo are as follows. It grows in size, and in the case of *C. pisiformis* becomes elongate, and the hooks are lost. The central cells enlarge and become clear. The subcuticular muscles are differentiated, and at a later period a system of more deeply placed muscles. Between the two layers of muscles intervenes a layer of cells. It is from a meniscus-like thickening of this cell-layer, which is developed at the anterior end, the end where the hooks remain attached in *C. Arionis*, that the head and neck of the future Tapeworm are developed. The head may be formed however, as in *Archigetes Sieboldi*, at the opposite end, the one at which Moniez asserts that it is always formed<sup>1</sup>. At the same time a network of excretory vessels appears. It opens to the exterior by a posteriorly placed pulsatile vesicle. The finer vessels end in ciliated funnels. When the organism has attained a length of 4 mm. the central clear cells break down and give rise to a central accumulation of liquid. In some instances this change takes place at a much earlier period: in others, e.g. in *Piestocystis* or in the *Cysticercus Taeniae ellipticae*, or of *Tetrarhynchus*, in a word, in the majority of Cestoda the central cells do not thus liquefy<sup>2</sup>.

When *C. pisiformis* is about 2 mm. long, the meniscus of cells above-mentioned begins to develope. It grows inwards, pushing before it the deep layer of muscles which form a receptaculum capitis. When it has reached a certain size, a depression appears externally, and thenceforth the meniscus grows inwards as a hollow cone. The cavity of this cone widens at its inner or deep end, and here the rostellum, hooks, and suckers are developed; but it is only when the cone is wholly or partly evaginated that they appear in their ordinary shape. In the position in which they are developed they are, as it were, inverted. When the head and neck are evaginated the *Cysticercus* appears to be divisible into three parts, (1) the head and neck proper, or scolex; (2) the basal part of the invagination or hollow cone, and (3) the proscœlex or vesicle. When such an encapsuled *Cysticercus* is transferred to the stomach of a dog, the inclosing cyst is digested together with the parts, (2) and (3) *supra*: and only the head and neck pass on into the intestine. Here the head attaches itself by its hooks and suckers, and in forty-eight hours growth has proceeded so far that there are well-marked indications of 12-18 joints.

<sup>1</sup> Leuckart states that the excretory system of *Archigetes* opens externally near the posterior end of the scolex or sexual worm, i.e. the end to which the proscœlex or vesicle is attached. The excretory system of the scolex and proscœlex, e.g. of a *Cysticercus*, opens externally at the end of the proscœlex opposite to that at which the scolex is attached. If Leuckart's statement is correct, it shows that the scolex of *Archigetes* develops from the proscœlex in an unusual position and tends, therefore, to invalidate the assertion of Moniez referred to in the text.

<sup>2</sup> Moniez states that the proscœlex when 1 cm. long and less than 1 mm. broad divides transversely, the two parts being connected by a slender pedicle which ruptures. The anterior half develops the head: a rudiment of a head (?) was observed only once in the posterior half. The point of attachment of the pedicle to the anterior half is marked by a persistent depression, the foramen caudale. The fate of the posterior half is not known for certain. Non-division of a *Cysticercus* is, according to Moniez, the reason why the proscœlex sometimes attains such large dimensions.

The proscölex in *T. serrata* gives origin to a single scolex, and the resulting organism is therefore termed *Cysticercus*. When it produces a number of scolices, the resulting organism is a *Coenurus*, e.g. *C. cerebralis* of the Sheep, the cause of the disease known as 'sturdy,' 'gid,' or 'staggers;' and when scolices are produced not directly by the proscölex, but indirectly from 'brood-capsules,' which originate from the proscölex in the first instance and remain attached to it, the organism is an *Echinococcus*.

For Figure of *Coenurus*, see Pl. xiv. fig. 5.

The cyst in which the *Cysticercus* lies is formed by the irritated tissues of its host. Its inner surface is covered by a layer of epithelioid cells: its walls are composed of connective tissue and contain blood-vessels. The whole structure is produced, apparently, by the metamorphosis of lymph-cells.

The life-history of *T. serrata* and of other Cestoda is generally supposed to include three successive generations: two asexual, the proscölex and the scolex; one sexual with numerous individuals, the proglottides. The last-named are supposed to be produced, one after another, by posterior gemmation of the scolex, from which they are detached in many instances either singly or in groups. Many interesting features of resemblance between a fully-formed proglottis and a Trematode have been pointed out by P. J. Van Beneden (cf. *Vers Intestinaux*, p. 251, and Pl. xxvii). But the facts do not appear to necessitate the view that the proglottis is an individual: and Riehm especially has drawn attention to certain particulars. The setting free of a proglottis may be paralleled with the setting free of the hectocotyliised or sexual arm of many male Cephalopoda: the formation of new proglottides with the re-development of this arm, or to the building up of a complete worm from two or three somites, as in the Oligochaete *Lumbriculus variegatus*. Considered as an organism, a proglottis is unable to maintain its own existence: it has no organs of adhesion, and as a rule it is placed by its detachment under destructive influences. If however it remains under favouring circumstances, i.e. within the intestine, it may increase in size (*Vers Intestinaux*, p. 249; *Vers Cestoides*, pp. 123, 143), just as the fragments of a Nemertean may continue to live and mature sexual products. However, both Leuckart and Van Beneden are inclined to regard this fact as decisive for the zooid-nature of a proglottis. But it is not clear from Van Beneden's account to what the increase is due; nor perhaps is it absolutely certain that dissection of the host may not cause separation of the joints from the strobila. Such separation often occurs with the slightest disturbance (cf. *Vers Cestoides*, p. 139). Turning to anatomy;—though the deep longitudinal muscles do not extend across the interval between successive joints, and are interrupted even in *Ligula*, yet there are longitudinal muscles which do so (Riehm); the nervous system is continuous throughout the worm: so too the excretory system, but the transverse anastomoses of the *Taeniae* do not exist in other forms; the ovaries of *Ligula* appear to be continuous (Moniez), and discharge of the proscölices from the uterus may take place long before the joints are detached, e.g. in *Bothriocephalidae* and *Ligulidae*. Moreover the primitive terminal joints may remain barren or develop sexual products at a relatively late period. The degree to which segmentation is marked externally is variable: and in *Triaenophorus* and *Ligula* is scarcely discernible, much less so in the latter than in the former. The formation of joints is usually held to depend on the evolution of the sexual organs. It is

however well marked in the young *Ligula*, much less so in the sexual worm: so too *Triænothorus*. It exists in the barren posterior region above-mentioned, but this may be considered as arrested in growth. The setting free of the joints may well be an adaptation, and is possibly due to the completed development of the embryos and consequent regressive metamorphosis of the genitalia.

Other regressive changes appear to occur at the same period. Hamann states that the nerves degenerate in the ripe joints of *T. lineata*: and Megnin contends that the scolex may lose its hooks and its suckers, and may even atrophy away completely. See Journal de l'Anat. et Physiol. xvii. 1881. Such changes may occur, according to him, in *T. serrata* and *T. solium*. Donnadieu found that *Ligula* sometimes undergoes digestion when its ripe ova are discharged. Facts such as these show that no absolute conclusion can be based on the growth of joints after their detachment in the tapeworms of some fish (*supra*).

As to the two supposed asexual generations, the proscölex and the scolex, the question appears to turn on the following points: the asexual reproduction of the proscölex as proscölex: the mode in which the scolex takes origin from the proscölex: the character of the connection between proscölex and scolex: and the apparent necessity for two hosts.

The proscölex does not generally multiply itself asexually, but gemmation takes place in the *Staphylocystis* of Villot, in *Echinococcus* (?), and in an Echinococoid form discovered by Metschnikoff (cf. Leuckart, 'Parasiten,' i. p. 464); and it is possible that an imperfect fission may sometimes occur, e.g. in *Coenurus*. Such increase may be compared with the fission of a Trematode *Sporocyst*, e.g. of *Fasciola hepatica*, an undoubted representative of a generation, or with its gemmation as in *Leucochloridium*: with the division of the embryo *Lumbricus trapezoides*, an immature individual: with the formation of germs by the tail, i.e. an organ, of the *Cercaria*-larva, *Bucephalus polymorphus*, or of *Cercaria cristata*, according to the observations of Ercolani: or with the separation of parts of the hydrocaulus or stem which develop into individuals in a Campanularian, the *Schizocladium* of Allmann. In other words, the occurrence of asexual reproduction does not necessarily prove that the proscölex is an individual.

The scolex is derived from a local thickening of a layer of cells, part of the body-wall of the proscölex: but its muscular layers and its excretory system become completely continuous with the corresponding structures of the proscölex. This mode of origin is utterly unlike the way in which germs originate from the walls of a Trematode *Sporocyst* or *Redia*, viz. by the growth and division of a cell from the layer lining the coelome, or from the mass filling it at first (cf. Thomas, Life History of the Liver Fluke, Q. J. M. xxiii. 1883, p. 125, and figs. referred to): nor does it resemble the mode in which buds are formed in the Metazoa with the participation of all the germinal layers. With reference to this last point, however, it must not be forgotten that the germinal layers are at no period distinct in the Cestoda. It may be added that in a form discovered by Gruber (Z. A. i. 1878) in *Cyclops serrulatus*, there is no apparent proscölex at all, and the scolex develops without invagination.

The proscölex and scolex may remain permanently attached to one another as in *Archigetes Sieboldi*. The connection may only be severed when the first joints are detached, as in many Phyllobothrians and Phyllacanthians which infest fish.

Or the scolex may separate from the proscœlex, and either enter an intermediate host, e.g. some species of *Tetrarhynchus*, or even in rare instances remain free (cf. Moniez, Travaux, &c. iii. 1, p. 142). Finally, the proscœlex may be digested in the stomach of the second host, but so also are the barren joints formed by the scolex of *Cysticercus fasciolaris* (= *Taenia crassicollis*) while still encapsuled in the Mouse. There is evidently much variety observable with reference to the character of the connection between the two structures.

It is a general fact that two hosts are necessary for the evolution of a Cestode. *Archigetes* however is an example of the sufficiency of a single host. *Ligula* attains immature sexuality in a fish, its first host, so that a few days' sojourn in its second host, a water-bird, brings about sexual maturity. *Taenia solium* may exist in the flesh of man in the Cysticercus-stage, in the alimentary canal as a Tapeworm; and it has been shown by Riehm and Leuckart that the scolex of *C. pisiformis* may develop into a jointed and sexless worm in the intestines of the Rabbit, but whether it would ever attain sexual maturity under these conditions is doubtful. That the proscœlex may develop in an alimentary canal is proved by P. J. Van Beneden's discovery of proscœlices with scolices in all stages of growth in the intestine of the Lump-fish (*Cyclopterus*). The same thing possibly occurs also with other Tapeworms inhabiting fish. Why there should be two hosts is a most obscure question. Leuckart appears to think that there is a physiological connection between the two, inasmuch as one is the prey of the other. Moniez has broached the idea that a change from one to another host is, in these animals, which are so completely parasitic and therefore dependent, necessary to maintain their vigour.

The facts adduced certainly weaken the generally adopted view as to the existence of an Alternation of Generations in the Cestoda. There can be little doubt that the strobila is to be regarded as a single organism, and the same statement is probably true of the scolex and proscœlex<sup>1</sup>. It is evident that the Cestoda are profoundly modified by parasitism, not only structurally but developmentally. The study of lower forms in the class may throw more light on the many obscure points connected with its evolution, but unfortunately there are great intrinsic difficulties in the way of such an investigation.

*Development of scolex and life-histories.* Leuckart, op. cit., Moniez, Les Cysticerques, and P. J. van Beneden, Vers Intestinaux and Vers Cestoides; see p. 228, ante.

*Archigetes Sieboldi*, Leuckart, Z. W. Z. xxx. (Suppl.), 1878; Gruber, Z. A. iv. 1881.

*A Gemmating proscœlex, Staphylocystis*, Villot, Ténias des Musaraignes, A. Sc. N. (6), viii. 1879; *Urocystis*, Id. A. N. H. (5), vii. 1881.

*On the question of Alternation of Generations in Cestoda*, see Riehm, Zeitschr. f. d. ges. Naturw. (Giebel), 54, 1881, p. 590; Moniez, Les Cysticerques, op. cit. pp. 135-154; Leuckart, Die Parasiten (ed. 2), pp. 488-490; P. J. van Beneden, Vers Intestinaux, p. 242 et seqq. *Comparison with Trematoda*. Van Beneden, ibid. p. 251 et seqq.

*Parasitism.* P. J. van Beneden, Animal Parasites and Messmates, Internat. Series, xix. 1876.

<sup>1</sup> Moniez regards the scolex simply as an organ of adhesion. To this view Niemiec opposes the character and degree of development attained by the central nervous system which is always lodged in it.

48. BROAD-LEAFED HORNWRACK (*Flustra foliacea*),

With Figure 10.

A seaweed-like Polyzoan, universal in European seas and widely spread over the world. It is colonial, like the vast majority of Polyzoa, and the colony or zoarium forms erect fronds which spring from a small basal portion, spread over some foreign object in the fashion of a *Membranipora*. The fronds vary in outline in different specimens: they are flexible owing to the small amount of calcareous matter deposited in the chitinous walls of the zoëcium, i.e. the resistant part of the ectocyst of the individuals making up the colony. They are composed of two lamellae, in which the zoëcia are placed back to back. Some species of the genus, however, have the zoëcia disposed in only one lamella. The zoëcia themselves are arranged in parallel longitudinal rows, and the zoëcia in one row alternate in position with the zoëcia of the adjoining rows to either side. An individual zoëcium is elongate in shape, with one, the distal, end curved or rounded, and the other, the proximal, end somewhat contracted. The margin of the rounded distal end bears two spines to either side the middle line, and in some cases a fifth single spine placed centrally. A whitish spot near this end, readily visible under a lens, marks the position of the retracted fore-part of the individual or tentacle-sheath which bears the circlet of tentacles. New zoëcia are added to the colony at the curved edges of the fronds.

*Flustra foliacea* generally grows upon stones or shells at moderate depths, but may occur in deeper water (sixty-two to seventy fathoms). It possesses a strong and peculiar smell when first taken from the water, and its fronds form a favourite resting place for other Polyzoa and various Hydroids.

The anatomy of *Membranipora (Flustra) membranacea* has been well studied by Nitsche, and is illustrated in Fig. 10 A. It is abundant and universal on our coasts. The colony is composed of a single lamella in which the zoëcia are disposed in parallel series, alternating as in *Flustra foliacea*. The zoarium is attached to the fronds of *Laminaria* and *Fucus*, and may attain the length of several feet.

The zoëcium or cell is in outline a parallelopiped. One surface, the lower, is attached; the other, the upper, is free. It has two elongated sides and two short ends. Of the two ends, one, that to the left in the figure, is proximal, i.e. near to the original parent zooid; the other distal, i.e. near to the growing free edge of the colony. A spine (*Sp.*) projects from the free surface at each of the two proximal angles. The mouth so-called, or aperture made by the retraction of the flexible fore-part or tentacle-sheath of the zoëcium, is placed distally on the free surface. It is crescentic in outline, and its proximal edge or lip (*op.*) is thickened, forming the operculum, a structure from which the suborder *Cheilostomata* takes its name.



The wall of the zoëcium is composed of a cuticle or ectocyst and an endocyst. The former (*e.*) is chitinous, and the chitin of the base of the two spines, of the two ends with their angles, are strengthened by calcareous matter, and a calcareous plate also occupies the greater portion of each side. Each end is perforated in two places, each side in four places, by a set of pores. These pores are grouped within circular areae with raised margins, and are known as 'rosette' or 'communication' plates (*r.*). The endocyst (*e'*.) is thin and delicate. Over the rosette plates it consists of columnar cells. Elsewhere it is membranous, containing scattered nuclei surrounded by masses of protoplasm. Two cords of fusiform cells, applied to the endocyst of the lower surface, connect the rosette plates at one end with the corresponding plates at the other end. These cords anastomose *inter se*,

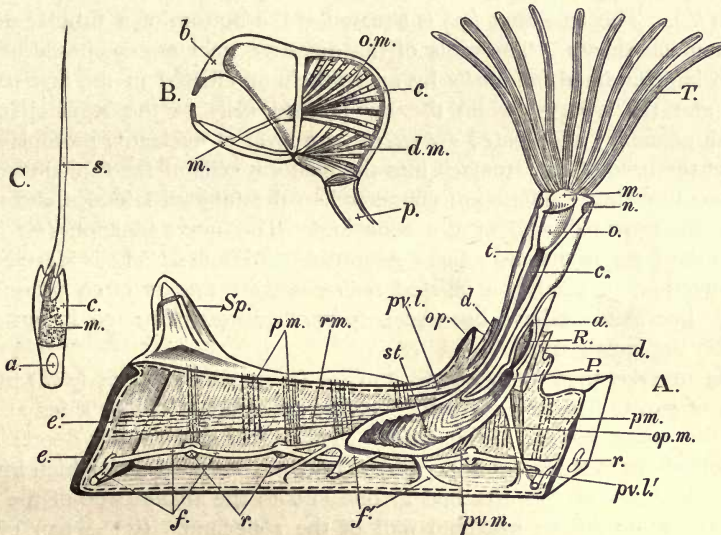


Fig. 10. *A.* Longitudinal section, magnified, of *Membranipora (Flustra) membranacea*, after Nitsche.

*B.* Avicularium (typical), after Hincks.

*C.* Vibraculum of *Scrupocellaria scruposa*, after Hincks.

and with the lateral rosette plates. Other cords, the funiculi laterales (*f.*), composed of superficial fusiform cells surrounding a granular axis, run from one to the adjoining rosette plate, and are connected also to the funiculi of the stomach (*f'*).

The fore-part of the body or tentacle-sheath<sup>1</sup> when retracted is contained within the basal part. In Fig. 10, *A.* it is represented as fully expanded. Its

<sup>1</sup> The term 'polypide' is often used to denote 'the zooid, consisting of alimentary canal, with tentacles, nervous ganglion, &c., which is developed within the zoëcium;' and then 'zoëcium' (=cell, auct; cystid, Nitsche; Brutkapsel, Reichert) denotes 'the chamber in which the polypide is lodged' (Hincks). The term zoëcium is used here and in the general account of Polyzoa to denote the thickened part of the cuticle which persists after the death and decay of the rest of the organism. It is simply a skeletal structure. The term polypide is discarded altogether. For the view that a Polyzoan consists of two distinct animals, i. e. zoëcium, and tentacle-sheath + digestive tract, is now known to be erroneous, and the use of the word only tends to maintain the error.

proximal portion is retained in a folded condition by certain ligaments and muscles. The summit of the fold forms a circular 'diaphragm' (*d.*), which contains a muscular sphincter, and closes over the tentacle-sheath (*t.*) when it is invaginated. The walls of the tentacle-sheath are homogeneous and contain nuclei, and are probably covered, as in other Polyzoa, by a delicate cuticle. It is crowned by a cirlet of hollow, ciliated tentacles (*T.*), usually eighteen in number. The mouth (*m.*) lies in the centre of the cirlet, and the cilia on the oral surfaces of the tentacles which work towards the mouth are longer than those on their aboral surfaces. The digestive tract consists of a more or less cup-shaped pharynx or oesophagus (*o.*) separated by a constriction from the stomach, which is divisible into a cardiac tubular portion (*c.*), a caecal sac (*st.*) and a pyloric region (*P.*), which is bent upwards on the distal or anal surface of the cardia. It ends with a short rectum (*R.*). The true anus (*a.*) is situated at the bottom of a tubular depression of the tentacle-sheath. The walls of the digestive tract are composed of a homogeneous lamella, lined *internally* by an epithelium, ciliated in the first part of the cardia, and the pylorus, while the non-ciliated cells of the stomach contain a brownish pigment; and coated *externally* by a layer of nucleated protoplasm, which passes at the base of the stomach into the fusiform cells of the funiculus (*f.*) with its various branches. These are connected to the funiculi laterales and the endocyst of the proximal wall of the zoëcium. The nerve-ganglion (*n.*) is placed between the oesophagus and anus. According to Hincks (British Marine Polyzoa, i. Introduction, p. lxxxix), a ciliated *intertentacular tube* is often present in this species. Spermatozoa have been seen to pass outwards through it, but it is also present in the female zooid.

The muscles present in a zoëcium are (i) parietal muscles (*pm.*) formed by bundles of two to five fibres, attached to the basal angle of the sides at one end and to the upper surface at the other. This upper surface they depress. (ii) A pair of opercular muscles (*op.m.*). (iii) A retractor muscle (*rm.*), which invaginates the tentacle-sheath and is attached at one end to the abanal side of the oesophagus, at the other to the proximal wall of the zoëcium. (iv) A pair of parieto-vaginal muscles (*pv.m.*) attached to the base of the fold surrounding the tentacle-sheath, and situated close to the opercular muscles on the anal side of the digestive tract. (v) The muscles of the tentacle-sheath. These are arranged in two layers—a circular, which forms a sphincter near the base of the circle of tentacles; a longitudinal, the fibres of which are collected towards the base of the sheath into four bundles—two on the abanal, two on the anal side. The two first form the superior parieto-vaginal ligaments (*pv.l.*), and are attached to the upper zoëcial wall; the two latter form the inferior parieto-vaginal ligaments (*pv.l'.*), and are attached to the inferior zoëcial walls close to the angles of the distal end.

The parent zoëcium of the colony has a rounded outline, and gives off numerous buds. In the colony, when once established, new zoëcia are formed as buds in the same linear series as the old zoëcia. A bud of unusual width may divide longitudinally, thus originating two parallel series in the place of one. The endocyst of the growing bud is composed of two distinct cell-layers—an outer set of columnar cells, an inner set of fusiform cells. The latter persist in the funiculi laterales, and other cords of cells, but are indistinct in other parts of the zoëcium. In the fresh-water Polyzoa there is an inner layer of ciliated cells. The new

zoöecium is cut off in the bud by a double fold of the endocyst, which grows inwards from all sides simultaneously, and finally closes in the centre. The dividing wall of ectocyst is formed between the two halves of the fold.

If a zoöecium is situated at the free edge of the object on which the colony grows, or is in contact with some obstacle, its upper surface develops a large cylindrical outgrowth three to four times as high as the zoöecium is long, with a thickened ectocyst, in which, however, no calcareous matter is deposited. Such zoöecia are termed by Nitsche 'Turret-zooids.' They possess neither tentacles, tentacle-sheath, nor digestive tract. Under normal conditions these organs are developed within the new-formed zoöecium by a process perhaps not yet fully explained. Every zoöecium remains in connection with its neighbours by means of the 'rosette' plates, the columnar cells covering them, and the system of funicular cords (*supra*), to which a nervous function was at one time assigned.

*Flustra foliacea* resembles *Membranipora membranacea* in all essential features. It possesses thirteen to fourteen tentacles; its tentacle-sheath and digestive tract are long, and much bent and folded in the retracted condition. It possesses Avicularia, but they are not much modified in shape from the ordinary zoöecium. An Avicularium is a zooid in which the digestive tract is aborted with the tentacles and tentacle-sheath, whilst the rest of the zoöecium and the operculum persist. In its most specialised form, e.g. in *Bugula* (Fig. 10. B.), one of the *Cheilostomata*, the avicularium is borne upon a moveable peduncle (*p.*); the operculum has become a moveable mandible (*m.*), the zoöecium a hollow chamber (*c.*) bearing the mandible, containing posteriorly a set of divaricator (*d.m.*) and occlusor (*o.m.*) muscles, and anteriorly fashioned into a beak (*b.*). Between this highly specialised form and the simple form seen in *Flustra* all degrees of specialisation may be found. In some *Cheilostomata* another remarkable form of zooid, shown in Fig. 10. C., occurs. This is the Vibraculum. It possesses a moveable seta (*s.*), the homologue of the operculum carried on a simple chamber (*c.*) containing the muscles (*m.*) that move the seta. A long tubular appendage originates in many instances from such a Vibraculum in the lower part of the chamber. Transitional forms from such a Vibraculum as this of *Scrupocellaria* to the Avicularium or zoöecium are to be found. The function of the Avicularium is doubtful. In the most specialised forms the surface of the beak turned to the mandible has a small depression, from which project a number of tactile (?) setae with a cellular ganglionic (?) body at their base. The mandible is in constant motion, and the Avicularium has been observed to catch and retain small worms. In the less specialised forms, however, such an action would be impossible. The Vibracula are swept from time to time over the surface of the colony, sometimes with apparently concerted action, as e.g. in *Caberea*, and probably remove foreign bodies, &c. They appear to act as locomotor organs for the free colony of the *Selenariidae*. See Hincks, *Marine Polyzoa*, i. Introduction, p. lxxiii. to p. lxxxiii.

*Flustra* also possesses Oöecia, or marsupial chambers, into which the ovum passes and undergoes its development. These Oöecia are produced at the distal end of the zooid. For their structure and development, see Nitsche, *Z. W. Z.* xx. 1870, p. 3, pl. i. figs. 10-13, and Vigelius, *Biol. Centralbl.* iii. 1883-84, p. 710. The zoöecial character of these organs is doubtful. In some Polyzoa the zoöecium is modified into a Stem-cell or a generative zooid (= Gonöecium or Gonocyst). The

'Root-cells,' like the Oöecia, are regarded by Vigelius as organs, not as modified zoöecia (Bijdrag tot de Dierkunde, xi. 1884). They are, however, often jointed and branched, and may serve as connecting links between adjoining branches in a colony. See Busk's article on *Kinetoskias*, Q. J. M. xxi. 1881.

The Avicularium, Vibraculum, and Stem-cell, together with the Oöecium and Radicle-fibre according to some authorities, are zooids modified from the ordinary structure to discharge certain special functions. Modifications of this character constitute *Polymorphism*. They must be carefully distinguished from modifications of outward form *not* accompanied by a specialised function, such as are found in many *Calcispongiae*, and have been termed by Haeckel *Polymorphosis*.

When only two organisms or three, differ by way of polymorphism, the terms *Dimorphism* or *Trimorphism* are sometimes used. Instances are not uncommon in the animal kingdom. There can be no doubt that the Medusa and Hydroid polype are dimorphic forms, and there are other modifications of the hydroid, such as the Blastostyle, the Dactylozoid, the Snake-like zooid of *Ophiodes*, &c. The worker bee is a dimorphic female; the soldiers and workers among the Termites are trimorphic with the fully-formed male and female.

The phrase *sexual dimorphism* is used to denote the differences other than the usual anatomical characters which separate the two sexes. Such differences are exceedingly common, and are sometimes carried to an extreme; e.g. among *Lepidoptera* species or genera have been based on characters which are really only distinctive of sex. And in the Insectan order named the individuals of broods appearing at different times of the year often differ from one another in a marked manner. In this case the phrase *seasonal dimorphism* is employed.

*Polyzoa*, Ray Lankester, Encyclopaedia Britannica (ed. ix), xix. *British Marine Polyzoa*, Hincks, 2 vols. London, 1880. *British Fresh-water Polyzoa*, Allman (Ray Society), 1856; cf. Hyatt, Proc. Essex Institute (U. S.), iv. 1865; cf. Allman, *Recent progress of knowledge of Fresh-water Polyzoa*, J. L. S. xiv. 1879; of *Marine Polyzoa*, *ibid.* xv. 1881. Vigelius, Bijdrag tot de Dierkunde, xi. 1884 (not seen).

*Membranipora* (= *Flustra*) *membranacea*, Nitsche, Z. W. Z. xxi. 1870-1871. *Flustra membranaceo-truncata*, Vigelius, Biol. Centralbl. iii. 1883-84, and *Id.* Bijdrag tot de Dierkunde, xi. 1884. *Kinetoskias*, Busk, Q. J. M. xxi. 1881. *Hypophorella*, Ehlers, Abhandl. k. Gesellsch. der Wissenschaften. Göttingen, xxi. 1876 (not seen). *Halodactylus diaphanus*, Kohlwey (Inaug. diss.), Halle, 1882. *Alcyonella fungosa* (freshwater), Nitsche, Archiv für Anat. Physiol. 1868.

*Avicularium and Vibraculum*. Hincks, Introduction to 'Marine Polyzoa' (*supra*). *Relation of two*. *Id.* A. N. H. (5) ix. 1882. *Movements of Vibracula in Caberea*. *Id.* Q. J. M. xviii. 1878.

*Endosarc*, &c. Joliet, Bryozoaires d. Côtes de France, A. Z. Expt. vi. 1877.

*Formation of generative products in Cheilostomata*. Vigelius, Biol. Centralbl. ii. 1882-83.

*Oöecium*. Vigelius on *Flustra membranaceo-truncata* (*supra*); Nitsche, Z. W. Z. xx. 1870; Hincks, xiii. 1873, p. 30.

*Budding in Polyzoa*. Haddon, Q. J. M. xxiii. 1883.

*Discussion of Affinities*. Harmer on *Loxosoma*, Q. J. M. xxv. 1885, p. 304 et seqq.

49. SEA ANEMONE (*Tealia crassicornis*).

THE animal has been bisected vertically: and one of the halves thus obtained has been suspended with the *peristome* or mouth-disc pointing to the right, and the *base* of attachment or pedal disc to the left. The preparation shows the chief features characteristic of the class Anthozoa, as well as of the *Actiniaria*, to which suborder the Sea-Anemone belongs.

The animal creeps about upon the base, which is here much contracted, so that the free edge or *limbus* is scarcely discernible. At the *limbus* the base passes into the *wall* or *column*, which is naturally more or less straight but owing to muscular contraction is convex in this specimen. The wall has a distinct *margin* where it passes in its turn into the *peristome* which supports a marginal series of tentacles and has the mouth in its centre. The tentacles are contracted to short conical stumps. In the living animal they appear to be arranged in four circles, but are really disposed in five. Of these the innermost contains forty tentacles; the fourth twenty; the third ten, and the two external circles five apiece. The area of the *peristome* is naturally flat or even slightly concave. It has a slight furrow concentric with the mouth, which may be seen on the surface of the section to correspond with a round spot, the cut surface of a strong circumoral sphincter muscle. The mouth is naturally a long slit, the edges of which are kept apposed, save at the two *extremities* or *oral angles*. The margins of these angles are prominent, and the open spaces they border are the *pharyngeal* or *oesophageal grooves*—the *gonidial canals* of Gosse—or *siphonoglyphes* of Hickson. These grooves or furrows are lined with long cilia which create currents of water to, and perhaps from, the interior. They cannot be seen here. The tube which leads inwards from the mouth is the *oesophagus* or *stomodaeum*. Its lower edge is at some little distance from the base, and is prolonged into two lappets which correspond to the *oesophageal grooves*. Food passes down it into the central region of the *coelenteric space*. This space extends outwards and upwards between the *oesophagus* and the wall, and into the tentacles, at the tips of which it opens by a pore. But the space in question, as may be seen here, is not a simple space: it is broken up into a series of radial chambers by radial mesenteries or sarco-septa, one of which is reflected at the lower part of the preparation. These mesenteries are attached above to the *peristome*, below to the *pedal disc*, and externally to the wall, of which they are really processes. A certain number of them are complete, i.e. are attached to the *stomodaeum*; they are sometimes termed primary. The remainder fail to reach the *stomodaeum* and are hence incomplete. Some fall short of reaching it by a little distance;

others by a greater, &c. : hence they are often termed secondary, tertiary, &c. The mesentery exposed in the upper part of the preparation is complete: the one reflected in the lower part is incomplete. As the greater portion of the substance of the wall has been removed, the external edges of the mesenteries are clearly visible and it may be seen how great is their number. They are really grouped in pairs, and the space between the two members of a pair is known as the intra-septal, that between two adjacent pairs as the inter-septal, chamber. The pairs are also so grouped that between two primary pairs there is one secondary pair; between a primary and a secondary pair one tertiary, and so on.

If the complete mesentery in the upper part of the preparation is carefully examined it will be seen to have two perforations. One of these, the inner septal stoma, lies about  $\frac{1}{4}$  inch from the circumoral sphincter and is found universally among Sea-Anemones piercing the primary or complete mesenteries. The other perforation or outer septal stoma occurs in very few instances. It pierces all the mesenteries and lies just within the little curve made by the margin external to the outermost tentacle. Its presence indicates the existence of a very well developed marginal sphincter, 'Rötteken's ring-muscle,' which contracts the margin over the tentacles when the peristome is retracted, but it is, however, not visible in this preparation.

The incomplete mesentery which has been reflected has a thickened inner free margin. This thickening is the mesenterial filament or craspedon; it is slightly convoluted. The free edges of all the mesenteries, complete and incomplete alike, are similarly bordered; and the convolutions of the filaments are very visible on the inner surface of the coelenteric space or stomach below the free edge of the stomodaeum.

All Anthozoa possess a wall, a peristome with marginal tentacles, a stomodaeum, and a coelenteric space subdivided by mesenteries. The *Actinaria* or *Malacodermata* possess simple non-pinnate tentacles; the number of their mesenteries is usually some multiple of the number six; and there is no hard skeleton. But some corals, e.g. *Caryophyllia cyathus* and *Madrepora variabilis* (Koch, M. J. v. 1880), possess the same paired mesenterial arrangement as do the *Actiniae*.

The oesophagus or stomodaeum is formed as an invagination of the oral disc, and is consequently lined by ectoderm. In the development of a Hexactinian (in Hertwig's sense) twelve mesenteries appear, which group themselves in pairs. These are, properly speaking, the primary mesenteries. The remaining mesenteries of the adult appear in pairs in the primary inter-septal chambers. A certain number of these mesenteries which are really secondary generally fuse with the stomodaeum, thus becoming as it were primary. In *Sagartia* the really primary mesenteries are alone thus connected.

If the surface of a mesentery be carefully examined,—and it is always with

the exception of the 'directive septa' (*infra*) the surface turned towards the intra-septal chamber—a more or less pronounced ridge may be seen traversing it from peristome to base. This ridge indicates the position of the retractor or tentacular muscle of the peristome. In the case of two pairs of primary mesenteries (in the strict sense) this muscle runs on the inter-septal surface. The two pairs in question correspond one to each oral angle, and are known as 'directive septa.' They divide the animal into a right and left half, and extend downwards along the lappets of the oesophageal groove.

The innermost circle of tentacles is the oldest. There are in a few instances circum-oral and intermediate tentacles, i. e. tentacles placed round the mouth and between the mouth and marginal tentacles respectively.

The marginal sphincter muscle is rarely completely absent as in *Corallimorphus*, but the degree of its development varies very much. In *Tealia* it is remarkably strong.

The mesenterial filament which borders the free edge of each mesentery consists typically of three processes—one median covered with thread-cells and gland cells, and one on either side of the median with ciliated cells. The two lateral processes are present at the peristomeal end of the mesentery while they die out gradually towards its basal end.

In some forms, e. g. *Sagartia*, there are long vermiform mobile filaments attached to the surfaces of the mesenteries—close to the basal end of some of the mesenterial filaments. These threads are the *acontia*. They can be protruded from the mouth or from a series of apertures—the *cinclides*—near the base of the animal. One surface of an *acontium* is loaded with many thread-cells. The *cinclides* are certainly in some cases, e. g. *Sagartia*, *Adamsia*, genuine preformed apertures. It is not certain however that accidental ruptures of the wall may not take place occasionally.

*Tealia* and some other forms have the sexes separate. The male and female elements are alike derived from the endoderm. They occur only on the tertiary mesenteries or mesenteries of a lower order. They are situated between the mesenterial filament and the tentacular muscle. Many Sea-Anemones produce living young, resembling in shape the parent form.

It has been proved that some Anemones possess the power of multiplying by 'scissiparity.' A small portion of the limbus grows and separates itself from the parent, taking away a part of at least four mesenteries.

The tissues present in *Tealia* are an ectoderm, a supporting lamina or mesodermic layer, and an endoderm. The latter clothes the whole coelenteric space, central and peripheral, including its extension into the tentacles.

The ectoderm consists of (i) ciliated cells, with flat triangular bases; (ii) gland cells; (iii) sense-cells which end internally in fine filaments connected to a nervous plexus; (iv) cells containing thread-cells or nematocysts, perhaps similarly connected; (v) muscle and ganglion cells placed sub-epithelially. Both (iii) and (iv) are provided with a fine tactile bristle. The muscle- and ganglion-cells lie next to, or are actually imbedded in, the supporting lamina, the latter especially in the peristome. The ectoderm is unilaminar in the wall, base, and stomodaeum. In none of them does it possess muscle-cells; and in the two former no ganglion cells. The mesodermic layer or supporting lamina is laminated; is thickest in the

wall and base, and contains fibrils and stellate or fusiform cells. The supporting lamina of the mesenteries is continuous with that of the wall. The endoderm is unilaminar, its cells are flagellate, and the majority possess basal muscle-fibres. These fibres are disposed in a circular direction on the wall, peristome, stomodaeum, and the base where they are sometimes wanting. They are longitudinally disposed on the intra-septal surfaces of the mesenteries; transversely on the inter-septal. The ridge forming the tentacular muscle is produced by folds of the supporting lamina on which the muscle-fibres lie. A parieto-basilar muscle running obliquely from the side of the wall to the base is developed similarly from the transverse muscle layer on the inter-septal surfaces. These two muscles, tentacular and parieto-basilar, are reversed in position on the surfaces of the directive septa. The endoderm also possesses gland cells and sense-cells. Ganglion cells with nerve fibrils have been found in it, but not so numerous as in the ectoderm of the peristome. Sense-cells and nerve-fibres are found most plentifully in the median process of the mesenterial filaments and the acontia.

Ectodermal muscle-cells occur in some forms on the wall and stomodaeum, ganglion cells on the wall and base.

The surface of the body, as in *Tealia*, is sometimes roughened by tubercles, which are local elevations of the supporting lamina. The coloured 'marginal spherules,' which are found outside the tentacular circle in *Actinia mesembryanthemum*, &c., are evaginations of the whole body wall. Their ectoderm is thickened, and contains many thread-cells. Gland cells are especially numerous near and round the base of these bodies, which must be regarded as *batteries* of thread-cells.

Unicellular Algae, the well-known 'yellow cells,' live in the endoderm cells of many Actinians, but not in *Tealia*. They are never found in those Actinians which have a red colour, only in those which are colourless, e.g. *Aiptasia diaphana*, &c., or in the colourless parts of a coloured Actinian, as in the tentacles of *Ceriatia aurantiaca*. The association between the two organisms is known as Symbiosis.

The term 'Symbiosis' was first used by the botanist, De Bary, to denote the association together *inter se* of different animals, or of different plants without reference to the character of the association. The term has also been used in the same manner by Hertwig. It is now very generally restricted to mean the association together of two different organisms which are physiologically the complements of one another. Such an association may be formed between two plants, or between a plant and an animal.

Among plants the group of Lichens consists of an assemblage of forms in which a fungus grows in the thallus of an alga. Both fungus and alga are capable, at least in some instances, of living and growing independently of one another. A single alga may act as host to a large number of different fungi; and *vice versa*, a single fungus may affect a number of different algae. In some instances the alga grows more vigorously when surrounded by the hyphae of the fungus; in others the hyphae have been observed to penetrate the algal cells and destroy their contents after the manner of a parasite. Another remarkable instance of symbiosis among plants is the growth of a fungoid mycelium round the rootlets of certain Phanerogams—*Orchidaceae*; *Monotropa*; the *Cupuliferae*, e.g. oak, hazel, beech; *Abietinae*, *Salicaceae*, and *Betulaceae*, e.g. alder, birch.



Many marine animals belonging to different groups, e. g. many *Radiolaria*, many *Anthozoa*, especially Sea-anemones, some species of *Convoluta* among *Turbellaria* are infested with 'yellow cells.' These bodies have a distinct cell membrane, except in the case of the yellow cells of *Acanthometridae* (*Radiolaria*), a nucleus, two colouring matters, one of them chlorophyl, which resemble the colouring matters of certain brown algae, and they are capable of living and multiplying after the death and destruction of their hosts. Under the influence of sun-light they exhale oxygen and form starch both when in and when out of their hosts. It appears probable that they are the swarm spores of various olive-green Sea-weeds (*Melanospermeae* or *Fucaceae*), rather than a distinct genus of algae (*Zooxanthella* of Brandt = *Philozoon* of Geddes). Marine sponges, it may be added, are infested by various algae, green, blue, red, or brown.

The marine Turbellarian *Convoluta Schultzei*, and several Turbellarians of the fresh water, e. g. *Vortex viridis*, the Coelenterates *Hydra*, *Spongilla*, and many *Protozoa*, e. g. *Rhaphidiophrys viridis*, *Stentor polymorphus*, are of a bright green colour; and it is a matter of much dispute whether the green chlorophyl bodies (the *Zoochlorella* of Brandt) do or do not belong to the organisms in question.

It appears to be certain from Geza Entz's researches that many *Infusoria* may be either green or colourless; e. g. *Stentor polymorphus* is the green variety of *Stentor Mülleri*. *Coleps viridis*, *Ophridium viride*, *Vorticella chlorostigma* stand in a similar relation to *Coleps hirtus*, *Ophridium versatile*, *Vorticella campanula*. In some instances the green variety is rare. The chlorophyl bodies have a cellulose membrane, a nucleus, two contractile vacuoles, paramylum (starch) bodies, and green chlorophyl as an envelope, or in plates. They multiply outside the body of their host after its destruction and appear to belong to different genera of unicellular algae (*Palmella*, *Tetraspora*, *Glaeocystis*, &c.). Under certain conditions they multiply within their host and are digested by it. Miss Sallitt, however, who has examined some of the same *Infusoria* as Geza Entz, states that the chlorophyl bodies resemble those of *Hydra*, and consist of a non-nucleate ball of protoplasm, with a cup-like investment of chlorophyl containing protoplasm. They occur in the endoplasm and increase by division. In *Vorticella chlorostigma* the chlorophyl is diffused through the protoplasm. If the *Volvocina* are rightly included among *Protozoa*, it must be admitted, without reserve, that there are green-coloured animals which are nourished like plants.

Professor Ray Lankester's researches on *Hydra* and *Spongilla* establish clearly the fact that the green bodies of those animals have not the value of cells. They are devoid of nucleus and membrane. The same specimen of *Spongilla* may be green where fully exposed to light, colourless or flesh-coloured where in shade. But the colourless part turns green on treatment with sulphuric acid exactly as does the colourless plant *Neottia*, and microscopic examination shows that colourless representatives of the chlorophyl bodies are present. These bodies in *Hydra* closely resemble the corresponding structures in plants, and appear, like them, to multiply by fission. The ovum, which is the only ectoderm cell in which they are present, is at one time devoid of them. Kleinenberg has traced their origin in it from colourless bodies. Hamann, on the contrary, states that they migrate into it from the endoderm; but he appears to start from the point of view of their algal nature, and to be, like some other observers, ignorant of the fact that the

chlorophyl bodies of plants multiply by fission. It may be added that *Hydra viridis*, unlike *Spongilla*, when confined in the dark, does not lose its colour, and that in some varieties green angular bodies have been found similar to the colourless angular bodies of *H. fusca*.

With reference to *Vortex viridis*, von Graff states that green-coloured examples were observed by him to give origin to colourless young; that green examples, confined in the dark, became colourless in seven days. He also states that the green *Mesostoma viridatum* sometimes occurs almost devoid of chlorophyl coloured cells. These facts, according to him, point to the algal nature of the green bodies in these animals, and raise a similar presumption with reference to *Convoluta Schultzei*.

As to the physiological side of the question, it has been proved that, under the influence of light, oxygen is given off by the yellow cells, as well as by most animals of a green colour, by *Hydra* among the number. *Spongilla* and *Vortex viridis* do not seem to have been investigated in this respect. Starch also is formed in the yellow cells; in the chlorophyl bodies of many *Protozoa*; in the cells of *Spongilla*, but not in intimate connection with the green bodies; in the green cells of *Convoluta Schultzei*, while glycogen in plenty occurs in the colourless mesoderm cells, internal to the layer of green cells in this animal. It has been detected also, but not often, in the protoplasm of the endoderm cells of *Hydra viridis*. Starch vacuoles, however, it must be added, are found in colourless *Spongillae* in as great abundance as in those of a green colour.

The theory of symbiosis is that, while the animal supplies carbonic acid, and probably nitrogenous matters to the alga, the latter, under the influence of light, yields a supply of oxygen, of starch, and possibly other substances to the animal. Brandt's experiments appear to prove that those species of Sea-Anemones which contain yellow cells can get a supply of oxygen and of food from the algae, and live at least for a longer time under circumstances in which the same species speedily die if deprived of their yellow cells by confinement for a time, e. g. eight weeks in the dark. *Convoluta Schultzei*, according to Geddes, seeks the lightest spots, and can live without food if exposed to light for four to five weeks. And it has been noted that many green *Infusoria* and *Radiolaria* containing yellow cells appear not to require any food supply *ab extra*. The fungus in the lichen appears to play the part of an animal, and it is supposed that the mycelium surrounding the rootlets of the oak, &c., acts as an intermediary between a rich soil and the rootlets. The subject of symbiosis, however, is one involving many difficulties, and a student who consults the literature of the subject will find discrepancies in the accounts given by different observers. The literature is a large one, and the sketch given above, the barest outline.

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## 50. SEA-FIR (*Sertularia abietina*),

With Fig. 11, illustrating the structure of a Craspedote Medusa.

THE Sea-fir belongs to the class Hydrozoa and order *Hydroidea*. It forms a fixed colony or *hydrosoma*, which is protected in all its parts by a yellowish chitinous *perisarc*. The hydrosome consists of a number of *hydranths* or nutritive zooids collectively forming the *trophosome* and connected to one another by a branching *coenosarc*. The hydranths are lodged in perisarcular cups or *hydrothecae* (= *calyces*), and are borne by a supporting plant-like structure or *hydrophyton*. This hydrophyton consists of the coenosarc above-mentioned and its perisarcular investment. It is divisible into a system of stems with branches, the *hydrocaulus*, and of rooting fibres, the *hydrorhiza*, by which the colony is attached to some foreign object. Numerous rooting fibres are to be seen at the base of this specimen. The stems, with their branches, rise vertically from the root: they are somewhat flattened and their two opposite edges are beset by the thecae for the hydranths. The thecae on one edge of a branch or stem alternate more or less accurately with the thecae on the other edge. The hydranths can be completely retracted into their thecae and may be seen in this specimen as opaque spots. The branching coenosarc is tubular. The walls of the

tube are composed of a delicate supporting lamina separating a layer of ectoderm and endoderm cells, the latter being ciliated. Consequently the products of digestion, a process which goes on only in the hydranths, are conveyed along the coenosarc tube through branches, stems, and roots, in brief, through the whole hydrophyton. The ectoderm of the coenosarc is separated from the perisarc by a space, but the ectoderm of each hydranth remains in contact with its chitinous theca at the base of the cup. Wherever growth is taking place, i.e. at the tip of a root, or in a developing hydranth, the perisarc is in close contact with the ectoderm by which it is formed.

There may be noted in this specimen, towards the tip of the branches and upon the side turned uppermost, certain pear-shaped bodies, the *gonothecae*, *gonangia*, or *capsules*. Each gonangium contains a modified hydranth, the *blastostyle*, which bears the generative zooids. These zooids are never set free in the family *Sertularidae*, and have, as in the family *Plumaridae*, with few exceptions, the structure of a *medusoid gonophore*. The fertilised ovum in *Sertularia abietina* and some of its allies passes into a small cyst, the *acrocyst*, formed at the apex of the gonangium. Here it undergoes development and is set free as a ciliated *Planula* which, after leading a wandering life, settles down, and by growth and budding establishes a new colony.

The hydranth resembles *Hydra* in all essentials (see Plate xiv. Fig. 6, and description). Like that organism it consists of a *hydrocephalis* (= oral and stomachal regions) and a peduncle or *hydrocope* which is very short. The *hypostome* or oral cone is conical, the tentacles filiform and arranged in a single circle. They are solid and their axis is composed of a single row of vacuolated endoderm cells. The blastostyle is borne on a short peduncle or *gonocope*.

Representatives of two other Phyla may be seen to have affixed themselves to the main stems of this specimen. One of them is a *Spirorbis*, a small Tubicolar Annelid with a discoidal shell somewhat like that of the freshwater mollusc *Planorbis*: the other is a Cyclostomatous Polyzoan, *Diastopora Patina*, which with its aggregated calcareous cells presents an appearance not unlike that of a small tubiflorous flower belonging to a plant of the order *Compositae*. Coelenterata with an external perisarc and a single circlet of tentacles bear a superficial resemblance to many Polyzoa, a group formerly classed with them. A Hydroid may however be readily distinguished at once from a plant-like Polyzoan by the presence of thread-cells on the tentacles as well as by other anatomical features. Compare Fig. 10, p. 235, *ante*, and description.

The order *Hydroidea* is divisible into the sub-groups (1) *Hydrocorallina*, colonial organisms with an external calcareous skeleton; (2) *Tubulariae* or *Gymno-*

*blastea*, with fixed plant-like colonies and all parts save the hydranths protected by a perisarc; (3) *Campanulariae* or *Calyptoblastea*, with fixed plant-like colonies, the hydranths lodged in chitinous thecae formed by the perisarc; and (4) *Trachymedusae*, a group of Medusae which have no fixed colonial forms, but develop as Medusae from the egg. The Sea-fir belongs to the *Campanulariae*.

In addition to the possession of hydrothecae, a Campanularian differs from a Tubularian in three important respects: the terminal hydranth of a stem or branch is the youngest and not the oldest in the stem or branch; the generative zooid is with few exceptions borne on a blastostyle; and when that zooid is a Medusa it is furnished, as a rule, with auditory sacs, and not with eye-specks. Hence the Medusae of Campanularians are classed as *Vesiculatae*, those of Tubularians as *Ocellatae*.

The Medusa-form in the order *Hydroidea* has the following general characters:—

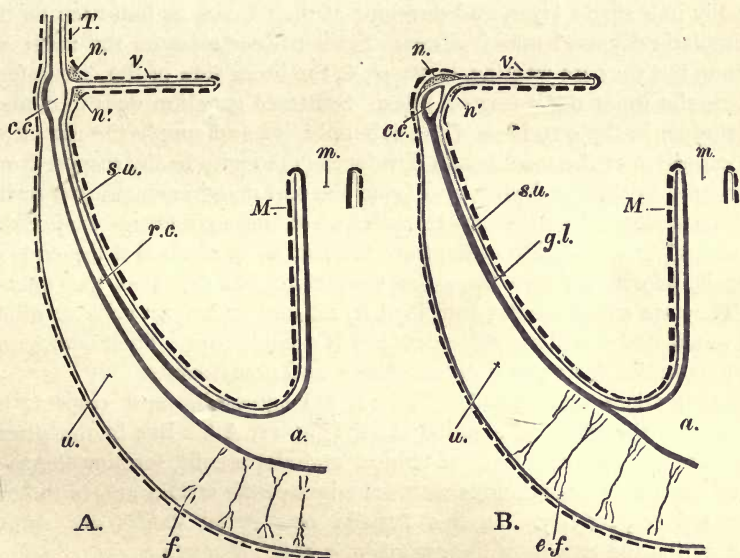


Fig. 11, illustrating diagrammatically the structure of a Craspedote Medusa.

A, a radial, B, an inter-radial section.

The ectoderm is indicated by a broken line. The dashes are thicker where it consists of columnar cells (over *n* in B), or where it develops muscular fibres. The endoderm is indicated by a thick dark line.

The shape is that of a bell, from the concavity of which depends a hollow tubular process, the manubrium (*M*). At the free end of the manubrium is the mouth (*m*); at its base a cavity more or less dilated, the atrium (*a*). From this atrium radial canals (*A*: *r.c.*), varying in number, pass outwards in the substance of the bell, and are united by a circumferential canal (*A*: *c.c.*), which runs circularly round its apparent edge. The true edge or rim of the bell is turned horizontally inwards, and forms the velum (*v*). The whole system of cavities is lined throughout by a ciliated endoderm, represented by a thick dark line, the cells of which vary in size and character in different regions. This endoderm is everywhere separated from the ectoderm, represented as a broken line, by a supporting lamina.

The lamina, which lies externally to the endoderm, i.e. on the convex side of the bell, is very much thickened, and forms the umbrella (*u.*), the substance of which is watery, jelly-like, and as a rule traversed by elastic fibres (*e.f.*). The umbrella is thickest in the region of the atrium, thinnest at the apparent edge of the bell, close to the circumferential canal. The lamina placed internally to the endoderm, i.e. on the concave surface of the bell, is very thin, like that of the manubrium and tentacles. It forms the sub-umbrella (*s.u.*). The umbrella and sub-umbrella pass round the circumferential canal, and unite to form the simple supporting lamina of the velum. The ectoderm varies in character in different regions. On the convex surface of the bell the cells are flat, except to the outer side of the circumferential canal, where there is a ridge of columnar ciliated cells, some of which send processes to the outer nerve-ring (*n.*), which lies at their base. The cells of the outer surface of the velum are cubical. On the concave surface of the bell they are disposed usually in a single layer, and develop at their bases, as indicated by thicker dashes, circularly disposed muscle-fibres. Similar fibres exist on the inner surface of the velum, but they are wanting, however, to the inner side of the circumferential canal, where the inner nerve-ring (*n'*) lies. Scattered ganglion cells in connection with this ring lie in the ectoderm of the sub-umbrella, and supply the muscle-fibres.

The ectoderm of the manubrium develops (1) longitudinally disposed muscle-fibres, indicated by thicker dashes, and (2) at the oral margin nematocysts or thread-cells, which are situated on the oral tentacles when these structures are present.

Tentacles (A: *T'*) usually spring from the margin of the bell at the ends of the radial canals, sometimes also from the circumferential canal in the inter-radial spaces. They are either tubular and lined by ciliated endoderm cells, or solid with a core of vacuolated endoderm cells arranged in a single row. Their ectoderm cells develop longitudinally arranged muscle-fibres, and nematocysts.

A section taken inter-radially (Fig. 11, B.) agrees in most respects with a section taken in the plane of a radial canal (Fig. 11, A.). But in the place of a radial canal it shows a single layer of cubical endoderm cells, forming the so-called gastral lamella (B: *g.l.*), continuous with the edges of the atrium and of the circumferential canal respectively. In this lamella new radial canals are sometimes developed during the growth of the organism, e.g. in *Aequorea*.

The eye-spots in an Ocellate Medusa are generally placed at the base of a tentacle on its *outer* side, sometimes, however, on the inner. The eye has retina cells, supporting cells, basal ganglion cells, and sometimes a cuticular lens. The auditory vesicle in a vesiculate Medusa is developed close to the inner nerve-ring, from a pit of the inner surface of the velum, which projects towards its outer surface. It has otolith cells and sense-cells, derived from the ectoderm of the inner surface of the velum.

A Medusa with a velum is said to be Craspedote. Such Medusae characterize the *Craspedota*, one of the two main sub-divisions of the class Hydrozoa. The other division is known as *Acraspeda*.

The gonads or generative organs are situated on the manubrium in an ocellate Medusa; at the base of the manubrium or on the course of a radial canal in a vesiculate Medusa. The spermatozoa and ova often arise and invariably ripen in the ectoderm, though they may take their origin in the coenosarc or the blastostyle, and by what is apparently an abbreviation of development, from the endoderm.

Under these circumstances they go through active migrations. In *Sertularia pumila* the generative zooid is a reduced medusoid gonophore; the ova arise in the endoderm (? from wandering ectoderm cells) of the branch or stem below the spot from which the gonangial bud springs, wander through the endoderm of the blastostyle and gonophore, pierce the supporting lamella, and ripen in the ectoderm of the gonophore. The generative zooid of *S. abietina* requires investigation.

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*Water in umbrella of Medusae*. Krukenberg, Z. A. iii. 1880; Möbius, Z. A. v. 1882.

*Sexual cells, origin, &c.* Weismann, Sexual-zellen (male and female) bei Hydromedusen, Jena, 1883; cf. Moseley, Nature, xxix. 1883-84; de Varenne, A. Z. Expt. x. 1882; cf. Bourne, Q. J. M. xxiii. 1883. *Female cell*. Hartlaub, Z. W. Z. xli. 1884. *Male cell*. Thallwitz, J. Z. xviii. 1885.

## 51. FRESH-WATER SPONGE (*Spongilla lacustris*),

From the Isis, growing on the wall of a lock, with Figure 12, illustrating the structure of *Euspongia officinalis*.

THIS specimen, like the preceding Hydroid (Prep. 50), is plant-like in appearance, consisting, as it does, of a base of attachment and two upright stems arising close together. *Spongilla lacustris* often attains a large size. Owing to its having been preserved in spirit, this specimen has the surface more fenestrated than in the living condition; its protrusible oscula or

exhalent apertures are no longer visible; and its natural emerald-green colour is lost. The surface is rough with protruding bundles of the siliceous spiculae which make up the skeleton of this sponge. The small inhalent orifices or 'pores,' characteristic of the class Porifera, are not distinguishable: indeed they are of microscopic size. It may be noted that the two stems have come into contact by their sides, and that at the point of contact they have fused or undergone 'conrescence.' Conrescence of this kind is an exceedingly common phenomenon in Porifera, and is one of the causes of the great variability in form of the species. But it does not occur between sponges of different species. Yellow seed-like bodies, the gemmules (*statoblasts*), may be seen in the substance of the base of attachment: they are formed at the approach of cold weather in the European, at the approach of the dry season in the Indian, fresh-water sponges.

There appear to be two fresh-water Sponges in Great Britain—*Spongilla lacustris* and *Meyenia (Spongilla) fluviatilis*. The former is branched, the latter massive and lobate. The principal distinction between the two rests on the structure of the gemmule or statoblast. These bodies are more or less globular in shape, and possess at some one point a pore which is placed at the bottom of a funnel-shaped depression, through which the inclosed mass of sponge cells makes its exit at the proper season. A delicate membrane, finely reticulate, immediately invests this mass of cells, and protrudes slightly into the pore. Externally to it lie two coats—a yellowish chitinous coat and a 'crust,' both of which are deficient at the pore. The crust varies in thickness. In the two British sponges it consists of a granular cell-like structure, which appears to contain silica. In *Spongilla lacustris* it lodges curved stout fusiform siliceous spicules, the surfaces of which are beset with stout recurved spines. They are arranged tangentially, and give the outer aspect of the crust an appearance like the lines of a so-called 'engine-turned' watch-case. In *Meyenia fluviatilis* the spicules of the crust are *birotulate*, and are known as amphidiscs. They consist of a shaft terminated at each end by a disc deeply and irregularly denticulate at its margin. The amphidiscs are set parallel to one another, and vertically to the outer surface of the crust. Marshall states that the gemmule is formed thus. In autumn a number of amoeboid wandering cells collect <sup>together</sup> in the inhalent canals or ampullae (*infra*), pass into the mesodermic tissue, and group themselves round one or two mesodermic cells. A pellicle appears on the surface of the mass. Mesodermic cells next form a capsule round it, and are transformed into the crust and its spicules. The parent sponge then dies away. The cells of the gemmule, at first distinct, gradually swell and form a syncytium, which emits a pseudopodium through the pore. In April or May the mass escapes, remains seated on the empty gemmule case, then floats for a couple of days, and finally comes to rest. A clear ectoderm is distinguishable from a more granular internal mass. An enteric cavity appears, before or after the osculum and inhalent pores, both of which may be absent. The young *Spongilla* becomes sexual. The sexes are separate. The males have no osculum or enteric cavity (?); the females have them. The ovum is fertilised, and the ciliated embryo is set free.



The males appear to perish, but the females grow, and are stated to lose their oscula and enteric cavities (= ampullae) more or less completely. The ciliated embryo produces an individual which is never sexual, but gives origin in autumn to gemmules. There is therefore an alternation of generations (Marshall).

The green colour of *Spongilla* is developed only when the sponge grows freely exposed to light. If it is shaded, a pale flesh-colour takes the place of green. However, a piece of such a pale-coloured sponge turns green when dipped into sulphuric acid, as does the colourless saprophyte plant *Neottia*. A flesh-coloured sponge contains in its cells angular particles; these in pale-green specimens are found mixed with green concavo-convex discs, which appear to be derived from them, and which are present in great abundance in an ordinary full-green specimen. These green bodies have been considered by Brandt (op. cit. p. 245 *ante*) to be symbiotic algae. The green colouring matter itself appears to have a similar constitution to that of higher plants, but the proportions of the constituents are different. The cells of *Spongilla*, whether flesh-coloured or green, contain starch in solution.

The structure of *Spongilla* has not been properly worked out, and the anatomy

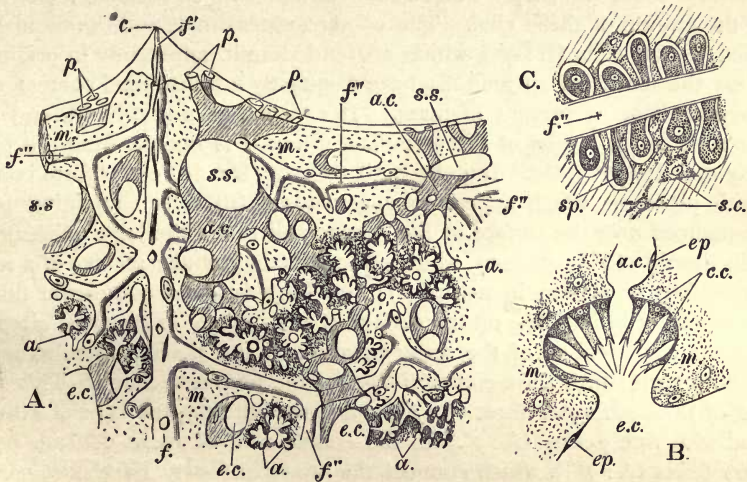


Fig. 12. A. Section of *Euspongia officinalis*, after Schulze, op. cit. *infra*, Pl. xxxvi. Fig. 2. B. Ampulla of same (Schulze, Pl. xxxvii. Fig. 11 in part). C. Young secondary spongin fibre surrounded by spongoblasts (sp.) of same (Schulze, Pl. xxxvi. Fig. 6 in part).

of a sponge (Fig. 12, A.B.C.) is best illustrated by that of the sponge of commerce, *Euspongia officinalis*, which grows in quantity in the Mediterranean Sea. There are, according to Schulze (op. cit. *infra*), six varieties of it, differing in external shape, disposition of the oscula, and of the fibrous skeleton.

The living organism is dark violet-grey, passing into yellowish brown where the light does not reach it freely. The surface is beset with minute elevations or conuli (A: c.), and is marked by fine close-set ridges which divide it into areae. Within these areae are situate the microscopic pores (A: p.) by which the sea-water finds its entrance. The number of oscula or exhalent apertures varies in a given specimen. The pores lead either into the dilated commencement of an afferent

water-canal or into a system of 'subdermal spaces' (A : *s.s.*). The afferent canals (A and B : *a.c.*) branch, and penetrate the substance of the sponge. The ultimate branches, .01 mm. in diameter, open two to four together, into the globular portion of pyriform ampullae or ciliated chambers (A : *a.*, B.). The stalk of the pear opens either directly into an efferent water-canal (A and B : *e.c.*) or into one of its rootlets. The branches of the efferent canals unite *inter se*, and finally open into an oscular canal. This canal is straight, two to three mm. wide, and rises vertically to the surface, where it opens by an osculum, which is limited by an iris-like membrane.

The sponge-substance is composed of three tissues: ectoderm, endoderm, and mesodermic tissue. The ectoderm consists of flat nucleated cells covering the outer surface. It is not certain whether the cells coating the subdermal spaces and afferent water-canals belong to the ecto- or to the endo-derm. They appear at any rate to absorb solid particles and hand them over to the cells of the mesodermic tissue. The ampullae are lined by cylindrical granular endoderm cells—about sixty to each ampulla—with a basal nucleus, single cilium surrounded by a hyaline protoplasmic collar (B : *c.c.*). The currents of water which traverse the sponge are due to the motion of these cilia. The efferent water-canals and the oscular canals are lined by flat cells (B : *ep.*), which are endodermic apparently in origin. The cells near the mouth of an ampulla have frequently a transitional character. The mesodermic tissue is present in mass. It consists of a matrix (A and B : *m.*) hyaline save in the region of the ampullae, where it is opaque from the presence of many rounded granules. It imbeds (i) stellate (C : *s.c.*) or fusiform connective cells with processes which appear to anastomose; (ii) cells containing pigment, most numerous near the surface of the sponge and round the large afferent canals; (iii) cells devoid of all processes, which often contain globular masses of a refractile substance, fatty or starchy in nature (?); (iv) long fusiform contractile fibre-cells, either isolated or in bundles, on the surface of the sponge, or disposed circularly in the annular constrictions of the water-canals, and the iris-like membrane of the oscula, both parts which show contractility; (v) the fibrous skeleton. This skeleton consists of thick *principal* fibres (A : *f.*), which radiate from the base of attachment and end with fine points (A : *f'.*) in the conuli, and of more delicate branched *secondary* fibres (A : *f''.*), which connect the principal fibres. Each fibre consists of a central granular axis surrounded by hyaline strongly refracting lamellae of Keratin or Spongin, a substance near akin chemically to silk, and which in most instances polarises light. The principal fibres have a rough exterior, and their axes contain foreign bodies, chiefly sand-grains, apparently taken in by the mass of irregular cells surrounding the tip of the fibre wherever the fibre is lengthening. The hyaline lamellae are secreted by pear-shaped cells or *spongoblasts* (C : *sp.*), which are probably modified connective tissue or mesodermic cells. The secondary fibres arise independently, and become connected subsequently to the principal fibres.

*Euspongia* may be propagated artificially from fragments. The sexes appear to be separate, and the male sponge rare. The sexual elements, derived probably from mesodermic cells, undergo development in spaces of the mesodermic matrix lined by flat cells. The ripe ovum is .25 mm. in size, is impregnated and developed into a larva *in situ*. The free larva is .4 mm. long, .35 mm. broad, shaped like a conical bullet and composed of an external layer of ciliated, and pigmented cells,

an internal layer of small cells, and a central mass of cells separated *inter se* by well-formed membranes.

*Spongilla* appears to possess a distinct ectoderm, and a mesodermic tissue containing little matrix, but many cells and silicious spicules. Of the latter, some are scattered as flesh-spicules irregularly in the matrix, others—the skeleton spicules—aggregated by a cementing material into fibres. There appears also to be a system of subdermal spaces. Afferent and efferent water-canals lead to and from ampullae lined by the collared cell characteristic of sponges.

For the vexed question as to the homology of the tissues here termed ectoderm, endoderm, and mesodermic tissue, with the parts so termed in other Metazoa, see a paper by Marshall, Ontogenie von *Reniera filigrana*, Z. W. Z. xxxvii. 1882. He appears to prove that afferent and efferent canals are alike lined by endoderm. Schulze, on the other hand (Die Plakinidae, Z. W. Z. xxxiv. 1880, pp. 416 and 436), appears to find that a part at least of the afferent canals are formed by invaginated ectoderm. Ganin's observations on the development of *Spongilla* show that in that organism the afferent and efferent canals with ampullae are lined by endoderm, but the subdermal spaces (= Leibeshöhle) are lined by an epithelium derived from neither ecto- nor endo-derm. Götte has recently published an account of observations quite at variance with Ganin's, and hard to reconcile with facts observed in the development of other sponges. Cf. Z. A. vii. 1884 (A. N. H. (5) xv. 1885); Z. A. viii. 1885.

*Porifera*, Vosmaer, Bronn's Klass. und Ordnungen des Thierreichs, ii. (in progress). *A monograph of Australian Sponges*, von Lendenfeld, Proc. Linnean Soc. of New South Wales, ix. 1884.

*Spongilla and its fresh-water allies.* The following references are for convenience given to one work, where the titles of the originals will be found. Carter, A. N. H. (5): *gemmule of Carterella*, vii. 1881; ix. 1882; *fossil spicules*, x. 1882; xii. 1883. Notes, &c., xv. xvi. 1885. Dybowski, *ibid.*, xiv. 1884. Hilgendorf, *ibid.*, xii. 1883. Marshall, *ibid.*, xii. 1883; (*gemmule*), xiii. 1884. Potts, *ibid.*, ix. 1882; xiii. 1884; xv. 1885; xvii. 1886. Vejdovski, *ibid.*, xiii. 1884; xv. 1885.

Retzer, Deutschen Süßwasserschwämme, Inaug. diss., Tübingen, 1883.

*Reproduction of Spongilla.* Marshall, SB. Natf. Gesellsch., Leipzig, 1884, (Journal Roy. Micr. Soc. v. 1885, p. 1011); Ganin, Z. A. i. 1878; Götte, Z. A. vii. 1884 (A. N. H. (5) xv. 1885); Id. Z. A. viii. 1885; Id. Abhandl. Entwick.-geschichte der Thiere, iii. Leipzig, 1886.

*Chlorophyl corpuscles and amyloid deposits.* Ray Lankester, Q. J. M. xxii. 1882. *Chromatology.* Sorby, Q. J. M. xv. 1875.

*Euspongia*, Schulze, Die Spongiden, Z. W. Z. xxxii. 1879.

*Growth of spongin fibres*, Von Lendenfeld, Z. W. Z. xxxviii. 1883, pp. 265, 285, Pl. xiii. Figs. 25-32.

*Colouring matter of Sponges.* Krukenberg, Vergleich. Physiol. Vorträge, ii. 1882, p. 51. *Digestion in Sponges.* Id., op. cit. iii. 1884, p. 125. Von Lendenfeld, Proc. Lin. Soc. N. S. W. ix. 1884, p. 434. *Vital phenomena of Sponges*, Solger, Biol. Centralblatt, iii. 1883-84.

*Coelenterate nature of Sponges.* Marshall, A. N. H. (5) xvi. 1885 (transl.). *Relation to Choano-flagellata.* Schulze, A. N. H. (5) xv. 1885 (transl.).

52. *Paramecium Aurelia* and *Amoeba Proteus*.

With Figure 13.

*Paramecium Aurelia*, the Slipper Animalcule (Fig. 13, A. B. and 1, 2, 3, 4), is commonly found in pond water and vegetable infusions. The length of its body varies from  $\frac{1}{120}$  to  $\frac{1}{80}$  of an inch. It is more or less asymmetrical in shape, and one surface is slightly convex, the other flat. As the latter is pierced by the pharynx it is generally termed ventral. The exact outline varies somewhat with the state of contraction of the animal.

The surface of the body is covered by a very delicate cuticle (B: *cu.*) secreted by the underlying protoplasm and pierced by pores through which pass the cilia. *Paramecium* is holotrichous, i. e. the cilia covering the body are equal in size. There are larger adoral cilia leading to the pharynx, as there are in some *Holotricha*. The cilia (A: B: *ci.*) are disposed in longi-

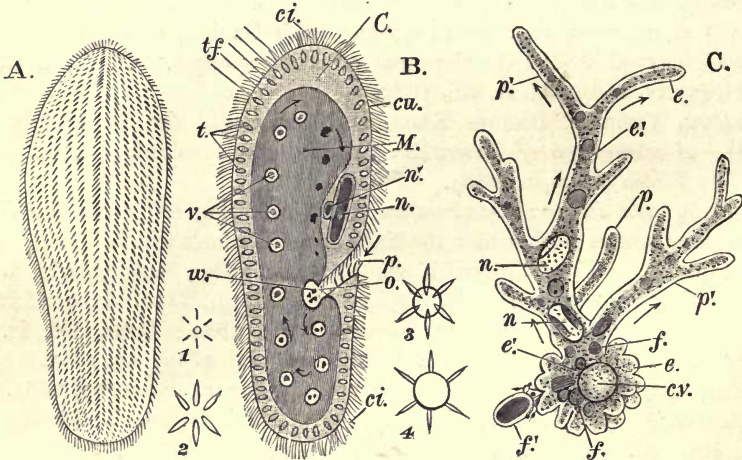


Fig. 13. A. and B. *Paramecium*: from Ray Lankester, op. cit. *infra*, Fig. xxv. 1 and 2. 1, 2, 3, 4. Formation of vacuole: (after the same Fig. xxv). C. *Amoeba Proteus*: from Leidy, op. cit. *infra*, Pl. i. Fig. 4.

tudinal lines on the surface of the body (A.) and extend into the pharynx (B: *p.*), in which they create a current, up one side and down the other. They are, therefore, not only organs of locomotion but also of alimentation. They are structurally filamentous extensions of the cortical layer of the protoplasm, and undergo alternate movements of flexion and erection, which commencing at one pole of the organism, are propagated in successive waves to the other pole. The protoplasm which makes up the whole substance of this unicellular animal is divisible into two parts, an external cortical layer (B: *C.*) surrounding a central medulla (B: *M.*). These two parts are sharply contrasted. The cortex is contractile, dense, hyaline, and of great

refractile power, while the medulla is fluent, soft, more or less granular, and opaque. The cortex is marked in many Infusoria, but not evidently in *Paramecium*, by alternate light and dark lines, e. g. in *Stentor*. The former corresponds to lines in which the cortex is thicker, and hence contraction of the body takes place in a direction coincident with their length. The cortical substance is doubly refractile, and hence depolarises light. This fact is especially evident wherever it is thickened.

The cortex contains the trichocysts, contractile vacuoles, nucleus, and paranucleus. The trichocysts (B: *t.*) are not present in all Infusoria. They are numerous in *Paramecium*, and form a superficial layer beneath the cuticle. They are minute sacs containing a simple spirally coiled filament which is eversible (B: *tf.*), and therefore they closely resemble the nematocysts of many Coelenterata. The contractile vacuoles are two in number, one in front of the other. Saville Kent states that under normal conditions they are evenly spheroidal in outline: but that under slight pressure they are formed in a manner normal to certain types and exemplified in Fig. 13, 1, 2, 3, 4. Minute pyriform drops make their appearance pointing towards a common centre. They enlarge, and their inner ends approaching give origin to a central drop which swells as the radiating spaces disappear and bursts externally, discharging its contents completely and disappearing in its turn. During the process of transverse fission two vacuoles make their appearance in the anterior region of the body, forming the vacuoles of one of the two new individuals, the other retaining the two previously existent vacuoles. The vacuoles are constant in position: their function is to discharge superfluous water, containing perhaps soluble excretory products. It has been observed by Mr. A. G. Bourne that when the organism is fed on food-particles stained with aniline blue soluble in water, the dye is rapidly excreted by the vacuoles in a concentrated form.

The nucleus or endoplast (B: *n.*), and paranucleus or endoplastule (B: *n'*), sometimes erroneously termed nucleolus, lie in a thickening of the cortex. In some instances they lie in the medulla and circulate with its movements. They were at one time regarded as ovum and testis respectively. In fission and during conjugation they divide, in fission once, in conjugation twice at least: and in the latter case the segments of the twice divided nucleus are usually further broken up. During the process of division nucleus and paranucleus alike have been observed to become striated. After conjugation, a process which is only temporary in *Paramecium*, and in which protoplasm is certainly exchanged between the conjugating individuals, both structures are reconstituted. The new nucleus is said to be formed by the fusion of two portions of the twice divided paranucleus. Some of the fragments of the nucleus are stated to be expelled, while the remaining fragments of both structures disappear unless a few of them fuse to form a new paranucleus. But in *Stylonychia* this

body has been observed to arise by fission from the nucleus. The facts stated lead to the opinion that the paranucleus is nothing more than a small nucleus. *Paramecium* is therefore bi-nucleate. Paranuclei are commonly found in Infusoria; but in some multinucleate forms, as e.g. *Opalina*, the nuclei are not only numerous but alike in size and other characters.

The medulla (B: *M.*) forms the central portion of the body. It is digestive in function and receives food-particles through a pharynx or tubular prolongation inwards of the cuticle (B: *p.*). A groove commencing on the left side of the animal leads obliquely to the entrance of this pharynx. At its base is the cell-mouth or *cytostome* (B: *o.*), where the medullary protoplasm is bare. The food-particles collect here in a minute drop of water (B: *w.*). Water and food enter the medulla, where they circulate together as food-vacuoles (B: *v.*), in the direction shown by the arrows in the figure. The water in these vacuoles is slowly absorbed, while the nutritive portion of the food is removed by a process not understood. In some instances an acid reaction has been observed in the inclosing water. The particles that remain are faecal, and, according to Saville Kent, are expelled midway between the mouth and posterior extremity of the body. It is not clear that *Paramecium* possesses a cell-anus or *cytopyge* lined by cuticle such as exists in some forms. The granules in the medulla are albuminoid and fatty in nature. When the organism has been starved for a time the medulla becomes nearly hyaline: when full-fed, on the contrary, perfectly opaque with granules.

Reproduction takes place by the transverse division or fission of the organism into two new individuals. The process is repeated for some time, the resulting organisms gradually diminishing in size. Conjugation then takes place. Two individuals fuse temporarily by their oral regions: and during fusion there is a division of both nucleus and paranucleus (*supra*), and apparently an interchange of protoplasm. When the conjugating individuals separate, 'rejuvenescence' sets in, i. e. the nuclei and paranuclei are reconstituted, and each individual regains the full dimensions of the species. Multiplication by fission then re-commences as before.

*Amoeba Proteus* or *A. princeps*, the Proteus animalcule (Fig. 13 C.), agrees with *Paramecium* in being a unicellular organism: it differs from it in the absence of a permanently fixed cortex, and in the character of its organs of locomotion, which are non-vibratile lobes of the protoplasm known as pseudopodia (C: *p.* and *p'*). It is to be found in the upper layers of soft ooze at the bottom of still clear lakes, ponds, and ditches, or creeping on the under surface of the fronds of Duckweed and the floating leaves of various aquatic plants.

The body consists of a pale, jelly-like, finely granular protoplasm, capable of both extension and contraction at the will of the animal. The outer layer of protoplasm retains a clear aspect and firm nature and con-

stitutes the ectosarc (C:e.): but it forms no definite cuticle, though it is possible that the surface in contact with the water coagulates into a pellicle more resistant than the underlying strata. The interior portion, the endosarc (C:e'), is fluent and watery, and by contrast more or less opaque, owing to admixture with various elements partly formed by the chemical activity of the protoplasm itself, partly taken up by it from without<sup>1</sup>. The substances of the former class, according to Leidy, who has carefully studied this organism, consist of (1) minute granules, pale or dark: (2) spherical corpuscles of largish size, homogeneous character, and either colourless or feebly yellow, liquid or semiliquid: (3) round or oval bodies resembling starch grains both in appearance and chemical reaction: (4) colourless, yellow, or brown oval globules, with dark border, highly refractile and apparently fatty in nature (C:f.): (5) minute crystals and (6) water drops, colourless or feebly yellow. Substances taken up from without are (1) food balls, soft, generally spherical and uniform in size but very variable in colour and composition, according to the nature of the organism (Rotifer, Infusorian, &c.) from which they are derived: (2) food materials of a firmer nature such as Diatoms, Desmids, Unicellular Algae, which retain their shape owing to the presence of a skeleton or firm cuticle: (3) various foreign bodies, organic and inorganic, picked up from the surface on which the animal happens to be creeping. The food materials are frequently but not invariably inclosed in a vacuole. They as well as other substances can be taken up at any point in the body, either by the union of two inclosing pseudopodia or by the protoplasm flowing over and around them. Expulsion of faecal and other materials as a rule takes place at the posterior extremity (C:f.) when the animal is in motion. 'The discharge is rather sudden and is often accompanied with the escape of some viscid fluid' (Leidy). The rift in the protoplasm closes at once, leaving no trace of its existence. It is a noteworthy fact that, in spite of the soft nature of the inclosing protoplasm, the food-balls, vacuoles contractile and non-contractile, retain their shape and integrity in every movement of the endosarc and animal.

There is always one nucleus, and sometimes more than one (C:n.), and a contractile vacuole. The position of the nucleus varies, but it is generally somewhere about or behind the centre of the body. It is colourless, homogeneous, finely or coarsely but uniformly granular: in shape a compressed sphere or disc with convex, flat, or concave surfaces and rounded edge. The contractile vacuole (C:c.v.) is a clear globe usually placed behind the nucleus at the posterior extremity. It enlarges slowly

<sup>1</sup> The distinction of the protoplasm into ecto- and endo-sarc is probably, strictly speaking, accidental; and there is nothing to prove that the ectosarc cannot and does not mix with the endosarc. In other words, the distinction is not to be regarded as permanent, in the same sense that the distinction between cortex and medulla in *Paramecium* is permanent.

and collapses suddenly. A new vacuole is formed at or near the spot occupied by its predecessor. There is rarely more than one of these pulsatile spaces present.

The animal when in a state of repose or after being disturbed forms a spherical or oval ball, about  $\frac{1}{125}$  of an inch in size. It sometimes occurs in this condition surrounded by a delicate membrane forming a 'hypnocyst.' It is then 'resting' owing to drought or plentiful nutrition. When it passes into a state of active motion, the surface of the body is covered with numerous clear protrusions of ectosarc. Certain of these elongate into pseudopodia while the remainder are withdrawn, and at the same time the animal begins to flatten out. The endosarc flows into the growing pseudopodia, which at first extend in various and opposite directions. But sooner or later one or two elongate in a given direction, and the rest retract, and the animal moves in a determinate course. It is now, according to the phase of shape assumed by the pseudopodia, either ramose, as in Fig. 13, C., dendroid, or palmate. When it floats freely suspended in water the pseudopodia extend in all directions, giving it a radiate or stellate appearance. The pseudopodia attain in their growth characters which are distinctive of the species or the group to which these *Rhizopodan* organisms belong. In *Amoeba Proteus* they are finger-like, i.e. digitate, simple (C: *p*.) or branched (C: *p'*). Their tips are either blunt or tapering. Elongation takes place by an onward flow of ectosarc followed by the extrusion into the ectosarc of a current of endosarc. The flow is, as a rule, not even but more or less sudden, as though there were a surface-resistance to be overcome. The posterior part of the body, where the protoplasm is receding, has often a lobed or mulberry-like appearance, as shown in Fig. 13, C. Similar lobes may be observed on a pseudopodium during its retraction. Any single lobe in the posterior mass might commence to elongate, and grow into a pseudopodium: and the direction of the animal's movement, indicated in C. by the arrows, might be thus reversed. In the extended condition this species may measure the  $\frac{1}{50}$  of an inch.

An *Amoeba* has been observed dividing into two. The protoplasmic bridge or filament connecting the two halves, gradually becomes more and more delicate and lengthened, and then finally snaps. It is uncertain whether or no *Amoeba Proteus* ever forms spores in the shape of minute *Amoeba* or *Amoebulae*, such as have been observed in *Pelomyxa palustris*.

*Protozoa*, Ray Lankester, Encyclopaedia Brit. (ed. ix.) xix. 1885.

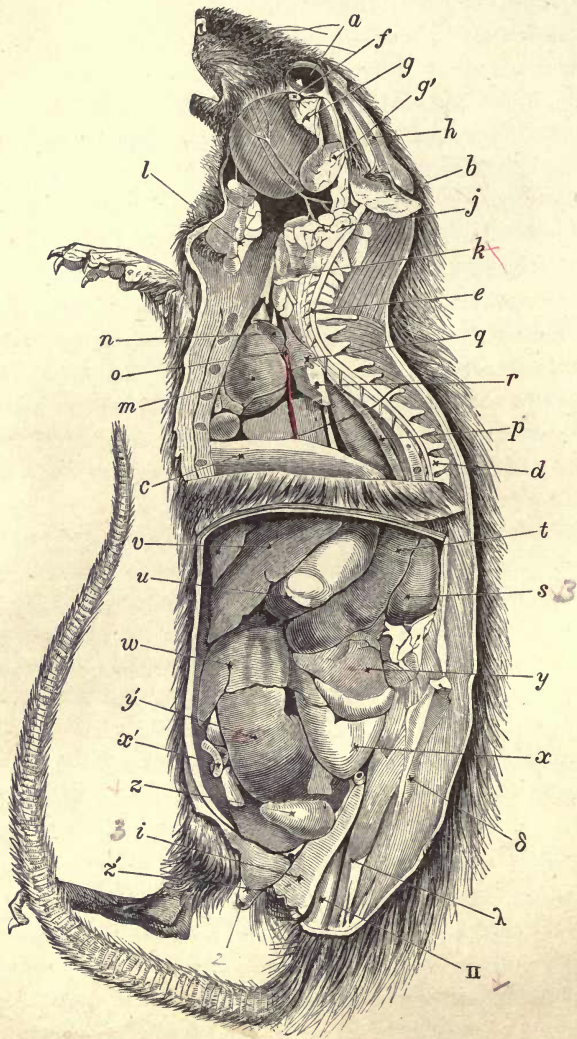
*Infusoria* (= *Ciliata*), Saville Kent, Manual of the Infusoria, 2 vols., and Plates, London, 1880-82. For *Paramecium*, see vol. ii. p. 483; Pl. xxvi. Figs. 28-30.

*Amoeba*. Leidy, Fresh-water *Rhizopoda* of North America, United States Geological Survey, xii. 1879. For *A. Proteus*, see p. 31; Pls. i; ii; iv, Fig. 25; vii, Figs. 13-19; viii, Figs. 17-30. Cf. Gruber, Z. W. Z. xli. 1885.





PLATE I.



COMMON RAT, *Mus decumanus*.

# DESCRIPTION OF THE PLATES<sup>1</sup>.

## PLATE I.

### COMMON RAT (*Mus decumanus*),

Dissected so as to show, superiorly, the cerebrospinal nervous system lodged in the cranio-spinal cavity, and, inferiorly, portions of most of the organs of vegetative life.

CHARACTERS distinctive of Mammalia shown in this figure are the following: the epidermic exo-skeleton in the form of hairs; the suspension of the lungs freely in closed 'pleural' sacs; the perfect diaphragm (*c*) separating the cavities of the thorax and abdomen; the smooth external surface of the kidney; the single aorta crossing the left bronchus; and the presence of an omentum or epiploon (*w*).

The scalpriform incisors characteristic of the order *Rodentia* are concealed in this profile view by the lips, but the figure shows well the great size of the masseter muscle which is crossed by the duct of the parotid gland (*j*) and by the facial nerve. The great size of the organs of special sense relatively to the entire bulk of the animal, and of the hind limbs relatively to the fore limbs, are characteristic, though not universally nor exclusively, of Rodents.

Points of less classificatory importance are furnished to us by the presence of a vena cava descendens on the left side; of smooth cerebral hemispheres (*h*); of a uterus all but completely bifid (*y* and *y'*); of a Harderian gland (*f*); of a hibernating gland (*k*); and of a double lacrymal gland (*g* and *g'*).

The left halves of the parietes of the craniospinal, thoracic, abdominal, and pelvic cavities have been removed to expose the parts shown in this figure. The integument has been removed from the greater part of the facial region, but a narrow strip has been left connecting the concha of the

<sup>1</sup> Plates I, VI, VIII, and X, are taken from the specimens described in the first part of this work. Plates II, III, XI, XII, and XIII, are from specimens of the same animals as described in the first part, but prepared differently, and therefore often displaying new points. In describing these Plates repetition is avoided as much as possible. Plates IV, V, VII, IX, and XIV, relate to animals or groups not described before. The descriptions of these Plates are therefore supplementary to the descriptions of specimens in the first part.

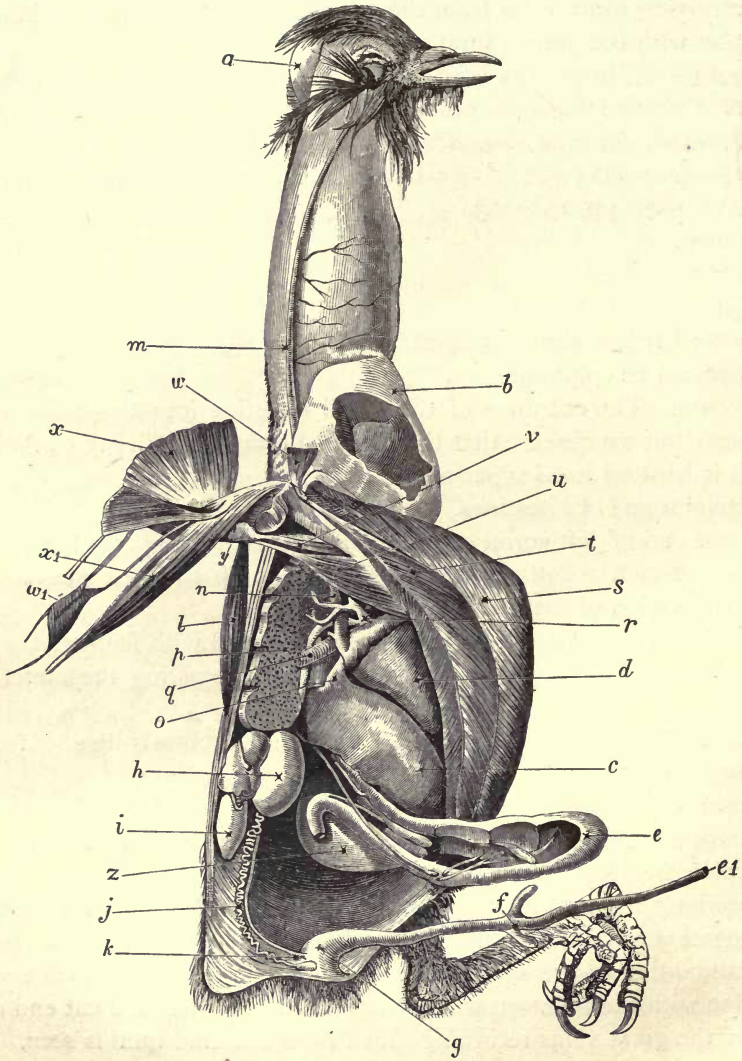
ear with the upper eyelid. A similar strip has been drawn as left *in situ* overlying the costal attachment of the diaphragm.

- a. Left eye.
- b. Left ear.
- c. Diaphragm forming a contractile dome-shaped floor between the abdominal cavity below and the thoracic above.
- d. Eleventh dorsal or anticlinal vertebra.
- e. Spinal cord. The part where it widens into the medulla oblongata is concealed by the large external ear.
- f. Part of Harderian gland, which discharges its secretion by a duct opening under the rudimentary third eyelid or nictitating membrane. This gland is found in most mammals, with the exception of *Chiroptera* and *Simiadae*.
- g. Intra-orbital portion of lacrymal gland.
- g'. Extra-orbital portion of lacrymal gland, lying upon the masseter muscle. It sends a duct with some glandular tissue inlaid in its walls to enter the orbit at its posterior angle, and receive the duct of the intra-orbital portion (g).
- h. Cerebral hemisphere of right side.
- i. Vagina.
- j. Parotid gland. Its ducts are seen to converge from its constituent lobules, which are loosely aggregated from the neighbourhood of the ear to that of the acromion, and to cross, when united, the ramifications into which the motor nerve of the facial muscles is seen to break up. The buccal pouch is wanting in the true *Mures*. Some lymphatic glands have been removed from the space between the masseter muscle and the parotid gland.
- k. Portion of 'hibernating gland;' a gland found in many *Rodentia*, *Chiroptera*, and *Insectivora*, and spreading in them into the axillary, the nuchal, the thoracic, and even occasionally into the abdominal regions.
- l. Submaxillary gland and duct.
- m. Heart; the line ends upon the left ventricle. The apex of the heart is not turned so much to the left as in man and in some of the lower mammals, e.g. the mole. The fold immediately below the point where the line abuts upon the ventricle is formed by the cut edge of the pericardium.
- n. Left auricle.
- o. Phrenic nerve.
- p. Aorta. A bristle has been passed between it and the left azygos vein, and abuts on the diaphragm where the left phrenic nerve enters it. Behind this bristle are seen, passing from the aorta to the sternum, first, the third lobe of the right lung; secondly, the oesophagus;

thirdly, the fourth lobe of the right lung within its own pleural cavity, in relation with which is the phrenic nerve; and, lastly, the lobules of fatty tissue, already spoken of, in apposition with the fourth and fifth of the six sternal bones.

- ✓ *q.* Left azygos vein joining the vena cava superior of the same side, and receiving some veins from the masses of fat just mentioned in connection with the pericardium.
- r.* Root of left lung: the lung of this side has been removed; it consisted of a single lobe, as is often, though not always, the case in *Rodentia*, *Marsupialia*, and *Insectivora*, though very rarely in *Carnivora* and *Quadrumana*; see Cuvier, Leçons d'Anatomie Comparée, tom. vii. éd. 2<sup>me</sup>, 1840, pp. 156-163.
- *s.* Kidney.
- t.* Spleen.
- u.* Stomach.
- v.* Liver; the line abutting upon its left lobe.
- w.* Omentum or epiploon.
- x.* Coecum. The entrance of the small intestine into the coecum is not seen, but we observe that the coecum becomes smaller in calibre where it is bent on itself superiorly.
- x'*. Convolutions of intestines.
- ✓ *y.* Upper end of left cornu of pregnant uterus, passing into the Fallopian tube, which together with the ovary fills up the space between this convolution of the uterus and the kidney.
- ✓ *y'*. Lower portion of same uterine cornu distended with foetuses.
- ✓ *z.* Bladder contracted into a conical shape and receiving the ureter at its base on the left side.
- *z'*. Outlet of urinary organs through a perforated clitoris distinct from the vagina.
- ✓ *π.* Rectum.
- λ.* Flexor muscles of the tail, which arise from the internal surface of the pelvic bones.
- δ.* Anterior portion of ilium, the posterior part of which has been removed, together with the pubis and ischium. From its internal surface the caudal flexors are seen to take origin, and in front of them and in a line with the point on which the letter *δ* is placed, the cut end of one of the great veins returning blood from the hind limb is seen.

PLATE II.



PIGEON, *Columba livia*.

## PLATE II.

COMMON PIGEON (*Columba livia*),

Dissected so as to show the main points characteristic of Aves, and the arrangement of the principal muscles of flight.

THE characters distinctive of Birds shown in this figure are the following: feathers; epidermic scales to the feet; musculature of the wing; characters of the brain; oesophageal crop (absent in some Birds); large size of duodenal loop; pancreas and the number of ducts to this gland; the two coeca; extremely short large intestine as compared with the length of the small intestine; heart resting in a deep notch of the liver; single aorta crossing the right bronchus; mode of division of the innominate artery; deep indentation of the lungs by the ribs; tubular structure of the lungs; and trilobed kidney adapted to the pelvic fossae.

There is no diaphragm as in all lower Vertebrata: the cloaca, as in *Crocodylia*, *Chelonia* and Amphibia, receives separately the rectum, urinary and generative ducts: the testes are permanently retained within the abdomen as in a few Mammals and all lower Vertebrata: the bladder is absent as in all *Lacertilia* and *Ophidia*.

In some Mammals a portion of the stomach is purely receptive, but no Mammal develops an oesophageal crop; and it is as rare for a Mammal to possess two coeca as it is for a Bird to possess one. The only Mammals—the *Prototheria*—which have a cloaca, have also a sinus urogenitalis.

a. Right cerebral hemisphere. Its surface is smooth, contrasting with that of the transversely laminated cerebellum seen behind in the median line.

b. The crop, which is bilocular in the *Columbidae*. A window has been made in its right wall to show its division into two compartments.

c. Right lobe of liver.

d. Heart. The ventricular portion is more acutely conical in most Birds than in Mammals, and the auricles are smaller in relation to the ventricles.

e. Loop of duodenum in which are contained the longitudinally arranged lobes of the pancreas. Into this loop of intestine three ducts open from the pancreas and two from the liver, which has no gall-bladder in this species. Two of the pancreatic ducts open near the middle of the distal segment of the duodenum close to each other and to one of the gall-ducts; the third pancreatic duct opens near the distal end of the loop, and the second gall-duct near its proximal end.

et. Terminal segment of small intestine ending in the large intestine at

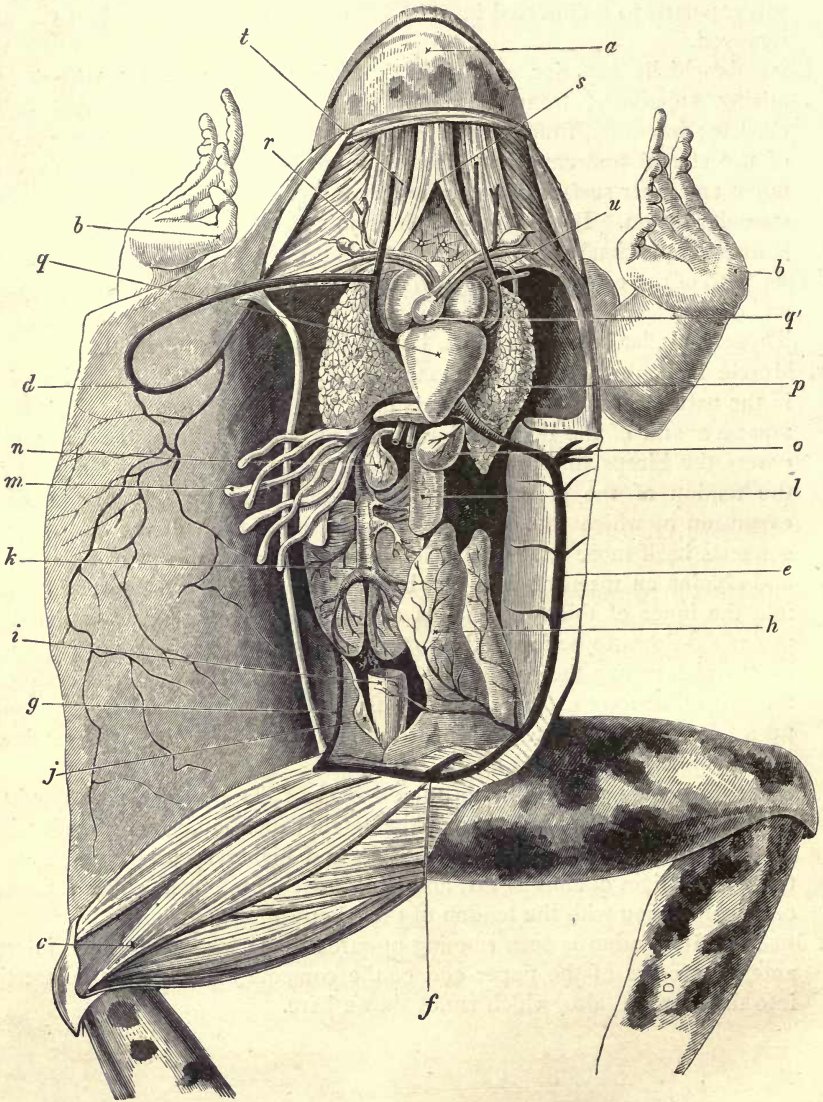
- f.* Two long coils of small intestine have been removed between this terminal segment and the distal end of the duodenum.
- f.* Large intestine, two coeca marking its commencement. In the small size of the coeca the *Columbidae* contrast with the majority of *Gallinaceae*.
- g.* Terminal dilatation of the large intestine receiving the vas deferens and ureter dorsally on each side. In this cloacal arrangement Birds resemble Reptiles and Amphibia; in all Mammals there is a *sinus urogenitalis* developed, into which these ducts open. In the absence of a urinary bladder Birds resemble Snakes and many Lizards.
- h.* Testis.
- i.* Kidney divided into three lobes, which are conformed to the sinuosities of the pelvic bones.
- j.* Vas deferens, dilating before its termination in the cloaca.
- k.* Ureter.
- l.* Teres major muscle, the subscapularis and great part of the scapula having been removed.
- m.* Right jugular vein receiving the veins from the oesophagus, and by virtue of these vessels, as also of a branch of anastomosis with the left jugular, attaining, as is usual in Birds, a larger size than that vessel.
- n.* Right jugular vein in thorax.
- o.* Vena cava inferior, entering the auricle to the right of and posteriorly to the entrance of the vena cava superior of the right side.
- p.* Lung, showing on its exterior surface indentations corresponding with the ribs.
- q.* Right bronchus entering the lung. Between the bronchus and the vena cava inferior we see a portion of the glandular proventriculus, and immediately above the bronchus and below the arch of the aorta, which has been displaced a little upwards, the junction with the jugular of the fragment of vein left to represent the subclavian trunk.
- r.* Right innominate artery, which is seen to break up into three main divisions, the common carotid, the axillary and the pectoral arteries.
- y.* Portion of inner tuberosity of humerus which overhangs the pneumatic foramen of the bone.
- z.* Gizzard.
- s.* Great pectoral muscle, the main depressor of the humerus and wing. Its main tendon is seen turned back at *x*; two other tendons which it gives, one to the long extensor, the other to the short extensor of the alar membrane, are not shown in this figure.
- t.* Second pectoral, the main elevator of the humerus.
- u.* Coracobrachialis inferior, a muscle arising from the inferior and outer three-fifths of the distal part of the coracoid, and inserted into the internal and



proximal lip of the cup-shaped pneumatic cavity of the humerus. The opposite lip of this cavity receives the tendon of the *teres major* *l*; and from the triangular space between the muscular bellies of these two muscles, the *subscapularis* muscle, together with the upper portion of the scapula, and a small muscle, the *serratus anticus*, which passes between the fibres of the *subscapularis* to be inserted into the inferior edge of the scapula, have been removed.

- v*. *Coracobrachialis superior*, a bicipital muscle with a very extensive origin; arising, superiorly, from the inner surface of the vertebral end of the clavicle; inferiorly, from a facet on the lateral aspect of the upper surface of the sternal rostrum; and between these two points of origin from the upper and inner surface of the ligament connecting the coracoid, clavicles, and sternal rostrum. Its tendon, which is joined by that of the *subscapularis*, is inserted proximally and anteriorly to that of the preceding muscle *u*.
- w*. One head of the *extensor plicae alaris anterioris longus*, arising from the upper end of the clavicle in continuity externally with a head of the *extensor brevis*. These muscular bellies appear to be divarications of the deltoid.
- w*<sub>1</sub>. Muscle in connection with the long alar extensor tendons. Its fibres have in the natural condition of the parts much the same direction as those of the muscle *w* and of the deltoid; but its origin is mainly from the fascia which covers the biceps in front, and being interposed between that muscle and the tendon of the great pectoral, it is continued up into the tendinous expansion by which the posterior layer of the tendon of the great pectoral connects itself more or less intimately with the coracoid head of the biceps and obtains an insertion into that bone. The muscle *w*<sub>1</sub> is inserted mainly into the inner of the two tendons at its distal extremity. This tendon is prolonged down to be inserted into the radial process of the carpo-metacarpal bone which carries the pollex. It is more or less intimately connected with the two other long extensor tendons from the muscle *w* and from the great pectoral, which are here drawn as one; as also with the *extensor brevis* which is not shown in this figure.
- x*. Tendon of great pectoral muscle turned back. The posterior portion of this tendon receives at its lower edge the tendon of a cutaneous muscle which is figured as attached to its outer angle, and higher up it receives the main tendon of origin of muscle *w*<sub>1</sub>, and is ultimately prolonged either separately or in connection with the tendon of the biceps up to the coracoid.
- x*<sub>1</sub>. Biceps. Its tendon is seen running upwards to be inserted into the internal anterior process of the upper end of the coracoid; it has a small insertion into the humerus also, which is not shown here.

PLATE III.



COMMON FROG, *Rana temporaria*.

## PLATE III.

COMMON FROG (*Rana temporaria*),

Injected and dissected to show the chief features of the circulatory organs, and especially the connected systems of the renal-portal and epigastric veins, together with certain portions of the muscular system, the renal and reproductive organs.

THE integument has been turned back on the right side, together with the musculo-cutaneous vein, the superficial branches of which extend from the knee to the shoulder ; part of the muscular wall of the body has been removed on that side, but part has been left *in situ* ; and the main trunk of the musculo-cutaneous vein is seen crossing a slip which the *obliquus externus* muscle receives from the scapula ; on the left side the muscular and cutaneous elements of the wall have been turned back whilst remaining in their natural connection with each other and with the epigastric vein ; the shoulder girdle has been cut through the middle line, and fastened out on either side so as to expose the lungs, heart, and great vessels ; the liver has been removed with the exception of a small part of its substance, as have also the stomach and intestines down to the lower end of the rectum.

- a. Intermandibular space. The skin is left *in situ* anteriorly in the symphyseal angle ; immediately posteriorly to its cut edge is seen part of the mylohyoid or submaxillaris muscle ; and posteriorly again, and at a deeper level, the converging hyoglossi in the middle line, and on either side of them the geniohyoids.
- b. Tetractyle hand. The first finger, i. e. second digit, or 'thumb' so-called, has its basal joint more or less tumid in this, a male specimen.
- c. Muscles of thigh. The line points to the sartorius, which is bordered externally by the vastus internus, and internally by the adductores and recti interni. See Ecker, *Die Anatomie des Frosches*, p. 115.
- d. Point where the musculo-cutaneous veins, constituted by factors from the regions of the head and face, but mainly from those of the back and flanks, turn inwards to pass over a slip going from the scapula to the external oblique muscle and join the subclavian vein. As the skin is moist and glandular this vein has probably to a certain extent a respiratory function. See Ecker, *l. c.*, p. 88.
- e. Vein, called 'epigastric' by Rathke, 'umbilical' by Bojanus and Jourdain, '*vena portae accessoria*,' and '*vena abdominalis inferior s. anterior*,' by other authors. This vein is mainly constituted by the convergence of the two transverse branches from the femoral veins seen at *f* in the figure, but it receives twigs also from the abdominal parietes, and a factor of especial significance in the shape of the vesico-hemorrhoidal vein from the allantoïd bladder and rectum.

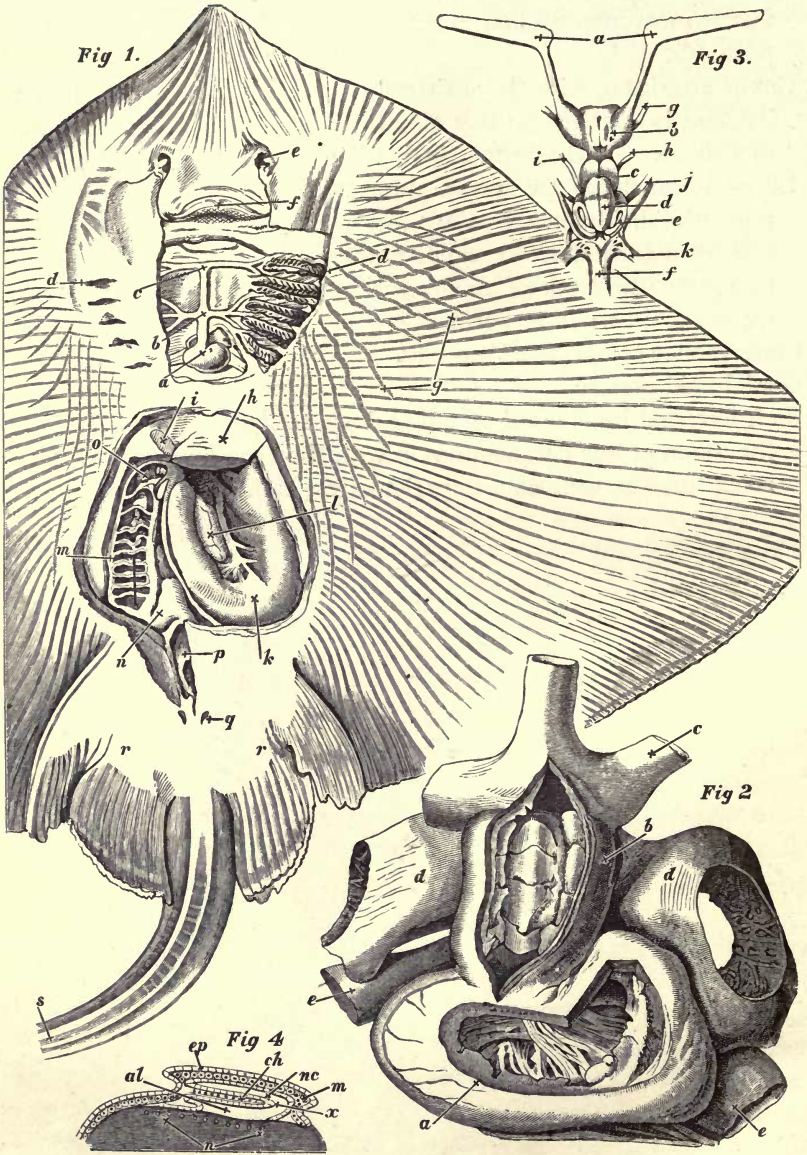
The occasional pathological distension in liver diseases of the veins of the anterior abdominal parietes in the human subject shows that an arrangement may exist in a rudimentary condition in the higher Vertebrata similar to that shown here to exist functionally between the epigastric and the parietal veins; and the connection with a vesico-hemorrhoidal vein, whilst it may be held to foreshadow the arrangement of the umbilical vein in the foetus of Mammals, puts prominently forward the fact that anastomoses exist between the portal and systemic veins. For the 'renal portal' of the Frog, see Jourdain, A. Sc. N. (4), xii., 1859, p. 180.

- f. Point where the transverse branch of the femoral vein of either side fuses with its fellow to form the trunk of the epigastric.
- g. 'Renal portal,' or renal inferent vein of the right side, being the other branch of the bifurcating femoral vein, which is thus seen to be continuous with the portal systems of both liver and kidney. Consequently there are two channels open for the return of the blood to the heart.
- h. Bifid allantoid bladder distended, with ramifications of the vesico-hemorrhoidal veins.
- i. The rectum, which is cut short.
- j. A vesicular, and in this species glandular, dilatation developed upon the Wolffian duct, by which both testicular and renal products pass down to the cloaca. A vein passes directly into the kidney from it.
- k. Vena cava inferior, constituted mainly by the efferent kidney veins, but receiving also those of the testes and fat bodies.
- l. Testis of left side. It has, together with its fellow and with the kidneys, been displaced a little to the right side.
- m. Fat bodies.
- n. Spleen. To the left and a little above the spleen are seen the cut ends of two vessels, one of which receives a factor from that organ, coming itself from the intestine, and the other of which takes origin from the stomach. Both veins join a branch of the epigastric, and are distributed to the liver, a small portion of which is seen left immediately above them.
- o. Gall bladder left attached to the epigastric vein by a vein which passes from it to that vessel.
- p. Lung of left side. The cavity seen on the outer side of either lung has its outer wall constituted by the internal abdominal muscle (homologous with the internal oblique and transversalis), which arches inwards in a dome shape, and is connected with the oesophagus and pericardium, the coracoid and hyposternum. In the natural condition of the parts these cavities are however mainly occupied by the lobes of the liver, which nearly entirely cover the lungs in an anterior view.
- q. Heart. The conus arteriosus takes origin from the base of the ventricle, a constriction known as the *fretum Halleri* marking the line of sepa-

ration of the two organs. The conus bifurcates into the two great divisions of the truncus aortae, which are each subdivided by internal partitions into three canals. These canals become three tubes, the carotico-lingual, the aortic, and the pulmonary trunks, of which the first is most internal and anterior, and the last the most external and posterior.

- q'. Conus arteriosus, with the auricles one on each side. It inclines to the left, and is attached on that side to the ventricle by the *frenulum bulbi* of Brücke. Denkschrift. Akad. Wien, Bd. iii. 1852, p. 355.
- r. Lingual branch of the first of three trunks arising just internally to a rete mirabile known as the 'carotid gland,' from the outer side of which the carotid artery, called sometimes the 'ascending pharyngeal,' passes to the back of the oesophagus in close apposition with the second main trunk or aorta.
- s. Convergence of hyoglossi muscles.
- t. Geniohyoid muscle.
- u. Left external jugular vein passing down to unite with a vein formed by the union of the cutaneous vein with the vena anonyma, and thereby constitute the vena cava superior of the same side.

PLATE IV.



SKATE, *Raja Batis*.

## PLATE IV.

SKATE (*Raja Batis*).

THIS plate, illustrating the anatomy of the Skate, is introduced for the purpose of supplementing the description of the Perch, a member of the order *Teleostei*, p. 83. The Skate belongs to the more generalised order *Elasmobranchii*. In addition to points characteristic of this order detailed below, note in the examination of a specimen the following:—the exoskeletal spines on the dorsal surface resembling teeth, not only in form but in structure, and attached to a basal plate of bone: the great extent of naked skin: the spiracle or visceral cleft between Meckel's arch (mandibular arch) and the Hyoidean arch—the partial homologue of the Eustachian tube—which opens from the mouth behind the eye: the minute apertures of the aquaeductus vestibuli, or pedicles of invagination of the inner ear, placed at the posterior and dorsal aspect of the cranium, one on either side: the skeleton, cartilaginous with the exception of the bodies of the vertebrae: the communication between the pericardial and abdominal cavities in the shape of a bifurcated canal: the presence of a posterior division of the kidney or metanephros, with a certain number of ureters passing off from the inner side of the organ to open into the dilatation, at the posterior end of the Wolffian or mesonephric duct: the union of a certain number of these ureters into a single duct, especially in the male: in the female the open conjoined mouths, situated ventrally at the root of the liver, of the two oviducts, Müller's ducts or Fallopian tubes; the 'nidamental' gland situated on each oviduct; the thicker posterior uterine portions of the ducts: the two oviducal openings, one on each side, into the cloaca: in the male the connection of each testis to the anterior part of the corresponding Wolffian body or mesonephros, thus forming an epididymis; the convoluted anterior portions of the Wolffian or mesonephric ducts forming vasa deferentia, and the claspers placed to the inner side of the two lobes of the ventral fins.

The Rays are peculiar in the slight development of the azygos system of fins, which is restricted to small lobes on the dorsal side of the extremity of the tail: in the enormous expansion forwards, outwards, and backwards, of the pectoral fins which gives the body its great width; and in the bilobed form of the ventral fins. The skin of one Ray at least possesses the minute close-set denticles which constitute shagreen. The degree of development and the arrangement of the large cutaneous spines varies much in different species. The prænasal cartilage is always large, often extremely prolonged, and forms the pointed anterior extremity of the body.

FIG. 1. Skate, *Raja Batis*, female, ventral view from a specimen, dissected so as to show the heart, gills, and digestive tract *in situ*.

- a. The line points to the spot where the conus arteriosus springs from the ventricle. This structure lies in front, with the auricle and ductus Cuvieri behind (see Fig. 2, *infra*).
- b. The line points to the base of the ventral aorta at the spot where it springs from the conus, and gives off the two posterior innominate arteries. Each of these vessels divides into three branches—the three posterior branchial arteries which run on the outer side of the three posterior (II–IV) branchial arches and supply with venous blood the two gill-laminae, anterior and posterior, borne by each arch. These laminae, together with the fibrous septum which supports them and is continued to the skin separating the so-called gill-pouches *inter se*, are seen on the right side of the diagram.
- c. The line points to the anterior termination of the ventral aorta where it gives off the right and left anterior innominate arteries. Each of these arteries divides into the two anterior branchial arches which supply—the anterior, the single gill-lamina (=opercular gill of *Ganoidei*, pseudobranch of *Teleostei*) borne upon the posterior aspect of the hyoidean arch; the posterior, the two gill-laminae borne by the first branchial arch (I). The fifth branchial arch in the Rays and most Sharks, as in *Teleostei* and *Ganoidei*, bears no gill-laminae. The mode in which the branchial arteries arise from the aorta is characteristic of Rays.
- d. The first of the five external gill-slits. The remaining four are seen arranged in a curved line behind. Gill-slits uncovered by an opercular fold are characteristic of all Sharks and Rays: their completely *ventral* position, of the latter only.
- e. The aperture into the olfactory pit. This aperture is placed ventrally in nearly all *Elasmobranchii*. A groove leads from the pit to the corresponding angle of the mouth. Such a groove exists in the embryos of all higher Vertebrata. The outer edge of the groove represents the fronto-nasal, the inner edge the praemaxillary, processes seen in the embryos of Vertebrata which possess praemaxillary and maxillary bones. If the roof of the olfactory pouch is examined in a specimen it will be seen to possess two series of transverse folds.
- f. The line rests upon the upper jaw, which is cartilaginous, and represents, as in all *Elasmobranchii*, a palato-pterygo-quadrangle cartilage. The transverse slit of the mouth and the under jaw (=distal end of Meckel's cartilage) are seen with the rows of diamond-shaped teeth set edge to edge. The retention of a ventrally placed mouth is characteristic of the *Elasmobranchii*.
- g. Jelly tubes or sensory ampullae. Only a certain number of these



structures which are peculiar to *Elasmobranchii* have been figured. They run towards the head, where their inner ends are situated in close contact. Their length varies, the most anterior being short, the posterior long. Their apertures are easily found. The tubes are dilated at their inner extremities and possess in this species numerous lateral saccules. The nerves pass along the septa between these saccules, radiating from the centre. They form a plexus in the walls of the saccules, the ultimate fibrils of which are probably continuous with hair cells in the lining epithelium. The jelly filling these tubes is firm, and is secreted by goblet cells scattered on the walls.

The lateral line is not indicated in this figure. See Merkel, *Endigungen der Sensibeln Nerven*, &c.; Rostock, 1880, p. 33, Pl. II. Fig. 10; and Leydig, *Beiträge zur Mikr. Anat. &c., der Rochen und Haien*, Leipzig, 1852, p. 37. The ampullae are also described by the same authors, see Merkel, p. 43; Leydig, p. 41.

*h.* Middle lobe of the liver, which is trilobed in this species, cut short. The right and left lobes are seen on either side of the aperture made in the abdominal walls.

*i.* Gall-bladder, in the fissure between the right and central lobes. The letters *h* and *i* are placed over the coracoidal bar.

*k.* Stomach, which has the form of a siphon. Blood-vessels are seen arising from the concave edge of the organ and uniting to form a vessel which passes towards the liver and is one of the factors of the portal system.

*l.* The spleen.

*m.* The intestine with its anterior wall removed to show the spiral valve formed by its mucous membrane. Such a valve is found in all *Elasmobranchii*, in *Ganoidei* (rudimentary in *Lepidosteus*) and *Dipnoi*. The inclination, &c., of the folds varies much in the different genera.

*n.* Rectum. The line points to the spot where the rectal gland, found in all *Elasmobranchii*, opens into it on its dorsal aspect.

*o.* Dilated duodenum or Bursa Entiana. It receives the bile and pancreatic ducts. The pyloric aperture is placed on a nipple-like projection.

*p.* The line points to the fold which lies dorsal to the anal aperture into the cloaca, and separates it from a recess into which open the two oviducts laterally and the urethral canal medianly. In the male there is a urogenital papilla on the dorsal wall of the cloaca.

*q.* Right porus abdominalis or external aperture of one of the two canals by which the abdominal cavity communicates with the exterior in *Elasmobranchii*, *Dipnoi*, some *Ganoidei*, and a few *Teleostei*.

*r.* The two-lobed ventral fins. In a male the claspers would be situated between the inner lobes of these fins and the root of the tail.

*s.* Tail cut short.

FIG. 2. Heart, with ductus Cuvieri and base of the ventral aorta of *Raja Batis*. The walls of the several sections of the heart have been removed in part to show points of internal structure. Ventral view. From a specimen.

- a. Ventricle, single as in all Pisces, Amphibia and Reptilia, with the exception of the Crocodile. The walls are thick, and the inner surface shows numerous bands of muscular tissue (columnae carneae). The cavity is curved and the entrance into it from the auricle is guarded by two large membranous valves, seen in the right upper corner of the diagram,—the left corner in the natural position.
- b. Conus or bulbus arteriosus. The aperture of the ventricle leading into it lies on the opposite side to the auricular aperture. Its walls are thick, composed of striated muscular tissue, and it is rhythmically contractile. Its cavity contains three longitudinal rows of pocket-shaped membranous valves, four in each row. The distal valve in each row is the largest. The number of valves in each row appear to vary in the different species of Rays.

The conus must be regarded as a part of the ventricle. It is present in *Ganoidei* and *Dipnoi* among Pisces, and in Amphibia. The number of rows of valves and of valves in each row that it contains is very variable. The distal valves persist and form the valves that guard the entrance to the aorta in those Vertebrata in which the conus is not present as a separate division of the heart.

- c. The line points to the left posterior innominate artery. It and its homologue on the other side of the body spring from the base of the median aorta. The aorta is composed chiefly of membranous tissue, and the muscular tissue present in its walls is unstriped. (Cf. Fig. 1, *b* and *c*).
- d. d.* The right and left pouches of the large thin-walled auricle. This structure is single as in all Pisces except *Dipnoi*. Its walls are thin and its muscles form a network of trabeculae.
- e. e.* The right and left ductus Cuvieri. These two vessels bring back to the heart the venous blood of the whole body. They fuse in the middle line posteriorly to the auricle forming the sinus venosus. The aperture of this sinus into the auricle is guarded by two membranous valves.

The cavity of the whole heart makes an S-shaped curve, much more distinct in some Sharks than in the Ray. This curve is an embryonic feature in other Vertebrata.

FIG. 3. Brain, with the roots of the chief nerves of *Raja Batis*. Dorsal view. From a specimen.

- a. The Lobi olfactorii connected by long olfactory tracts to the cerebral lobes from which they are outgrowths. Each lobe is lengthened out

- laterally, corresponding with the elongated nasal pit. In some Rays they are secondarily lobed. The olfactory tracts vary much in length in the *Elasmobranchii*. They are said to be wanting in *Raja miraletus*.
- b. The cerebral lobes or main part of the fore-brain. They are much compressed dorso-ventrally, triangular in shape, with the outer angles swollen where the olfactory tracts take origin. They are slightly notched in front and grooved ventrally, indicating their bilaterally symmetrical structure. Lateral ventricles are wanting, but the degree to which they are obliterated among *Elasmobranchii* is very variable. A triangular spot, shaded in the diagram, behind the cerebral lobes marks the position of the third ventricle. The filamentous pineal gland (*Epiphysis cerebri*) has been removed.
  - c. The mid-brain, corpora bigemina, or optic lobes. These bodies are large and hollow, and lie above the aqueductus Sylvii or passage between the third and fourth ventricles, with which their cavities communicate.
  - d. The cerebellum, or roof of the anterior portion of the fourth ventricle, the ventricle of the hind-brain. It is large in size in all *Elasmobranch* fishes, and often complexly convoluted. It consists here of two lobes in front and a long triangular lobe behind. It contains a large cavity, freely open to the fourth ventricle, which is just visible behind it, being for the most part covered by the posterior triangular lobe.
  - e. The convoluted corpora restiformia with which are connected the roots of the fifth, facial, and auditory nerves.
  - f. The commencement of the spinal cord. The medulla oblongata or the sides and floor of the hind-brain is remarkably short in the Rays. It is usually elongated in *Elasmobranchii*.
  - g. Optic nerves. There is a superficial chiasma to these nerves in *Elasmobranchii*, *Ganoidei*, and *Dipnoi*.
  - h. Third nerve or oculomotor. It springs from the base of the mid-brain, but its superficial origin is hidden by the saccus vasculosus.
  - i. Fourth nerve or trochlearis. It arises, as in all Vertebrata, from the roof of the aqueductus Sylvii behind the mid-brain, and in front of the cerebellum.
  - j. Roots of the fifth (trigeminus), seventh (facial or 'portio dura'), and eighth (auditory or 'portio mollis') nerves. The facial rises dorsally, the auditory posteriorly and ventrally, while the remaining roots belong to the trigeminus. This close connection of the nerves at their roots is generally found in Pisces. The trigeminus and facial are also closely connected in the Gasserian ganglion in *Anura* (Amphibia). The facial and auditory nerves also are often closely connected in Amphibia and Reptilia at their roots.

*k.* The roots of the vagus nerve or pneumogastric. The glossopharyngeal nerve forms the most anterior of these strands which rise close together from the medulla oblongata.

FIG. 4. Longitudinal section through an Elasmobranch embryo at a time when the neural canal, notochord, and alimentary canal are established. From Balfour, Development of Elasmobranch Fishes. London, 1878, Fig. 1 c, p. 58.

*ep.* Epiblast or superficial layer of cells formed from the blastoderm, and extending, with the mesoblast and hypoblast, round the ovum, to form the yolk sac. This growth or extension is greatest at the anterior end of the embryo. It is slight at the posterior end, where was situated the aperture of invagination, blastopore, or anus of Rusconi, beneath the embryonic rim.

*nc.* Neural canal which is formed first as a groove in the blastoderm (medullary groove), and is then converted into a canal by the closure of the sides of this groove. The medullary groove extends to the posterior end of the blastoderm and the dorsal edge of the blastopore. On its closure to form the neural canal a pore persists at this spot; and when the dorsal edge of this pore, continuous with the edge of the blastopore, grows down over the yolk, a communication is left between the neural and alimentary canals.

*x.* Communication between the two canals named, known as the neurenteric canal. It is a common feature in vertebrate development, and lies, as a rule, behind the spot where the anus is formed. Hence there is a post-anal extension, not only of the neural, but also of the alimentary canal. See Balfour, Comp. Embryology, vol. ii. p. 267, 268; p. 634-636. Cf. Spencer, Q. J. M. Suppl. 1885, p. 126-7.

*ch.* Notochord. A rod of cells differentiated at an early period from the layer of cells below the medullary groove, and therefore probably to be considered as of hypoblastic origin.

*m.* Mesoblast.

*al.* Alimentary canal, roofed in by cells which are derived together with the mesoblast from the original mass of cells underlying the epiblast. The mesoblast cells are wanting immediately below the medullary groove, but form two plates to either side of it. Both mesoblast and hypoblast extend with the epiblast round the non-segmented part of the ovum or yolk to form the yolk sac.

*n.* Nuclei in the yolk. These nuclei appear spontaneously (?) in the protoplasm of the yolk, i. e. in the network between the secondary yolk or deutoplasm. A portion of protoplasm separates round each nucleus. This process begins at an early stage, and the cells thus formed are added at first to the lower layer of blastoderm cells, and subsequently

to the hypoplast. They thus contribute to its growth, and especially to the formation of the floor of the alimentary canal.

The chief works on the Anatomy of the Skate and *Elasmobranchii* are the following:—

*Anatomy of Skate.* T. J. Parker, Zootomy, London, 1884.

*Zoological account of Rays.* Cf. Day, Fishes of Great Britain and Ireland, ii. 1884, p. 336. Couch, Fishes of British Islands (coloured figures), i. 1862, p. 78. Bell, British Fishes, ii. 1841, p. 550. Günther, British Museum Catalogue of Fishes, viii. 1870, p. 434.

*Skull.* W. K. Parker, Tr. Z. S. x. 1879. *Visceral arches.* Dohrn, Mitth. Zool. Stat. Naples, vi. 1885.

*Paired fins.* Balfour, P. Z. S. 1881. *Paired and azygos fins.* Mivart, Tr. Z. S. x. 1879 (see general remarks). *Azygos fins.* Mayer, Mitth. Zool. Stat. Naples, vi. 1885.

*Exoskeleton.* Hertwig, J. Z. viii. 1874. Benda, A. M. A. xx. 1882.

*Teeth.* Tomes, Ph. Tr. 1876. Id. Dental Anatomy, ed. 2, 1882, p. 215.

*Central nervous system.* Rohon, Dk. Akad. Wien, xxxviii. 1878. Viault, A. Z. Expt. v. 1876. *Système ganglionnaire.* Vignal, A. Z. Expt. (2), i. 1883, p. xvii. *Spinal cord,* Stieda, Z. W. Z. xxiii. 1873; Sanders, P. R. S. xl. 1886.

*Cranial nerves.* Marshall, Q. J. M. xxi. 1881. Cf. Beard, *Branchial sense-organs,* Q. J. M. xxv. 1885. *Vagus nerve.* Rohon, Arb. Zool. Inst. Wien, i. 1878.

*Gustatory organs.* Todaro, A. Z. Expt. ii. 1873. *Organs of lateral line.* Solger, A. M. A. xvii. 1880. *Do. and ampullae.* Merkel, Endigungen der sensibeln Nerven in der Haut, Rostock, 1880.

*Intestinal spiral valve.* T. J. Parker, Tr. Z. S. xi. 1880. *Rectal gland.* Blanchard, Journal de l'Anat. et Physiol. xiv. 1878. *Function of do.* Id. Bull. Soc. Zool. de France, vii.

*Rudimentary gill slits.* Van Bemmelen, Mitth. Zool. Stat. Naples, vi. *Histology of gills.* Dröscher, A. N. 48, 1882. *Rudiment of air bladder.* Miklucho-Maclay, J. Z. iii. 1867.

*Valves in conus arteriosus of Elasmobranchii and Ganoidei.* Stöhr, M. J. ii. 1876; for *Raja Batis*, see p. 219.

*Venous system of Skate.* T. J. Parker, Trans. New Zealand Institute, xiii. 1880.

*Urinary apparatus and genital ducts.* Balfour, Development of Elasmobranch Fishes, 1878, pp. 249–286.

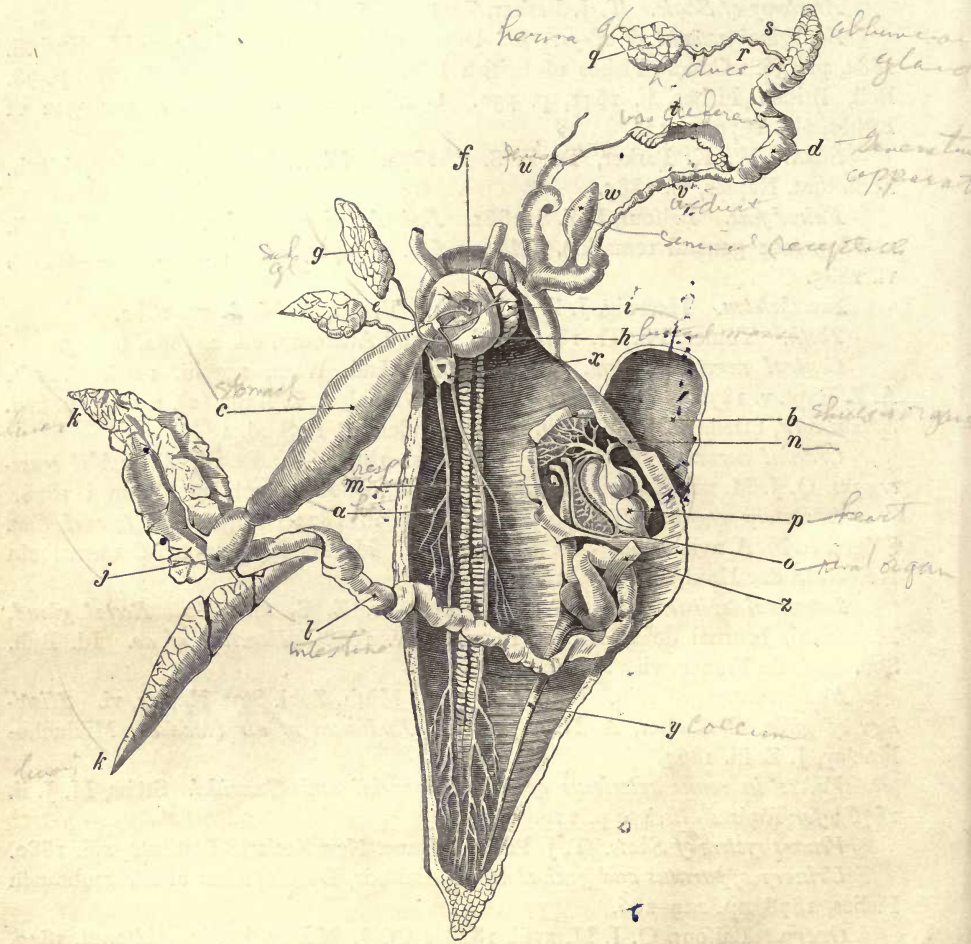
*Ovary.* Balfour, Q. J. M. xviii. 1878. Cf. J. Muller, Berlin, Abhandl. 1840, for forms of ovum, and Günther, Study of Fishes, 1880.

*Copulatory organs.* Petri, Z. W. Z. xxx. 1878; see Bolau, Z. W. Z. xxxv. 1881; and Schneider, Zool. Beiträge, i. 1. 1883.

*Pori abdominales.* Bridge, Journal of Anat. and Physiol. 1879. Cf. Ayers and Gegenbaur, M. J. x. 1884.

*Chemistry of horny fibres in Mustelus and egg-case of Scyllium.* Krukenberg, Mitth. Zool. Stat. Naples, vi. 1885.

PLATE V.



CELLAR SLUG, *Limax flavus*.

## PLATE V.

CELLAR SLUG (*Limax flavus*, s. *variegatus*),

Dissected so as to show its digestive, circulatory, respiratory, nervous, and reproductive systems.

THE muscular envelope has been separated from the foot along the left side, and turned over to the right, together with the shield-shaped mantle and the organs it overlies. The buccal mass and nerve collar, together with the salivary glands, have been displaced a little to the left, on which side of the animal's body the stomach and bilobed liver have been fastened out. Some of the nerves, muscles, and arteries have been cut away. The oesophagus and buccal mass have been pulled a little forward through the nerve-collar, and occupy much the same position relative to it that they do when in life the buccal mass and head are thrust forward. The two first convolutions of the intestine have been uncoiled, and it has thus been drawn as taking a much less sinuous course than it does in nature from its commencement at the pylorus to the point where it comes into relation with the dorsal integument and shield, and hooks round the muscle which retracts the buccal mass and tentacles. The generative organs have been detached from their normal connections, and are arranged on the right side of the animal's head. Their volume, as drawn here, is small in comparison with that which they attain in the breeding season. The upper tentacles, the nerves which supply and the muscles which retract them, have been cut through, and turned forward so as to lie between the generative apparatus on the right hand and one of the salivary glands on the left. The right lower tentacle is seen between the right upper tentacle and the vestibulum of the reproductive system.

a. Locomotive disk or 'foot' passing upwards at the sides into the general muscular envelope of the various organs of the animal's body, from which it is limited off by a furrow. Its internal circular coat is raised into two corrugated ridges along the greater part of the middle line of the body by the underlying supra-pedal gland. This gland is found in many *Gastropoda*, and is of very large size in this Slug. Its aperture lies above the foot and below the head, its duct is long, and lined by ciliated epithelium of two kinds, of which one is perhaps sensory (? olfactory). The gland cells are aggregated on either side of and below the duct. The supra-pedal gland must be carefully distinguished from the pedal which secretes the mucous thread by which certain *Prosobranchiata* suspend themselves to the surface of the water, and which opens on the sole of the foot anteriorly. See p. 110, and lit. p. 112.

- b. Shield and organs in connection with it.
- c. Stomach and bilobed liver, arranged upon the animal's left.
- d. Generative apparatus arranged upon the animal's right.
- e. Nerve-collar, consisting of two *cerebral* ganglia placed above, or rather at the sides of, the oesophagus, and two pairs of ganglia placed below it, and united with the upper pair by connectives. The two *cerebral* ganglia are connected by a flat commissure, and with the infra-oesophageal ganglia by a double connective, the posterior cord of which joins the posterior part of the mass or *visceral* ganglia, whilst the anterior cord joins the anterior or *pedal* ganglia from which nerves pass off to the foot.
- f. Stomatogastric ganglion of right side placed below the oesophagus, where it enters the buccal mass together with the duct of the salivary gland. The ganglion is connected by a long and delicate commissural cord with the supra-oesophageal ganglion of its own side, and it gives off nerves to the buccal mass, to the oesophagus, and to the duct of the salivary gland.
- g. Salivary gland.
- h. Buccal mass containing the 'tongue' or 'odontophore.'
- i. Semper's organ. It is of very large size in this Slug, small in *Helix*, *Arion*, *Lymnaeus*, and has only been detected in *Pulmonata*. It consists of four to five lobes composed of cells, resembling those in the salivary or supra-pedal glands, held together by a network of connective tissue and a membrane. According to Sochaczewer (*Z. W. Z.* xxxv. 1881, p. 35), it receives two nerve twigs from the labial nerves, and is *not*, as Semper supposed, richly supplied with nerves. A ganglion has been detected by Sarasin (*Arb. zool. zoot. Inst. Wurzburg*, vi. 1883, p. 95) lying in the oral lobes and sending processes into this gland. It occurs also in *Pulmonata Basommatophora*, in which Semper's organ is absent.
- j. Coecal projection at pyloric end of stomach.
- k. Liver consisting of two lobes opening each by a single duct close to the pylorus.
- l. Intestine passing from the pylorus to end a little in front of and above the respiratory inlet. Its two first convolutions have been separated from the liver and reproductive apparatus. As it approaches the dorsal integument and shield it describes a curve like an Italic S. In the first loop of this S is seen the origin of the retractor muscles of the buccal mass and labial tentacles; at its opposite extremity arises a straight coecum, *y*.
- m. Respiratory orifice, with the 'rectum' curving round to open a little above and anteriorly to it. To the right of the rectum is seen the duct of the renal organ.

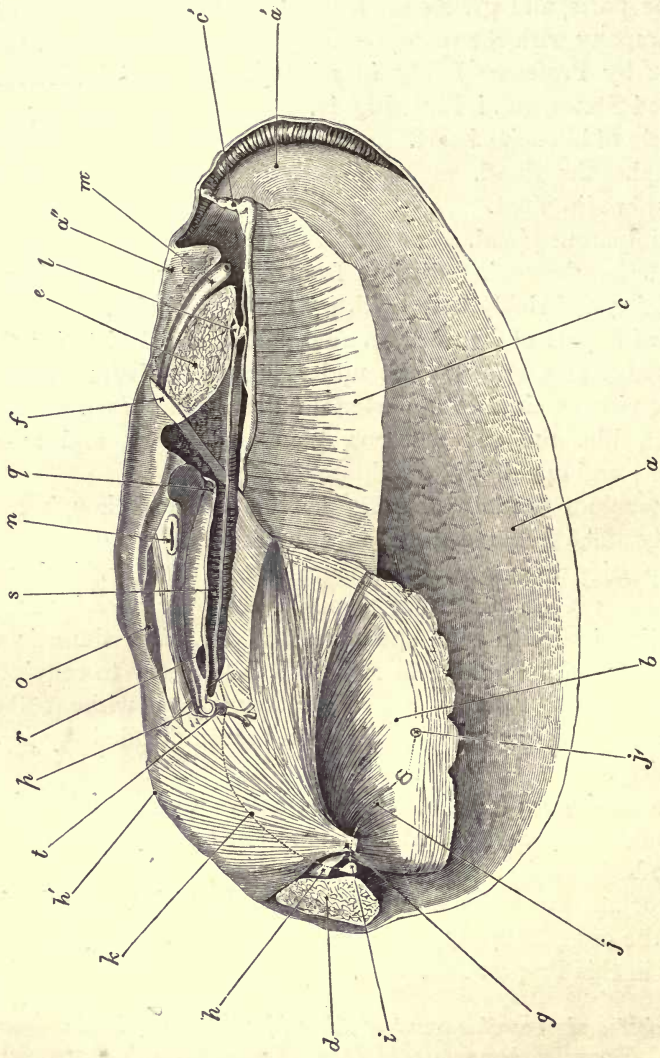


- n.* Portion of dorsal integument, an incision immediately to the right of which would disclose the shell. Internally to it is the respiratory sac, with the ramifications of the pulmonary veins.
- o.* Renal organ, placed to the right of the heart in the natural position of the parts, and giving off a duct which passes backwards, to run in company with the rectum and open near the anus. See enlarged figure by Professor Leidy in Binney's *Terrestrial Molluscs of the United States*, vol. i. Pl. I. Fig. iv.
- p.* Ventricle of bilocular heart.
- q.* Hermaphrodite gland.
- r.* Hermaphrodite duct.
- s.* Albuminiparous gland.
- t.* Vas deferens becoming distinct from oviduct *v* sooner than in *Helix* or *Arion*, and richly beset with prostatic glandules.
- u.* Penis, with part of its retractor muscle left attached to it; the muscle originates at a spot on the under surface of the muscular envelope of the viscera, close to the arterial outlet of the heart.
- v.* Oviduct, like the vas deferens, glandular above, and membranous below; and opening into a dilated vagina.
- w.* Receptaculum seminis, opening in this species, though not in the closely allied *Limax cinereus* into the vagina.
- x.* *Pedal* portion of the suboesophageal nerve mass, enclosing, together with the *visceral*, an orifice through which the anterior aorta passes. The line is drawn to a spot where in *Helicidae* the otic vesicle is readily found, but where in *Limax* it is not easy to convince oneself that it exists, even as a rudimentary organ, without the use of reagents, such as the oxalic acid recommended by de Lacaze Duthiers.
- y.* Coecum passing off from intestine just before it comes into relation with the pulmonary cavity, and extending back nearly to the termination of the body cavity.
- z.* Retractor muscle of the buccal mass and tentacles. Its fascicles pass with the oesophagus through the nerve-collar. They have been cut away in this Preparation.

*Anatomical and general account of Limacidae*, Simroth, *Nacktschnecken*, &c. Z. W. Z. xlii. *Figures of the anatomy of Limax*, Leidy, *Binney's Terrestrial Molluscs of the United States*, i. Pl. I.

*Reproductive system*, Baudelot, A. Sc. N. (4), tom. xix., 1863, Pl. III. Fig. 17.

PLATE VI.



FRESH-WATER MUSSEL, *Anodonta cygnea*.

## PLATE VI.

FRESH-WATER MUSSEL (*Anodonta cygnea*),

Dissected so as to show its muscular and nervous systems, as well as certain other organs in relation with them.

THE animal has been taken out of the shell; the gills and the mantle have been removed on the left side, together with the labial tentacles and parts of the pericardium, as well as of the organ of Bojanus or nephridium of the same side.

*a.* Right mantle lobe, free along its ventral edge.

*a'*. Fimbriated portion of mantle corresponding to the inferior siphonal notch by which water is drawn into the branchial cavity.

*a''*. Dorsal raphe along which the two halves of the mantle meet.

*b.* Foot. The muscular portion is strongly contracted.

*c.* Gills of right side.

*c'* Union of external gill to the mantle between the inferior and superior siphonal notches.

*d.* Anterior adductor.

*e.* Posterior adductor.

*f.* Posterior retractor of the foot, inserted into either valve, anteriorly and superiorly to the posterior adductor, the scar or muscular impression of the two being more or less confluent. Its muscular expansion in the foot is especially well developed along the free or ventral edge of the foot, and it inter-digitates very freely with the protractor pedis, though it lies for the most part at a lower level than that muscle.

*g.* Protractor of the foot. This fan-shaped muscle spreads over the external surface of the foot, from an insertion into the shell, a little superiorly to the point where the pallial line joins the impression of the anterior adductor. It acts, consequently, as an antagonist to the preceding and succeeding muscles. Its impression is distinct in this animal from that of the adductor.

*h.* Anterior retractor of the foot. The fibres of this muscle take origin from a point in the shell, towards the dorsal aspect of the anterior adductor, though some way from its dorsal border. They spread thence into the foot especially along its anterior edge, and down as far as its anterior angle, for the most part at a deeper level than the preceding muscle. Some of the fibres, however, spread over the visceral mass dorsally.

*h'* The line points to the position of the smaller retractor muscles with

- insertions just anteriorly to the umbones, whence they radiate over the regions of the stomach, and towards the pericardium.
- i.* Left cerebro-pleural ganglion lying in the angle between the anterior retractor and adductor, and the protractor pedis, above the entrance to the mouth.
  - j.* Connective passing from the left cerebro-pleural ganglion to the left pedal. The pedal ganglion of each side gives off twelve nerves, six from its neural, and six, more slender, from its lateral surface. They are not figured in this plate.
  - j'.* Auditory vesicle appended to pedal ganglion. This vesicle is ordinarily said to be appended to a branch given off from the most backwardly placed but one of the posterior pedal nerves. But Simroth states that its nerve is derived from the cerebro-pedal connective and so figures it. See Z. W. Z. xxvi. 1876, Pl. XVI. Fig. 56, and p. 138, *ante*. It is not always symmetrically developed on both sides, and, when present on one side only, it has been found to contain two otoliths. It is situated in a part of the foot narrow from side to side, at the junction of its anterior two-thirds to its posterior third, and near to its purely muscular portion into which the viscera do not enter.
  - k.* Commissure between the left cerebro-pleural and visceral ganglia. It passes between the fibres of the retractor pedis and the protractor through the upper part of the foot, internally to the generative orifice, *t*; then through the glandular portion of the nephridium, *s*; and across the tendon of the retractor pedis posterior where it bifurcates for insertion into either valve of the shell.
  - l.* Left visceral ganglion. Two nerves are figured in connection with it, one, a parietal nerve, going to the mantle, the other, a branchial nerve, going to the gill.
  - m.* Rectum ending in the cloaca. A delicate nerve is figured by Duvernoy, *op. cit.* p. 138, *ante*, as passing to it from the visceral ganglion.
  - n.* Heart; the letter pointing to the slit left by removal of the left auricle.
  - o.* Pericardial space into which opens the glandular portion of the nephridium.
  - p.* External opening of the nephridial duct.
  - q.* Opening by which the glandular portion of the nephridium communicates with the duct.
  - r.* Wide opening by which the ducts of the two nephridia communicate. This opening does not exist in *Unio margaritifera*.
  - s.* Secretory or glandular portion of the nephridium, reaching from the level of the anterior end of the pericardial space to the under surface of the posterior adductor. It opens into the pericardium by a canal

along which a bristle has been drawn as passing. The glandular portions of the two nephridia communicate freely with each other, as do also the excretory sacs in this species.

- z. Orifice of the duct of the generative gland. This orifice is concealed in *Anodonta*, though not in *Unio*, by the attachment of the inner gill-lamina to the visceral mass. See V. Baer, Meckel's Archiv. 1830, p. 318.



## PLATE VII.

## LAMELLIBRANCHIATA.

FIG. 1. The common Oyster (*Ostrea edulis*), dissected so as to show the principal features of its anatomy.

THE animal has been removed from its shell and dissected on its left side, the one that corresponds to the flat or free valve of the shell. It may therefore be compared without difficulty with the figure of *Anodonta*, Plate vi., which has been dissected in the same way.

- a. a. a.* Right lobe of the mantle which has been left entire, the left lobe being cut away save at its oral end.
- a'*. Anterior dorsal angle.
- a''*. Anterior ventral angle, which is produced a little beyond the dorsal angle. The part included between these two angles is fitted into a deep recess in the right valve, and the ligament of the shell, which is internal, corresponds to the straight edge uniting them.
- b.* The two oral tentacles of the left side. The tentacles are not quite symmetrical in this animal. Note the deep bay which lies between them and the cut edge of the left mantle which is remarkably thickened in this region.
- c.* The gills or branchiae. There are four of these as in *Anodonta*. They are not symmetrical *inter se*, and are fluted, i. e. the lamellae are not flat but undulated.
- c'*. The spot where the attachment of the gills to the mantle lobes ends. This attachment divides the mantle cavity into an inhalent, oral or infra-branchial chamber, of great length but shallow in the Oyster, and an exhalent, aboral or supra-branchial chamber, which is deep and of less extent than the oral chamber. Note the four lines of apertures into the interlamellar spaces of the gills.
- d.* The single adductor muscle, the sole adductor present in the families *Ostracidae* and *Aviculidae*. The Lamellibranchiata have been divided into the *Monomyaria* with one, and *Dimyaria* with two adductor muscles, as in *Anodonta*, but the division is not a good one. This single adductor corresponds to the posterior adductor of *Anodonta*. It is distinctly divisible into two parts, an opaque portion close to the pericardium, and a translucent portion behind. This division is observable in the adductors of many Lamellibranchiata, both anterior and posterior. Coutance has stated that the muscular fibres of the translucent portion in *Pecten* are striated, of the opaque, smooth; that the former contract rapidly, the latter slowly; that the opaque portion is more

like a ligament in function. But the histological difference between the parts does not extend to other Lamellibranchiata.

- e. The left auricle, and
- e'. The single ventricle of the heart. The auricles are fused together in the middle, while their two extremities are free, i. e. they receive blood from the gills by two channels and communicate with the ventricle by two short vessels, the ventricular orifices of which are guarded by two valves apiece. The ventricle is not perforated by the intestine, a point in which the Oyster resembles *Anomia* and *Teredo*. The heart lies in a pericardium situated anteriorly to the adductor and communicating with the exterior through the nephridium.
- f. The body of the animal which contains the digestive tract, the liver or hepato-pancreas, the organs of generation, and a part of the renal organ. A short 'oral process' of Hoek, which contains a loop of intestine (Fig. 2, c), projects from it just in front of the visceral ganglion, g.
- g. The left visceral ganglion, of very large size, and when seen from the surface instead of sideways, bilaterally symmetrical. It gives off posteriorly and laterally nerves which branch repeatedly, possess a muscular sheath (Hoek), and are connected at the margin with the pallial nerve. This nerve is complete, i. e. extends along the whole edge of the mantle. Anteriorly the ganglion gives off in addition to the cerebro-pleural commissure two nerves, one of which passes between the adductor and the pericardium to the mantle. The other is the branchial nerve, and is seen passing along the commissure of the two left gills. Between this nerve and the cerebro-pleural commissure, and behind the spot where they cross one another, is a depression, the common vestibule of the renal and generative ducts.
- h. Cerebro-pleural ganglion of the left side sending forwards branches to the pallial nerve. There is no foot and in consequence no pair of pedal ganglia. These ganglia are either fused with the cerebro-pleural or else aborted; but there is a nerve-cord passing *beneath* the mouth from one to the other cerebro-pleural ganglion which represents the cord connecting the two pedal ganglia of *Anomia*. In this animal they are approximated to the cerebro-pleural ganglia and are of large size.
- i. Commissure between the cerebro-pleural and visceral ganglia. Two nerves going to the body originate from it.
- j. Large funnel-shaped anus.

The organs of generation as described by Hoek extend over the surface of the body and the anterior surface of the pericardium. There are two glands, a right and left, but they are connected peripherally. They form a system of anastomosing and interlacing channels beneath the integument from which caeca descend vertically



into the body. In these caeca the generative products both male and female develop side by side. Each duct opens anteriorly into a recess common to it and the duct of the organ of Bojanus or nephridium of the same side.

The nephridium consists of long caeca which give origin to other caeca and extend even into the mantle. They lie in the body superficially to the genitalia. The renal channels open into a long chamber. This chamber or duct communicates with the recess above mentioned and by a reno-pericardiac canal with the pericardium. The nephridium of the Oyster differs strikingly from that of other Lamellibranchiata (Fig. 4) in not being compact. Some parts of the renal channels are covered with a ciliated, other parts with a stratified epithelium.

*Hoek*, Tijdschrift der Nederlandsche Dierkundige Vereeniging, Suppl. i. Leiden, 1883, (in French and Dutch).

*A resumé of anatomy of the renal and genital organs.* Abstract in Journal of Roy. Micr. Soc. (2), iii. 1883, pt. 1, p. 354.

*Nervous system.* Duvernoy, Mémoires de l'Institut, xxiv. 1854, Monograph, p. 61.

*Visual organs of O. Virginica.* Sharp, Mitth. Zool. Stat. Naples, v. 1884.

*Adductor muscle.* Plateau, A. Z. Expt. (2), ii. 1884.

*Sexes of oysters.* Ryder, A. N. H. (5), xii. 1883. *O. Virginica* and *O. angulata* have the sexes separate; Bouchon-Brandely, C. R. xcv. 1882.

*Development.* Horst, A. N. H. (5), ix. 1882; Brooks, Johns Hopkins Univ. Biological Studies, Report, Chesapeake Zool. Lab., Session 1878; Ryder, Report of U. S. Commission of Fish and Fisheries for 1882 (published 1884).

*Green colour in oysters.* Puységur, cf. Journal Roy. Micr. Soc. iii. 1880; Ryder, *ibid.* (2), iii. 1883; both in full in Reports of U. S. Commission of Fish and Fisheries for 1882 (published 1884). Ray Lankester, Q. J. M. xxvi. 1886.

FIG. 2. Digestive tract of the same, in the position it would occupy in a specimen placed like the one figured above (Fig. 1). After Brandt and Ratzeburg, *Medizin. Zoologie*, Berlin, ii. 1833, Pl. XXXVI. Fig. 4.

- a. The two pairs of labial tentacles.
- b. Anal termination of the intestine, lying to the dorsal side of the adductor muscle, *j*, Fig. 1. The anus is funnel-shaped.
- c. Loop of intestine occupying the 'oral process' of Hoek, which projects in front of the visceral ganglia (*g*, Fig. 1).
- d. Stomach, upon the side of which, turned towards the dissector, lies the coil of intestine immediately preceding the anus.

FIG. 3. Heart and principal vessels of *Arca Noë*. From Poli, *Testacea utriusque Siciliae*, ii, Parma, 1795, Pl. XXV. Fig. 2.

The heart is aberrant, inasmuch as there are not only two auricles as in other Lamellibranchiata, but the ventricle also is double.

- a. Branchial venous, i. e. efferent vessels. The shaded vessel below represents the branchial arterial, i. e. afferent vessels.
- b. Mantle vessels, entering with *a*.

- c.* The auricle of the left side.
- d. d.* The two ventricles, left and right, the former shaded. Each ventricle gives off
- e.* A single trunk which divides at once into two vessels, an anterior and posterior.
- h.* Anterior aorta formed by the fusion of the two anterior vessels from the left and right sides respectively. It passes forwards and supplies the viscera, labial tentacles and anterior part of the mantle.
- g.* Posterior aorta formed by the fusion of
- i.* The two posterior vessels.
- j. j.* The organ of Bojanus or nephridium.

FIG. 4. Longitudinal section, partly diagrammatic, of the left organ of Bojanus, or nephridium of *Unio pictorum*. From de Lacaze-Duthiers, A. Sc. N. (4), iv. 1855, Pl. V. Fig. 2.

- a.* Posterior adductor muscle.
- b.* Ventricle of heart traversed by the intestine, and giving off the anterior and posterior aortae.
- b'. b'.* Pericardial space, immediately beneath the dorsal surface of the animal.
- c.* Rectal termination of intestine with anus.
- d.* Dorsal edge of mantle in section.
- e.* External aperture of nephridium. It leads into the duct, a thin-walled sac lying immediately below, i. e. ventral to, the pericardial space. The two ducts, left and right, sometimes communicate beneath the pericardial space anteriorly, e. g. in *Anodonta*.
- f.* Internal aperture of the nephridium into the anterior extremity of the pericardial space. The arrow shows that the anterior part of the glandular or lamellate portion of the organ passes internally to the duct.
- g.* Aperture of the generative organ, lying close to but separate from the nephridial duct in this mussel, and in the majority of Lamelli-branchiata.
- h.* The aperture from the non-glandular into the glandular portion of the nephridium. The former has smooth walls, the latter walls produced into lamellae. The cells covering these lamellae are pigmented and contain phosphatic concretions.

It is clear that water set in motion by the ciliated epithelium of the organ can either enter or pass out of the pericardial space.

FIG. 5. *Veliger* of *Cardium pygmaeum* before it quits the egg. From Lovèn, copied in Bronn, *Klassungen u. Ordnungen des Thierreichs*, vol. iii. (1), 1862, Pl. XXXVIII. Fig. 31.

- a.* Entire circular velum, fringed with cilia, and bearing in its centre a long flagellum. The velum, according to Lovèn, is formed by the

coalescence of two papillae. It is never produced into lobes, as in Gastropoda and Pteropoda. In some fresh-water forms which have no free larva the velum is reduced (*Anodonta*, *Unio*, *Cyclas*), or aborted (*Pisidium*). In these forms, in *Teredo* and *Ostraea edulis*, the central flagellum is absent.

*b.* Archenteron inclosed by hypoblast cells.

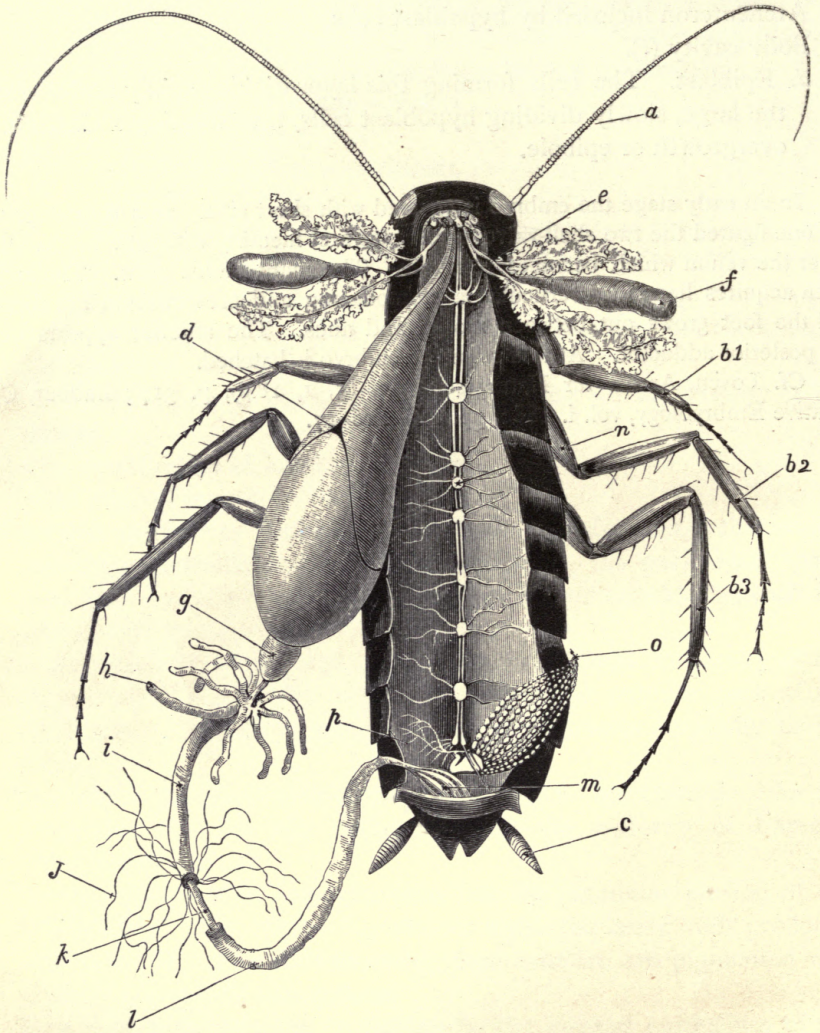
*c.* Body cavity (?).

*d. d.* Epiblast. The cells forming this layer divide rapidly and surround the large, slowly dividing hypoblast cells, thus forming a Gastrula by overgrowth or epibole.

In an early stage the embryo is covered with short cilia. In a later stage than the one figured the two shell-valves appear, at first meeting without a hinge. They cover the velum which becomes retractile. The mantle-folds grow. The archenteron acquires hepatic diverticula; a stomodaeum and proctodaeum are formed; and the foot grows out between mouth and anus. The anterior appears before the posterior adductor. At this stage the embryo is hatched.

Cf. Lovén, *Archiv für Naturgeschichte*, 15, 1, 1849, p. 317; Balfour, *Comparative Embryology*, vol. i. 1880, pp. 214, 216-17.

PLATE VIII.



COCKROACH, *Periplaneta orientalis*.

## PLATE VIII.

COMMON COCKROACH (*Periplaneta orientalis*), FEMALE,

Dissected so as to show its digestive, nervous, and reproductive apparatus; the 'fat body,' and a considerable portion of the dorsal integument having been removed.

OF the external organs are seen the multi-articulate antennae, the segmented anal appendages or 'cerci,' the compound eyes, portions of the epicranium, of the terga, of the pro-, meso-, and meta-thorax, and of the eight terga of the abdominal somites; and finally, the three pairs of legs articulated to the thoracic somites, and consisting each of a proximal segment known as the *coxa*; a second and much smaller segment, distinct in these, though not in the saltatorial *Orthoptera*, from the *coxa*, and known as the *trochanter*; a third, the *femur*, beset below with spines; a fourth, the *tibia*, more richly armed with spines than the *femur*; and the fifth, the *tarsus*, which is quinque-articulate.

- a. Antennae consisting of three elongated basal segments, and a multi-articulate appendage made up of as many as ninety-two joints.
- b. 1, b. 2, b. 3. Tibiae, sub-quadrangular in shape, and beset along their two narrower sides with spines.
- c. 'Cerci anales,' consisting of twelve segments, the terminal one conical, the others thickly beset with hairs. As sexual characters may be noted the absence of the sub-anal styles possessed by the male, and the median emargination of the supra-anal dorsal plate with which the cerci articulate. The cerci perhaps represent a pair of abdominal limbs. They are commonly found in *Orthoptera*, *Pseudo-Neuroptera*, and all *Thysanura*.
- d. Nerve ganglion developed upon the nervus recurrens, and seen to give off a nerve on either side, which passes backwards upon the crop to the gizzard and has itself fusiform dilatations of a ganglionic character developed upon it.
- e. Common duct communicating with the two lobes of the dendritic salivary gland. The ducts of the two salivary glands fuse mesially with each other, in the angle formed by the convergence and fusion of the ducts of the two salivary bladders or reservoirs with which they fuse in turn, so that the compound duct finds an outlet into the mouth by means of a short common canal. The figure does not accurately

reproduce this arrangement, which cannot be demonstrated to the unassisted eye.

- f. Salivary bladder.
- g. Gizzard communicating with the chylic stomach, *i*, through the intermediation of a short segment of small calibre.
- h. Whorl of eight caeca at the commencement of the chylic stomach.
- i. Chylic stomach, smooth externally as is the upper half of the homologous segment in *Grylotalpa*.
- j. Malpighian tubules, in number from twenty-four to thirty; inserted in a zone around the lower end of the chylic stomach. This insertion is unusual, and they generally open into the commencement of the intestine, from which they are developed as outgrowths in *Blatta germanica* and all Insecta.
- k. First portion of the intestine or 'small' intestine.
- l. Large intestine or colon; found ordinarily in its upper part distended with the refuse of the ingesta, and below of smaller calibre, and corrugated so as to present a beaded appearance.
- m. Rectum showing the longitudinal lines formed by internal ridges supplied with numerous tracheae. The ridges thus developed upon the rectum constitute in the larvae of the *Libellulidae*, together with a valvular apparatus developed from the caudal tegumentary skeleton, their aerating organ.
- n. First abdominal ganglion, closely approximated to the third thoracic, and placed at a slightly greater distance from the second abdominal ganglion. The sixth abdominal ganglion should have been drawn as somewhat heart-shaped, but laterally constricted so as to have the appearance of being made up, as it probably is, of more than one distinct ganglion. The two oviducts pass to their point of fusion from the outside of the angle bounded by the nerves, seen to spring from this ganglion. The sub-oesophageal ganglion is not seen in this figure, being, as always in Insects, in such close apposition to the supra-oesophageal or cerebroid ganglion, as to have been sometimes, but inconveniently, described as making up, together with it, a 'brain.' Counting, however, this ganglion whence the mandibles, maxillae, and labium receive their nerve supply, we find that the entire ventral cord is made up of nine ganglia, the last of which may be taken as representing more than one ganglion.
- o. 'Verticillate' ovary of right side, consisting of eight egg-tubes, connected by a suspensory ligament, which is made up by the fusion of filaments from their respective apices, and is attached to the dorsal region of the thorax. The proximal extremities of the oviducts vary in shape with their state of distension. Hence they have been described in very different terms by different authors. The

two oviducts pass ventrally to the terminal nerve structures, to form a common vagina, which opens between the sterna of the eighth and ninth abdominal somites.

*p.* Colleterial glands of the left side.

The tubules of each side join a single stem, and the two ducts thus formed open by a single orifice into the vagina within the angle bounded by the nerves of the last abdominal ganglion. The two glands (right and left) have, according to Kadyi, an identical structure, and consist of tubes dividing dichotomously. But the left gland is large and hides the right, and its secretion contains crystals of Calcium oxalate. The secretion itself is a yellow granular fluid which hardens on exposure to air and forms the cocoon. This cocoon lodges as a rule sixteen eggs disposed in two rows, an egg on one side alternating with an egg on the other. The spermatheca opens in front of the colleterial duct. It consists of two short tortuous caeca with a short common duct. Spermatozoa are said by von Siebold to be found in both these caeca. The usual structure in *Insecta* of this apparatus is a bursa copulatrix with muscular walls and chitinous lining and an appended gland. In thus possessing two receptacula seminis instead of one, as also in having eight ovarian tubules instead of twelve, as is usually the case in *Orthoptera*, the Cockroach presents more or less aberrant arrangements.

*Ovarial tubes.* Brandt, Mémoires de l'Acad. Imp. St. Pétersburg, (7), xxi. 1874. Id. Das Ei, Leipzig, 1878; Id. Z. A. viii. 1885. *Ovum of Nepa and Notonecta*, Will, Z. W. Z. xli. 1885; of *Colymbetes fuscus*, Id. ibid. xliii. 1886; *Of various Insecta*, Korschelt, Z. A. viii. 1885; Von Wielowiejski, Z. A. ix. 1886. *Microphyle and chorion*, Korschelt, Z. A. vii. 1884.

*Development of ovarian tubes in Insecta.* Jaworoski, Z. A. v. 1882. Cf. Balbiani, Recueil Zool. Suisse, ii. 1885; Schneider, Zool. Beiträge, i. 1885.

*Genital apertures in Insecta.* Palmén, Ueber paarige Ausführungsgänge der Geschlechtsorgane bei Insecten, Helsingfors and Leipzig, 1884; cf. Id. M. J. ix. 1883.

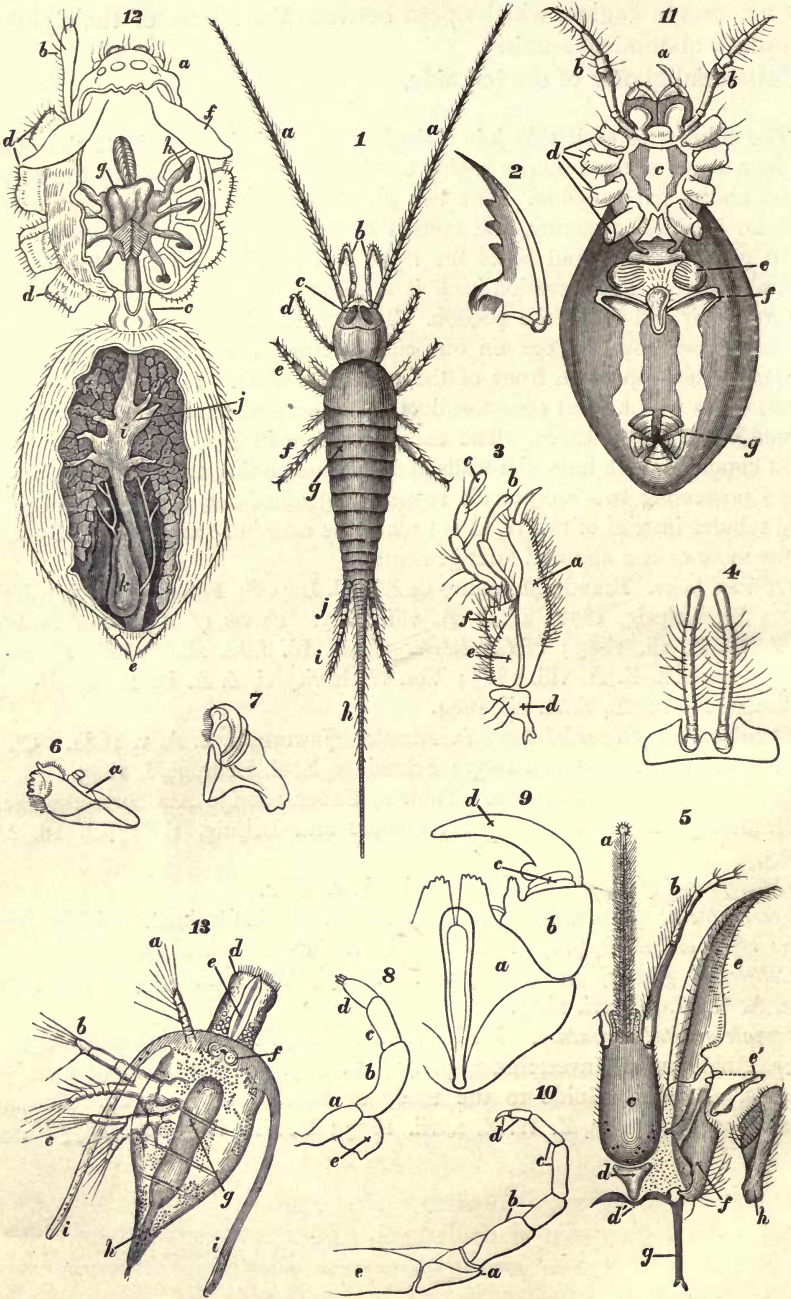
*Development of sex ducts.* Nusbaum, Z. A. v. 1882.

*Spermatheca.* Von Siebold, Müller's Archiv (Arch. für Anat. und Phys.) 1837, p. 393; of *P. orientalis*, p. 408. Leydig, Nova Acta, xxxiii. 1867.

*Colleterial glands, and egg-capsule.* Kadyi, Z. A. ii. 1879. *Egg-Capsule*. Hallez, A. N. H. (5), xvi. 1885.

*Female genital armature.* De Lacaze-Duthiers, A. Sc. N. (3), xvii. 1852. Cf. Huxley, Anatomy of Invertebrata, p. 405, p. 433. *Development of these parts in Insecta.* Packard, Guide to the study of Insects, 1872, p. 15. *In various Hymenoptera*, Kraepelin, Z. W. Z. xxvii. 1873; Dewitz, ibid. xxv. 1875; xxxviii. 1877.

PLATE IX.



ARTHROPODA.



## PLATE IX.

This plate represents points of interest in the anatomy of various groups of Arthropoda.

FIG. 1. *Machilis polypada*, from Sir J. Lubbock, Monograph of the *Collembola* and *Thysanura*, Ray Society, 1873, Pl. LIII. and p. 236.

THIS Insect belongs to the order *Thysanura*, family *Lepismidae*. The many jointed filaments borne by the last abdominal somite in this order are three in number, except in the genus *Campodea*, where they are two, and in *Iapyx*, in which they are represented by a pair of short stout unjointed forceps. In *Lepisma* the three filaments are equal in size; in *Lepismina* and *Nicoletia* the central filament is slightly longer, a difference much exaggerated in *Machilis*. In the family *Lepismidae* the maxillary palpi are long, and the body is clothed with scales.

*Machilis polypada* has only been found in Great Britain: it inhabits woods and dry places, is about half an inch long, and is brown in colour, with a metallic lustre.

- a. Antennae composed of many setose joints, tapering to their extremities and longer than the body. The terminal joints are united in groups of seven.
  - b. Maxillary palpi composed of six joints. The three terminal joints are recurved.
  - c. Eyes. Simple according to Packard, large and black; contiguous in this genus, but small and widely separate in *Lepisma*.
- The above described parts are borne upon the head, which is distinctly marked off from the thorax. The latter consists of three limb-bearing somites as in all Insecta, but it is not distinctly marked off by any constriction from the abdomen which has ten somites.
- d. Anterior or prothoracic legs. The prothorax is large and arched.
  - e. Meso-thoracic, or middle pair, and
  - f. Meta-thoracic, or posterior pair, of limbs.

These limbs in *Machilis* bear on their basal joints a short cylindrical appendage covered with stiff hairs and closely resembling the cylindrical appendages of the abdomen. The processes in question may be seen projecting in front of the corresponding limbs.

In *Scolopendrella*, a Myriapod (? Insect) classified by Packard with the *Thysanura*, there is a similar appendage internal to the bases of each of its twenty-two limbs. It may be noted also that *Scolopendrella* agrees with *Campodea* among *Thysanura*, and with the *Collembola* in having both mandibles and maxillae sunk in the head.

- g. The first of the ten somites composing the abdomen. The ventral surface of each, except the first, bears a pair of setose cylindrical appendages. The last pair is large. They are moved by the animal as it runs.

In *Lepisma saccharina* these appendages are present only on the last two somites, and are represented on the anterior somites by groups of stiff hairs. In *Camptodea* and *Iapyx* they are absent on the eighth and ninth somites. They appear to represent abdominal legs. Such legs are present in many embryonic Insects, and in larval *Lepidoptera*, *Tenthredinidae*, and *Panorpatae* are developed into prolegs on more or fewer of the abdominal somites. It may be noted that in *Machilis* the female possesses, in addition apparently to the abdominal limbs, two appendages, on the eighth and ninth somites, which form an ovipositor. As there is no reason to doubt the homology of these processes with the parts of the ovipositor similarly found in many other female Insecta, their homology with limbs appears doubtful, and in need of further elucidation.

h. Median and

- i. Lateral caudal filaments belonging to the tenth somite. The lateral filaments are perhaps homologous with the abdominal limbs present on the foregoing somites.
- j. Last and elongated pair of abdominal limbs.

*Anatomy of a Collembolan.* Sommer, *Macrotoma plumbea*, Z. W. Z. xli. 1885.

FIGS. 2-4. Mouth-parts of a Tiger-beetle, *Cicindela littoralis*. From Stein's figures in Carus, *Icones Zootomicae*, I, Leipzig, 1857, Pl. XIV. Figs. 12-14.

Fig. 2. The mandible, which consists, as in all Insecta, of a single piece. In this carnivorous biting animal, it is curved, pointed, and its inner edge is produced into four sharp teeth.

Fig. 3. The maxilla composed of six parts.

- a. The lacinia with a terminal hook which is moveably articulated, and distinguishes, among other points, the small family *Cicindelidae* or Tiger Beetles from the large family *Carabidae* or Ground Beetles.
- b. Palpiform two-jointed galea, which is distinctive of the tribe *Adephaga*, comprising the families *Cicindelidae*, *Carabidae*, *Dyticidae*, and *Gyrinidae* among the *Coleoptera Pentamera*.
- c. The four-jointed maxillary palp, articulated to
- f. The palpiger. This in its turn rests upon
- e. The stipes and
- d. The cardo, which articulates with the skull.

Fig. 4. The labium. It is much simplified as compared with the labium in *Periplaneta*. It consists of a transverse basal piece with two notches in the anterior border separated by a pointed process, and represents, according to Professor Westwood, the mentum. Two four-jointed

labial palpi are inserted in the notches. They are described by the authority quoted as three-jointed, with a moveable base. It is difficult to homologise with certainty the parts of so modified an organ. It is possible that this mentum may represent more than the part so termed in *Periplaneta*.

*Cicindelidae*. See Westwood, Introduction to Modern Classification of Insects, vol. i. p. 47, 1839.

FIG. 5. The mouth-parts of the Honey-bee, *Apis mellifica*, worker. Drawn from a specimen as seen from the aboral surface and removed from the head.

*a-d'. Parts of the labium.*

*a.* The lingua or tongue : a long, narrow organ covered with setae, which are arranged in transverse rows, and increase in length from the base to the apex of the tongue. In every fifth row there are touch (?) papillae mingled with the setae. The tongue ends with a concave disc, the aboral surface of which carries branched hairs. The whole aboral surface of the organ is traversed by a longitudinal groove. The sides of the groove are thin, but its floor is thickened, forming a grooved rod, which extends as far as the terminal disc. The groove and rod appear to be of functional importance in the act of gathering honey.

*b.* The four-jointed labial palp. The basal joint is long and grooved internally. The groove assists with the lingua to make a channel along which the honey flows. Between the bases of the palpi and lingua lie the paraglossae.

*c.* Mentum. The duct of the salivary gland opens on its inner surface at the root of the tongue and beneath a small valve.

*d.* Submentum.

*d'.* Lora of Kirby and Spence (Introduction to Entomology, vol. iii. 1826, p. 367), commonly found in *Hymenoptera*. It supports the submentum centrally, and at each extremity it is connected to the cardo of the maxilla. It pushes forwards the sub-mentum, mentum, &c., when the mouth-parts are protruded for the purpose of suction.

*e-g. Parts of maxilla.*

*e.* The lacinia, *e'* the palp.

*f.* The stipes and

*g.* The cardo of the maxilla.

The palp is generally stated to be one-jointed. It appears to be really imperfectly two-jointed. In some *Apidae* it has as many as six joints.

*h.* The Mandible. Its inner surface is concave, and bears two oblique ridges on which hairs are implanted.

When the mouth-parts are at rest the tongue is partially retracted, and together with the labral palpi and laciniae of the maxillae are recurved within the mouth. The sub-mentum, lora, and cardines of the maxilla are folded upon one another at the same time and hidden by the large mentum.

Briant, J. L. S. xvii. 1884.

Cook, Amer. Naturalist, xiv. 1880.

FIGS. 6-9. Appendages connected with the mouth, and Fig. 10, the first pair of ambulatory limbs of *Scolopendra morsitans*, after Savigny, Mémoires sur les Animaux sans vertèbres, Part I, Paris, 1816. Slightly altered from a specimen.

6. Mandible : *a.* small three-jointed palp.
7. Maxilla, consisting of a small soft external 'palp' and a median lobe which, as in *Myriapoda Diplopoda*, e. g. *Iulus*, is fused basally with its fellow.
8. Palp-like limb. In *Scolopendra audax*, according to Pagenstecher (Allgemeine Zoologie, ii. 1877, p. 131), it consists, like an ordinary walking limb, of seven joints. *a.* Basal joint fused to its fellow, *b* and *c.* two median joints. *d.* Claw terminated by two to three spines ; *e.* the sternum (?) displaced laterally.
9. Poison claw. *a.* Appears to represent the enlarged basal joint fused to its fellow medianly; its anterior edge is produced into a process bearing several stout spines. *b.* Joint prolonged internally into a spine-bearing process. *c.* Two folds in the soft membrane connecting *b* with *d* on the inner edge. They do not appear to represent joints as they have been supposed to do. *d.* Large claw with the opening of the poison duct at its apex. It is hinged at its outer side upon *b.*
10. First pair of limbs, with seven joints. *a, b, c, d.* The seven joints. It was supposed by Professor Rolleston that the double joints *b, c, d* are formed by division of the joints similarly lettered in Fig. 8. The terminal joint is generally regarded as a claw. It appears better not to use for these joints the designations coxa, trochanter, femur, tibia, and tarsus. They are all similar in aspect, not distinctly differentiated in shape as are the parts so termed in Insecta. *e.* The sternum. There is no tergum to this somite unless it is united with the tergum of the preceding somite.

The appendages, Figs. 8-10, are generally regarded as belonging to what is called the 'basilar somite.' But the appendage, Fig. 8, is distinctly connected with the head, and represents the labium of Insecta. In no Chilopod that I have examined is a tergum present corresponding to the limb, Fig. 10, and in some species this limb is absent. Balfour (Comp. Embryology, i. p. 325) is inclined to doubt the correctness of Newport's statement to the effect that the

basilar somite is composed of four embryonic somites to which the appendages Figs. 8-10 belong, one of the somites being limbless. He believes that the basilar somite corresponds to the poison claws, Fig. 9, alone, and that there is no somite without a limb. At any rate there is none in *Geophilus*, according to Metschnikoff.

Cf. Meinert, *Caput Scolopendrae*, Copenhagen, 1883; cf. Journal R. Micr. Soc. 1884, p. 374, and Amer. Naturalist, xviii. 1884.

*Poison glands.* MacLeod, Bull. Ac. Roy. Belg. (2) xlv. 1878.

FIG. 11. Geometrical Spider, *Epeira fasciata*, viewed from below. Règne Animale, Les Arachnides, by Dugès and Milne Edwards, Pl. XI. Fig. 1b.

a. The chelicerae or falces. These limbs are post-oral in the embryo but prae-oral in the adult. They consist of a large basal and a slender claw-like terminal joint, at the top of which opens the duct of the poison gland, seen at *f*, in Fig. 12. This joint moves horizontally in all Spiders with the exception of the *Tetra-pneumones* (*Mygale* and the Trap-door Spiders).

b. Pedipalpi, consisting of a limb-like terminal portion and an enlarged basal or masticatory joint. Between the two basal joints is the lower lip or labium of authors. It has nothing to do with the parts so termed either in Insecta or *Scorpio*, but represents the prosternite (cf. Ray Lankester, Q. J. M. xxi. 1881. p. 531, and Fig. 9, B.). The specimen from which this figure was taken was that of a female. In the male the terminal joint of the limb-like portion or 'palp' of this appendage is modified to receive the sperm and act as a copulatory organ.

c. Mesosternite, surrounded by

d. The basal joints of the four ambulatory limbs.

The part of the body bearing the above-described limbs constitutes the cephalo-thorax. It is followed by the soft unsegmented abdomen which, in the embryo Spider, consists of nine somites and a terminal azygos piece.

e. The stigmata leading to the two pulmonary sacs.

f. Those leading to the tracheae. Between them is the epigynal organ covering the sexual aperture.

g. The four spinning mammillae with the anal valve as a fifth lobe behind. Most Spiders, with the exception of the *Tetra-pneumones*, have six mammillae. The *Tetra-pneumones*, as a rule, possess only four.

*Auditory and olfactory organs.* Dahl, A. M. A. xxiv. 1885; cf. A. N. H. (5) xiv. 1884. *On an organ of sense.* Bertkau, A. M. A. xxiv. 1885, and Id. and Schimkewitsch, Z. A. viii. 1885.

*Respiratory organs,* MacLeod, Archives de Biologie, v. 1885.

FIG. 12. The digestive apparatus of *Tegenaria domestica*, the common House Spider, after Plateau, Bull. Acad. Roy. Belg. xliv, Pl. I, Fig. 2.

- a. The anterior part of the cephalo-thorax, carrying the eight uni-corneal or mono-meniscous eyes arranged in two transverse rows.
- b. Second joint of the right pedipalp.
- c. Peduncle connecting the cephalo-thorax with the abdomen.
- d. The basal joints of the four pairs of ambulatory limbs.
- e. Two of the six spinning mammillae.
- f. The poison glands. Their ducts open on the terminal joint of the chelicerae (a, Fig. 11).
- g. The anterior caecum of the cephalo-thoracic stomachal dilatation used in sucking up the juices of the prey. In front of it are the muscles of the pharynx; behind it, the dilatator muscles of the stomach; and at the sides it gives off,
- h. The caeca, eight in number, which enter the bases of the limbs and are recurved in the coxal joint.
- i. The chylific or abdominal stomach receiving
- j. The numerous ducts of the so-called liver or hepato-pancreas which secretes a digestive fluid. These ducts are numerous in Arachnida, and the glands large.
- k. Caecum, opening on the dorsal side of the proctodaeum or rectum at the point where the ramified Malpighian tubules, shown as white lines in the figure, enter it.

*Fore-gut and digestive organs in Arachnida.* MacLeod, Bull. Acad. Roy. Belg. (3), viii. 1884.

*Structure and function of Liver.* Bertkau, A. M. A. xxiii. 1884; xxiv. 1885. Cf. Dahl, Z. A. viii. 1885.

*Anatomy of Epeira.* Schimkewitsch, A. Sc. N. (6) xvii. 1884. *Development.* Id. Z. A. vii. 1884.

FIG. 12. *Nauplius* of *Lepas fascicularis*. Von Willemoes-Suhm, Ph. Tr., 1876, Pl. X, Fig. 11.

This *Nauplius* was taken in the Pacific Ocean during the passage of H. M. S. Challenger from Japan to the Sandwich Islands. It is but just hatched from the egg, and is still enveloped in a larval skin, destined to be shed in a few hours. In size it measures about  $\frac{1}{75}$  of an inch. In subsequent stages of the *Nauplius* form it grows immensely in size and acquires long dorsal, caudal, and ventral spines. It was originally described by Dohrn as *Archizoaea gigas*.

- a. The first uniramosse appendage. It represents the first antenna, and in the *Cypris*-stage of the Barnacle becomes four-jointed. The second joint bears a suctorial disc, in the centre of which opens the duct of the cement gland. By means of this apparatus, the *Cypris*-like

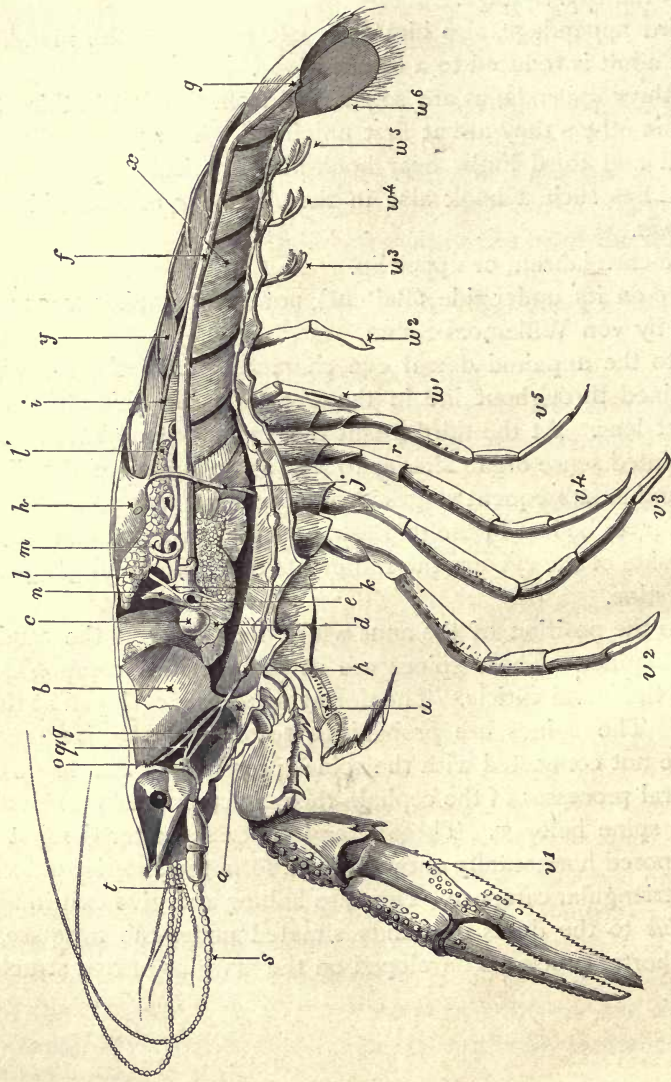
animal attaches itself to some foreign body. The terminal joint bears olfactory hairs, and, together with the third joint, is discarded in the pupa-stage.

- b. The second appendage, a biramose swimming foot. It represents the second antenna of other Crustacea, but in the *Cirripedia* is completely lost in the *Cypris*-stage.
- c. The third appendage, also biramose. It represents the mandible, but in the adult is reduced to a toothed lobe.

These three appendages are segmented from the first in this Cirriped. In some others they are at first unjointed. The protopodites of the second and third limbs bear hook-like masticatory processes. The second has such a hook also in the *Nauplius* of *Branchiopoda* and *Copepoda*.

- d. The immense labrum or upper lip.
- e. A groove on its under side (Balfour), not the oesophagus, as was supposed by von Willemoes-Suhm.
- f. Points to the unpaired dorsal eye characteristic of the *Nauplius*. It is retained throughout life in the *Copepoda*. In this stage it has a distinct lens. At the third moult there appears on either side of it a two-jointed sense organ similar to the sense organ of the *Branchiopoda*, and in subsequent stages a compound eye also appears on either side of it, to be lost in the pupa-stage. The two granular patches on either side of the eye are the rudiments of the cerebral ganglion.
- g. The intestine.
- h. Points to the position of the anus which lies between the caudal and ventral spines. These spines are at present in a compressed state within the larval cuticle. The dorsal spine is developed at the third moult. The spines are probably a secondary adaptive protection, and are not connected with the spines present in a *Zoea*.
- i. The lateral processes of the cephalo-thoracic carapace to which also the caudal spine belongs. These lateral processes, after the first moult, are disposed horizontally outwards, and form the anterior outer angles of the triangular carapace. They are hollow and give exit in an older *Nauplius* to the ducts of glands situated under the carapace, as do other shorter processes developed on the margins of that structure.

PLATE X.



COMMON CRAYFISH, *Astacus fluviatilis*.



## PLATE X.

COMMON CRAYFISH (*Astacus fluviatilis*), MALE,

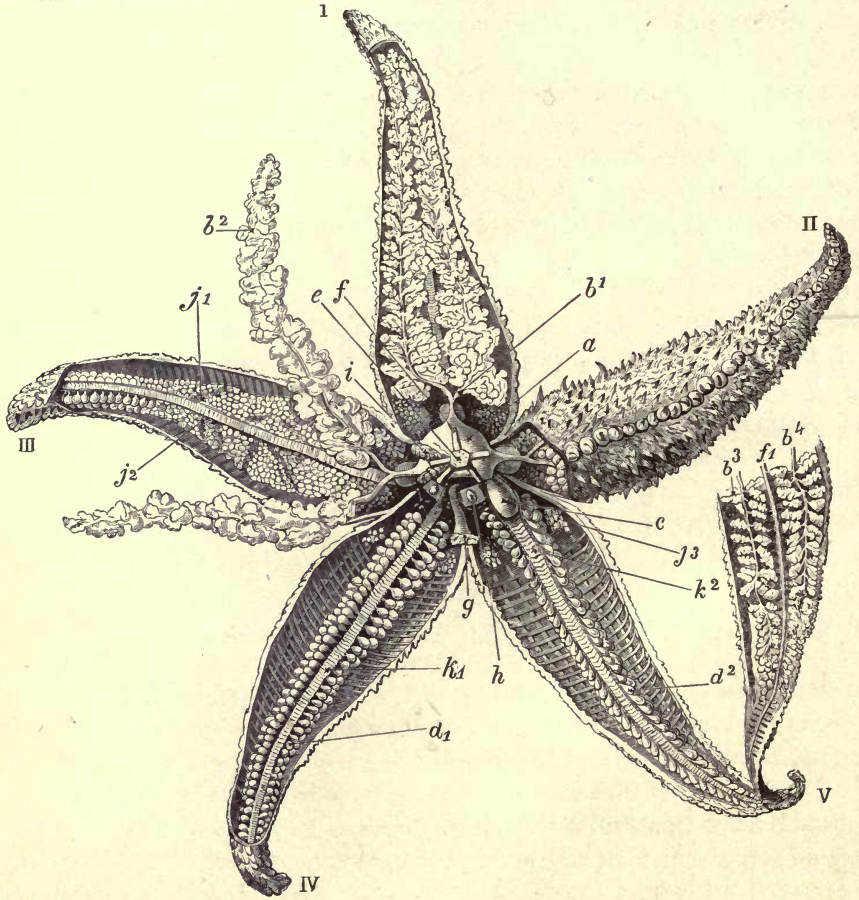
Dissected so as to show its nervous, digestive, circulatory, and reproductive systems *in situ*; the various organs having been exposed in a vertical section, by the removal of the tegumentary skeleton, the muscles, and the hepatic lobes of the left side. See Prep. 33, p. 177, *ante*.

- a. OESOPHAGUS leading vertically upwards from the mouth into the stomach. The labrum, the free edges of the mandibles, and of the two maxillae, are faintly indicated on the right side of the mouth anteriorly to the three foot-jaws.
- b. Cardiac portion of stomach. Superiorly and anteriorly the stomach is still retained in its natural position, the anterior gastric muscles, which took origin superiorly to the supra-oesophageal ganglia, *o*, from the under surface of the ventral wall of the hollow rostrum, and attached themselves to the cardiac plate, having been left intact; whilst the anterior wall of the stomach has been displaced a little backwards in order to give a better view of the stomato-gastric nerves.
- c. Lateral prominence of pyloric filter.
- d. Hepatic lobes of right side.
- e. Orifice by which the hepatic lobes of the left side opened into the digestive tract.
- f. Intestine passing with the straight course characteristic of Crustacea, with the exception of *Lynceus*, to the anus.
- g. Anus, opening on the inferior surface of the 'telson' in uncalcified membrane, anteriorly to the junction of its anterior and posterior halves.
- h. Heart, showing one of the lateral venous orifices, and the posterior aorta which divides into two main branches, *i* and *j*.
- i. Post-abdominal artery, taking a course superiorly to the intestine, and inferiorly to the extensor muscles of the posterior somites.
- j. Sternal artery passing down to the interval between the commissural cords connecting the third and the fourth abdominal ganglia.
- k. Hepatic artery of the left side, passing from the heart over the pylorus towards the left hepatic lobes which have been removed.
- l. Anterior left lobe of testis.
- l'. Azygos lobe of testis placed behind the paired lobes.
- m. Convolutions of vas deferens of left side, in length equal to that of the entire body. The agglutinating matter of the spermatophores is probably secreted in them.
- n. Coecal sac of mesenteron or archenteron.
- o. Supra-oesophageal ganglionic mass.

- p.* First post-oral ganglion, supplying the mandibles, the two pairs of maxillae, and the three pairs of foot-jaws, or thoracic appendages. In the developing *Astacus* this mass consists of six pairs of ganglia, in correspondence with the six sets of appendages it innervates. In Insects, the first post-oral ganglion is always distinct from the thoracic ganglia, whilst in other Arthropoda it is generally fused with more or fewer of them.
- q.* Median stomatogastric nerve formed by the fusion of four nerves, two from each oesophageal ganglion, to *q'*.
- q'*. Azygos nerve, passing downwards from the middle of the posterior edge of the supra-oesophageal mass to meet four nerves given off, two from each of the two oesophageal ganglia, developed upon the commissural cords of the nerve-collar. It forms with them the nerve, *q*. The nerve from the anterior edge of the supra-oesophageal ganglion is not shown. Cf. p. 189, *ante*.
- r.* Fifth thoracic, or sixth post-oral ganglion. Posteriorly to it are the six abdominal ganglia. From this ganglion and the two in front of it, long nerves pass off upwards to the reproductive organs and the superiorly placed muscles.
- s.* Multi-articulate flagellum or endopodite of second pair of antennae.
- t.* Exo- and endopodite of first pair of antennae or antennules.
- u.* Second joint of third thoracic appendage, 'maxilliped,' or 'foot-jaw.' This joint, as in the forceps *v* 1, next behind it, represents two joints, the basipodite and the ischiopodite of the normal seven-jointed endopodite, seen in *v* 2, *v* 3, *v* 4, *v* 5. Its antero-internal edge is denticulate, as in the Lobster, but its serratures are concealed by a fringe of setae.
- v* 1. Fourth thoracic appendage, or forceps, modified by the production of the distal outer angle of the propodite so as to form a pair of pincers with the opposed last joint, or dactylopodite. Two other joints, the 'carpopodite' and 'meropodite,' are shown in this figure.
- v* 2 and *v* 3. Fifth and sixth pairs of thoracic or first and second ambulatory legs, differing from *v* 1 in their smaller size, and in not having the second and third joints fused.
- v* 4 and *v* 5. Seventh and eighth pairs of thoracic or third and fourth ambulatory legs of the Decapod. The two terminal joints do not form pincers, otherwise they resemble *v* 2 and *v* 3. The vas deferens opens in the coxopodite or basal joint of *v* 5.
- w* 1 and *w* 2. The appendages of the two first abdominal somites modified so as to form an accessory copulatory organ in this a male specimen.
- w* 3, *w* 4, and *w* 5. Appendages of the third, fourth, and fifth abdominal somites, consisting each of two basal joints, which serve as a pedicle to two multiarticulate filaments, an exopodite and an endopodite.

- w* 6. Appendage of sixth abdominal somite, forming the right lateral element of the caudal fin. The telson is interposed mesially between the two appendages of the sixth abdominal somite.
- x*. Flexor muscles acting on the swimmeret and abdominal somites in the animal's rapid movements; its slower movements being dependent upon the ambulatory feet.
- y*. Extensor muscles, in two layers like the flexors, but of much smaller size.

PLATE XI.



COMMON STAR-FISH, *Asterias rubens*, LINN.

## PLATE XI.

COMMON STARFISH (*Asterias rubens*), LINN.,

Dissected so as to show its motor, digestive, and reproductive systems.

THE dorsal integument has been removed from the central ray of the trivium, I; from its left ray, II; and from both rays of the bivium, a part of it being left attached to the right ray, V, of the bivium at its apex, to show the attachment of the radial digestive coeca. The digestive and other viscera have been removed in great part from the interior of the two rays of the bivium and the ampullae *d* 2, and the ambulacral ossicles *k* 2 exposed *in situ*. The coeca attached to the pyloric portion of the stomach have been displaced from their attachments in the left ray of the trivium; they have been left undisturbed in the central ray; and in the right ray all the organs, with the exception of a small part of the dorsal integument next to the central disc, have been left undisturbed.

I. Central radius of trivium; a line drawn along the axis of this ray to the madreporic tubercle *g*; would, in the undisturbed condition of the parts, have the anus a little on its left; and if prolonged, would pass down the interradial space of the bivium (IV and V).

II. Right radius of trivium, with the greater part of the integument left *in situ*. The inward prolongation or angle of the integument is well seen in the interradial space between arm I and arm II. The dorsal integument contains a large number of ossicula, some of which carry small conical prickly spines, whilst others simply connect the spinigerous ossicles into a reticulation. Down the centre of each ray the spinigerous tubercles are in this species arranged with considerable regularity, so as to form a mesial series; in the other portions of the dorsal area, they are scattered irregularly. The intervals between the dorsal ossicula bear respiratory coecal processes of the integument.

III. Left radius of trivium. The two coeca of the pyloric division of the stomach have been displaced from their normal connections within the cavity of the ray, and are displayed in the interradial space on either side. In the middle line are seen the ambulacral ossicles, and on either side the generative glands, *j* 1, *j* 2.

IV and V. Left and right rays of bivium. The greater part of the reproductive organs and the whole of the digestive have been removed; and the ambulacral ampullae, *d* 1, *d* 2, corresponding to the rows of

sucker-like feet arranged on either side of the ventrally placed ambulacral furrows, are seen in two rows on either side of the middle line occupied by the mesial articulations of the successive pairs of 'vertebral' or 'ambulacral' ossicles, *k* 1, *k* 2.

If the results of Ludwig's researches on the development of *Asterina gibbosa* are applicable to all Asteroidea, a Starfish ought to be placed as follows to make it coincide with the position of the parts relative to the antero-posterior axis of the larva. The madreporite *g* must be placed to the left; and the anus *e* (figured too near the centre of the disc), with the interradius between III and IV, to which it belongs, must be anterior. This interradius coincides on the ventral surface of the adult with the position of the anterior appendage of the larva. Five processes develop on the right side of the larva, i. e. the dorsal or abactinal surface in the adult, and are arranged in a circle, open anteriorly. To form the arms they fuse with five similarly arranged processes of the left side, i. e. the ventral or actinal surface here. Both sets of processes may be numbered from 1-5, commencing with the anterior ventral process of the larva, and ending with the anterior dorsal, passing round the posterior extremity. In the fusion of the two sets of processes, abactinal and actinal, a curious twist of the one set upon the other takes place. The actinal process 1 coincides with III in the Plate, 3, which marks the posterior extremity of the larva, with II, and 5 with IV. The abactinal processes, which correspond at their first appearance with the actinal, shift so that 2 coincides with III, 4 with II, and 1 with IV. Consequently a line drawn through the anal interradius down arm II marks a line in the adult which coincides with the antero-posterior axis of the larva. The original antero-posterior axis of the abactinal surface passes, however, through the madreporite and arm I; for while this axis retains its position with reference to the larval antero-posterior axis on the actinal surface, it is shifted to the left on the abactinal. It may be noted that the larval anus or gastrula mouth lies between the actinal and abactinal processes 3, but closes before the twist takes place. The larval mouth lies similarly between the two processes 1, but closes, and a new mouth is formed in connection with a new oesophagus which grows out towards the left side of the larva.

It would be interesting to know whether the twist occurs in other Asteroidea, and in Ophiuroidea as well. See Ludwig, Z. W. Z. xxxvii. 1882.

- a*. Pyloric division of stomach, communicating freely with the cardiac, and giving off a stem which bifurcates as it enters each ray.
- b* 1. One of the arborescent divisions into which the radial diverticulum of radius I divides. It is only in the Asteroidea that the digestive tract has this radial arrangement of coeca.
- b* 2. Arborescent coecum of radius III, displaced, as is its fellow, into the interradiial spaces.
- b* 3 and *b* 4. Terminations of coeca of radius V attached to the dorsal integumentary skeleton by a mesentery.
- c*. Cardiac division of stomach, bulging, but only for a short distance, into the cavity of the several rays at a lower level than the coeca, *b*. To

the right of *c* is seen one of the interradial septa to which the ducts of the generative coeca on either side are attached.

*d* 1. Ampullae of ambulacral feet of radius IV.

*d* 2. Ampullae of radius V.

*e*. Subcentrally placed anus.

*f*. Origin of extensor muscle of radius I from inner surface of centre of dorsal integument. It is by the action of this muscle that the distal extremity of the rays and the eyes they carry, have their ordinary up-turned direction, as shown in this figure, given to them.

*f* 1. Distal termination of extensor muscle of radius V.

*g*. Madreporic canal and plate displaced backwards into the interradial space of the bivium, opposite to which it is placed in the natural position of the parts.

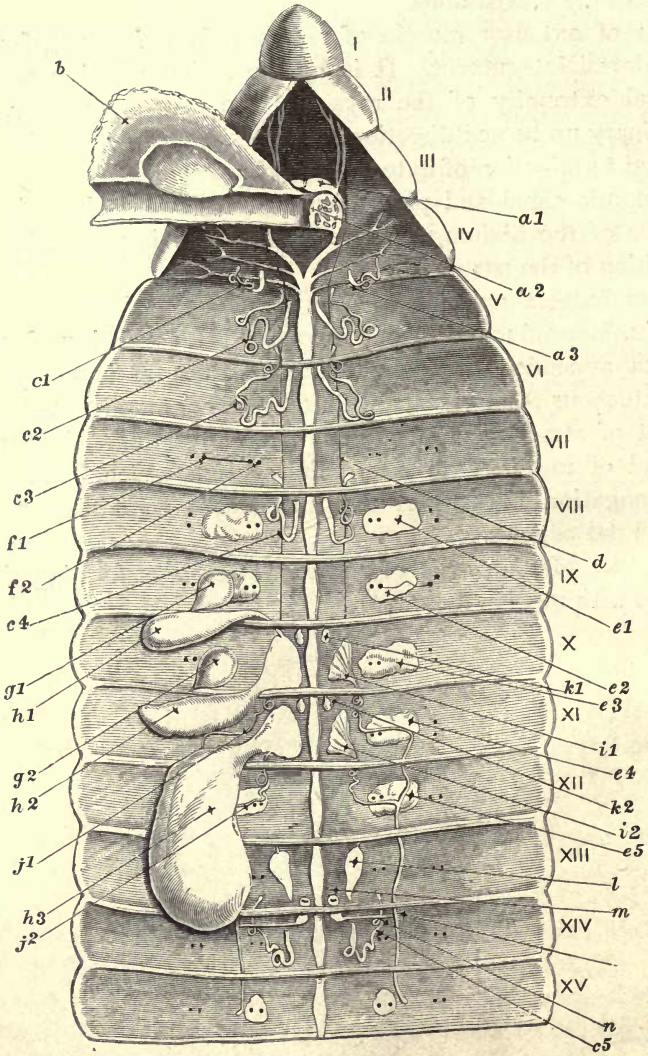
*h*. First ambulacral ampulla.

*j* 1 and *j* 2. Reproductive glands of radius III, consisting of multiramified coeca appended to a single efferent duct, as in many but not all proctuchous Asteroidea, and in *Ctenodiscus* amongst the aprocious.

*j* 3. Point of attachment of efferent generative duct of right generative gland of radius V to interradial septum, which is formed by the prolongation inwards of the integument containing a number of small flat ossicles.

*k* 1 and *k* 2. Median ends of ambulacral ossicles forming the *vertebral* ridge with median furrow.

PLATE XII.



EARTHWORM, *Lumbricus terrestris*.



## PLATE XII.

EARTHWORM (*Lumbricus terrestris*).

The fifteen anterior somites, numbered from before backwards, the 'prostomial segment' counting as the first.

THE integument has been divided, except in the prostomium, down the middle dorsal line, and the greater part of the digestive tract has been removed, together with the pseud-haemal vessels, so as to show the nervous, nephridial, and reproductive organs.

- a 1. Bilobed supra-oesophageal ganglionic mass ; giving off from either outer angle a nerve which bifurcates very soon after its origin, and distributes itself in the prostomium.
- a 2. Visceral or stomatogastric plexus of the right side. See p. 211, *ante*. Described by Quatrefages, A. Sc. N. (3) viii. 1847, p. 36.
- a 3. Commencement of ventral nerve-cord.
- b. Pharynx, turned aside to the left, the right half of the organ, except the small portion upon which the right stomatogastric plexus, a 2, is seen, having been removed.
- c 1. First nephridium, or 'segmental organ,' opening externally in somite iv. Ordinarily the thickened muscular portion of the tube opens externally in the somite immediately posterior to that in which its internal funnel-shaped opening is situated. But as somite iv is not cut off from somite iii by a perfect dissepiment such as limits the somites after somite v *inter se*, the anterior funnel-shaped termination is not in a different somite from the one in which the coils of the gland are lodged.
- c 2. Nephridium similarly modified to c 1.
- c 3, c 4, c 5. Normal nephridia. The opening on to the exterior is usually close to the inner row of setae, though it may vary considerably, and even come to lie exteriorly and superiorly to the outer row of locomotor spines. The funnel-shaped internal opening is seen a short way from the outer edge of the nerve-cord, and near the ventral surface in the somite anterior to that in which the gland communicates with the exterior. In these organs the coils of the posterior part, which is much the larger, are connected by a mesentery-like lamina to each other and to the dissepiments of the somites.
- d. Muscle passing up from one of the ventral muscles to attach itself to the capsule of the supra-oesophageal ganglion to which it stands in the relation of a powerful retractor.

- e 1, e 2, e 3, e 4, e 5.* 'Capsulogenous glands' of D'Udekem. These bodies are stated to be specially modified and greatly developed setiparous glands, which attain this prominence in the somites connected with the essential, and with the accessory organs of generation; amongst the latter of which the long inner setae of many somites may be reckoned, besides those here lettered *e 1* to *e 5*. At *e 2* we see a slip of muscle passing across the glandular mass, and connecting the inner with the outer row of setae.
- f 1.* Outer row of setae. Each seta is formed by a separate sac, and has a separate insertion. The setae of the aquatic *Oligochaeta* are, on the contrary, 'fasciculate' in their insertion. In the clitellum the outer row of setae may be enlarged to serve as copulatory organs.
- f 2.* Inner row of setae. The spines are solitary in their insertion as in the outer row, but they are enlarged so as to serve as organs of adhesion in many somites, as, for example, in the tenth and fifteenth, as well as in the somites constituting the clitellum.
- g 1.* Anterior receptaculum seminis of the left side, opening in the interval between the ninth and tenth somites, in the line of the outer row of setae.
- g 2.* Posterior receptaculum seminis, opening in the interval between the tenth and eleventh somites. These organs are very variable in size, according as they are full or empty.
- h 1.* Anterior vesicula seminalis of the left side. See p. 206, *ante*.
- h 2.* Middle vesicula seminalis of left side.
- h 3.* Posterior and largest vesicula seminalis.
- i 1.* Internal funnel-shaped orifice of vas deferens anterior of right side.
- i 2.* Similar orifice of vas deferens posterior of right side. Nephridia are present in these somites, and are disposed in the ordinary manner. Diagrammatic: see pp. 206-8, *ante*, and Q. J. M. xx. p. 80-82, with woodcut, p. 79.
- j 1.* Vas deferens from anterior spermatic infundibulum of left side.
- j 2.* Vas deferens from posterior spermatic infundibulum of left side. The junction of the two vasa deferentia to form one common canal is well seen in the twelfth somite on the right side, and the ending of the common canal there formed is well shown on both sides in the fifteenth somite. The external opening of the common vas deferens has the shape of an oval slit, with its long axis transverse to that of the animal's body, guarded at the breeding season by prominent tumid lips.
- k 1.* Anterior testis of right side.
- k 2.* Posterior testis of right side.
- l.* The single ovary of the right side, occupying the same position relatively to the nerve-cord and the inner row of setae as the testes.

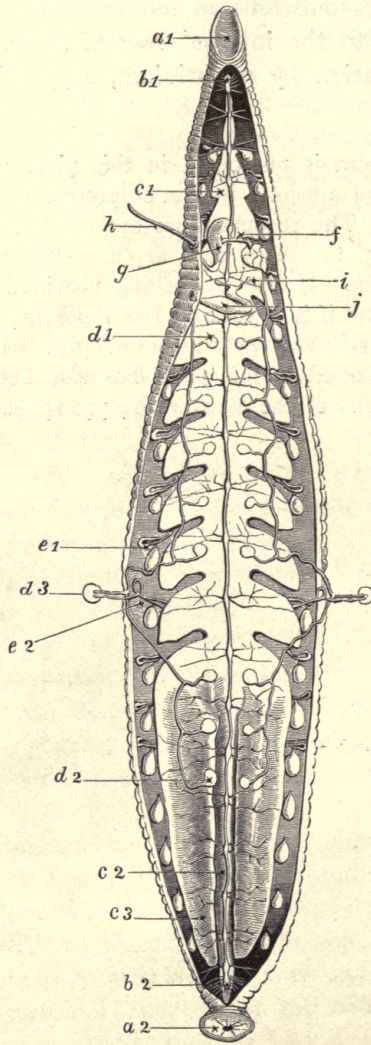
m. Infundibular ciliated mouth of oviduct.

n. Oviduct in the posterior of the two somites to which it is related.

As it passes through the dissepiment separating the thirteenth from the fourteenth somite, the oviduct has a saccular dilatation—a receptaculum ovarum—ordinarily found to contain ova, appended to it. It then passes outwards in relation with the dissepiment, and opens externally to the internal row of setae. It is crossed just before its termination by nephridium, c 5, which is related to the same somites.

*Note.*—The prostomium is numbered in this plate as the first somite. It appears, however, to be not a somite but an outgrowth of the somite numbered ii here. See p. 197, *ante*. The receptaculum ovarum is said, in Bergh's account, Z. A. ix. 1886, pp. 232-3, to belong to a septum—that which separates somite twelve from somite thirteen. It does so belong, provided the prostomium is not reckoned as a somite. But if it is reckoned as a somite, the septum in question is *that which separates somite thirteen from somite fourteen*. The usual mode of reckoning the somites followed in this plate has also been followed in the description of the preparations of the Earthworm, pp. 196-212, but it is probably wrong.

PLATE XIII.



MEDICINAL LEECH, *Hirudo medicinalis*.

## PLATE XIII.

FIGURE OF MEDICINAL LEECH (*Hirudo medicinalis*),

Dissected so as to show its nervous, digestive, reproductive, and segmental organs, as seen from below; slightly altered from Moquin Tandon's figure, Pl. VIII., Fig. 10, Monographie des Hirudinées, 1846.

THE integument is drawn as divided down the middle ventral line, from the posterior border of the buccal cavity or anterior sucker to the anterior border of the posterior sucker; two of the testes and two of the nephridia have been displaced outwards in the somite, lettered *d* 3, *e* 2; the rest of the organs have been left undisturbed *in situ*.

*a* 1. Anterior sucker.

*a* 2. Posterior sucker, formed by the fusion of seven distinct somites, to which as many ganglia, subsequently fused into the single posterior ganglion of the ventral chain, corresponded at one period of the animal's development. The anus is dorsal and anterior to the sucker.

*b* 1. Infra-oesophageal ganglion and first ganglion of ventral chain, very closely apposed to each other.

*b* 2. Last ganglion, the twenty-third of the ventral chain, composed of seven embryonic ganglia fused. This ganglion gives off from five to nine pairs of nerves, which are distributed to the posterior sucker. The penultimate ganglion gives off only one pair of nerves.

*c* 1. First lateral diverticulum of the portion of the digestive tract, which comes next after the pharynx.

*c* 2. 'Small intestine' of most authors, 'gastroiléal' portion of digestive tube of Gratiolet, in which the haemoglobin of the blood undergoes changes. It ends posteriorly in a short ovoidal colon, which again ends in a short rectum, turned slightly upwards to the anus. The small intestine is a little dilated at its commencement in the interval between the two terminal sacculi *c* 3. This dilatation is much larger and more distinctly bilobed in the Horse-leech (*Aulostoma Gulo*).

*c* 3. Eleventh lateral diverticulum of right side prolonged downwards on either side of the small intestine and colon, as far as the point where the rectum begins.

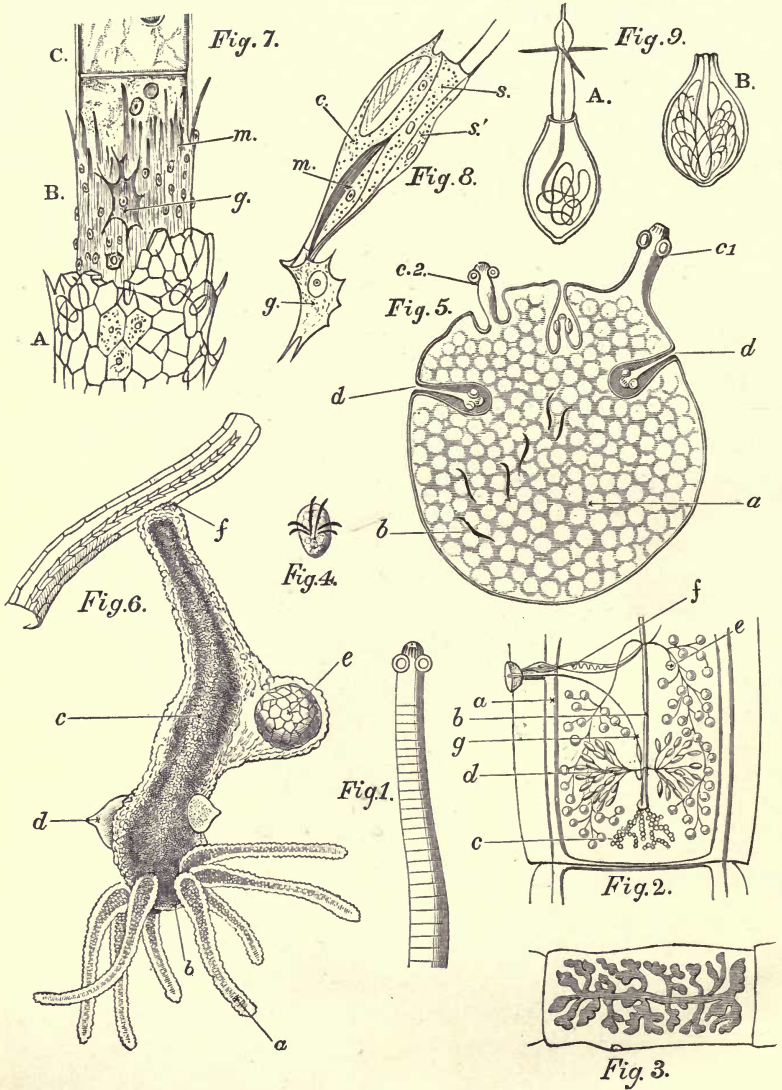
*d* 1. The most anteriorly placed of the nine testes of either side, communicating by a short transverse duct passing outwards, with a vas deferens common to it and the eight posterior testes, and anteriorly convoluted. These convolutions are seen in this figure in the space on the right side bounded by the lines lettered *i* and *f*.

- d* 2. Last or ninth testis of right side.
- d* 3. Sixth testis, displaced outwards so as to show its connection with the vas deferens.
- e* 1. Segmental organ or nephridium.
- e* 2. Segmental organ or nephridium. The testis is displaced outwards. In relation with it is a coecal process from the nephridium, the testis lobe, which is surrounded by the perinephrostomial sinus. The vesicle by which the nephridium opens externally lies just to the right of the line from the letter. See pp. 221-3, *ante*.
- f*. Ductus ejaculatorius of left side, leading from the convoluted portion of the vas deferens to the base of the prostatic body.
- g*. Prostatic body.
- h*. Muscular penis, surrounded where it passes out of the integument by a strong sphincter. This orifice lies in the second annulus of the eleventh somite (Whitman).
- i*. Ovarian sac of left side, carried upon one of the short oviducts. The ovarian sac of the other side is seen on the farther side of the nerve-cord, underneath which its oviduct passed.
- j*. Muscular vagina, in which after sexual congress the spermatophore is found. Between the vagina and the two oviducts, a common oviduct intervenes, which takes a tortuous course, and has its coils surrounded by a mass of loose tissue, composed of unicellular glands, which are probably the main agents in the secretion of the albumen which envelopes the eggs in the cocoon. The azygos character of the two generative outlets is especially noteworthy.

WILLIAMS

WILLIAMS ; GEORGE

PLATE XIV.



CESTODA: HYDROIDEA.



## PLATE XIV.

## CESTODA: HYDROIDEA.

THE figures 1 to 5 are intended to show diagrammatically the life-history of one of the typical *Cestoda*, genus *Taenia*. Figure 1 represents the sexual animal as it is found in the segmented form, called 'strobila' from the analogy of a fir-cone, in the intestinal canal of a carnivorous or omnivorous vertebrate 'host,' such as the dog, or human subject. Figure 2 represents the distal half of a segment, or 'proglottis,' as it may be seen before the great accumulation of ova in the uterus has caused the disappearance of the other sexual organs, male and female, which each segment contains. Figure 3 represents a ripe segment, so distended with embryos as to have caused the ripe proglottides, which retain considerable locomotor powers, to be called 'ovaria ambulancia.' Figure 4 shows one of the microscopic embryos, the so-called 'proscolex,' as it appears when set free from its shell within the stomach, into which it is introduced. Figure 5 shows the cystic stage or scolex into which such a proscolex as that shown in Figure 4 develops, when it belongs to *Taenia coenurus*, which differs from most other Tapeworms in having its proscolex proliferating as drawn in the figure, instead of producing a solitary 'new head' or 'scolex.' This cystic stage is passed in the tissue of some solid organ, such as the liver or the muscles; but in the particular case of *Taenia coenurus*, most usually in the brain of the sheep, though sometimes in other parts of the body of this ruminant, as also of rodents.

FIG. 1. Tapeworm, as found in the intestinal canal of man or of a dog, semi-diagrammatic; after Van Beneden, Mémoire sur les Vers Intestinaux, Paris, 1858, Pl. xxvi. Fig. 25.

THE 'head' or 'nurse' so-called is armed with a circlet of spines, as is the case with *Taeniae* which are harboured in the intestines of birds and of carnivorous mammals; whilst the *Taeniae* of Amphibians and herbivorous mammals are not possessed of this armature. Posteriorly to the circlet of spines is seen a circlet of four suckers. An unsegmented neck follows the suckers. The first segments are small, but as the distance from the head increases, so their size and development increase. A Tapeworm is not a colony composed of an asexual head and sexual proglottides or segments. The segmentation of the body is probably acquired, and not primitive as generally supposed.

FIG. 2. Posterior half of an unripe segment of *Taenia coenurus*, to show the generative organs, male and female; after Leuckart, Die Menschlichen Parasiten, ed. 2, p. 399, Fig. 165.

- a. Water-vascular or excretory canal. Two vessels, a dorsal and ventral, one of which is much larger than the other, and is not shown here, run along either side of each segment, parallel with and close to each other, and are connected with their fellows on the opposite side of each segment by a transverse anastomosis. This transverse connecting vessel takes in the last segment the shape of a median vesicle into which the lateral vessels converge, and through which they open to the exterior. In the larger *Taeniae*, e. g. *T. solium*, the dorsal longitudinal vessels are aborted.
- b. Uterus, in the unripe segment running as a straight tube from the posterior part of each segment to the anterior. In some *Taeniae* it is transverse. Where the genital pores are double (right and left), the uterus remains single, e. g. in *T. elliptica*.
- c. The albumen gland or vitellarium. In the small *Taeniae* the gland is saccular, in the larger tubular, and the tubes branched and anastomosing. They contain small nucleate cells which break down into a tenacious clear fluid. The gland is homologous with the bilaterally symmetrical yolk gland or vitellarium of other *Cestoda*. Its duct joins the 'fertilising' canal at the spot where the latter is surrounded by a mass of unicellular glands which make up the shell gland indicated in this figure by a slight expansion above the albumen gland.
- d. Germ-glands, one on either side, composed of tubes much branched in the larger *Taeniae*. They contain clear uninucleate ova or germs. The ducts unite in the middle line, and the common canal thus formed unites with the fertilising canal which connects the spermatheca to the uterus, before it is surrounded by the shell-gland.
- e. Testes appended in a racemose manner by very delicate ducts to the vasa deferentia. They occupy the 'dorsal' surface of the segment, whereas the female organs are confined to the 'ventral' surface, and were more abundant in the anterior half of the segment which is removed, than in this, the posterior.
- f. Intromittent organ, essentially a specialization of the muscular ductus ejaculatorius. It is armed with spines in some *Cestoda*, which favour its retention in the vagina of its own segment. It is here figured as retracted and coiled up spirally.
- g. Vagina dilating into an oval receptaculum seminis or spermatheca, before joining the duct of the two germ-glands. It opens externally in the posterior half of a saucer-like depression, the porus genitalis, on one side of a segment, in the anterior half of which the male outlet is situated. The generative outlets are similarly arranged in *Taenia elliptica*,

a Tapeworm commonly found in the dog and cat ; but the glandular organs being double, the outlets are double also, and exist on both lateral edges in each segment. In *Taenia mediocanellata* from the human species, the common generative depression is situated some way behind the middle of the lateral border of each segment ; in *Taenia solium* it is nearer to the middle line, whilst in *Bothriocephalus latus*, which, like the two Tapeworms named, infests the human subject, both sexual orifices are situated on the ventral aspect of the segment. The statement that the male orifice may occur in some cases on the edge, and the female on the surface of a segment appears to be erroneous.

A segment with the generative organs in the condition here figured, would be found in either *Taenia solium* or *Taenia mediocanellata*, the two common human Tapeworms, at about the 450th segment counting backwards from the head ; and the segments would assume the appearance given in Figures 3 and 4, after about 200 more segments in *Taenia solium*, and 360 to 400 in *Taenia mediocanellata*.

FIG. 3. Segment of *Taenia solium*, to show the dendritic outgrowths of the uterus, about twice the natural size ; after Leuckart, *l.c.*, p. 387, Fig. 156.

IN this segment the uterus and its contents have increased and encroached so much upon the rest of the generative organs, as to have caused their disappearance. In *Taenia solium*, its dendritic ramifications have a yellowish colour, and contain aggregations of embryos, such as the one figured at 4, enclosed in a hard resistant shell.

The uterus in the smaller *Taeniae* enlarges into a simple sac as the ova collect in it. In others again it acquires small lateral ampullae. The *Taeniae* possess no entrance to the uterus other than the vagina and fertilising canal. In some *Cestoda* the uterus possesses an aperture of its own. The ova acquire their shell within the uterus ; the germ segments, forms the proscolix (Fig. 4) and the shell of the embryo. As there is no uterine aperture the embryo shells with the proscolices are set free by the drying up and dehiscence of the proglottis, or rupture of the uterus, or by digestion of the soft tissues when the proglottis is swallowed entire by the host.

FIG. 4. Embryo or proscolix of an ordinary *Taenia*, armed, as it is normally in this genus and other *Cestoda*, with six spines ; after Van Beneden, *l.c.*, Pl. xxvi. Fig. 27.

SUCH an embryo as this is about three times the size of a human blood-corpuscle, 0.022–0.028 *Mm*, and when set free from the hard shell, which is not drawn in this figure, by the action of the digestive fluids of its host, it bores and pushes its way from the mucous surface of the stomach either into the blood-vessels, and so passes into the liver, a very common place for the development of the cystic stage, or into the connective tissues. The two spines of the central pair of the three are symmetrical, and, in

piercing the tissues, they have an antero-posterior movement. The two pairs of spines again on the right and left are symmetrical with each other. These two pairs move in piercing the tissues much as the fore-limbs do in swimming. The wound made is, on account of the small size of the embryo, invisible; and it has been incorrectly supposed that the embryos find their way into the liver by way of the bile-ducts. The six spines are recognisable up to a certain period, though dislocated from their position, in the more or less distended, cystic or cysticeroid vesicle, into which the proscotex may expand when it reaches its place of lodgment in the tissues. In *Cysticercus Arionis* the hooks are retained *in situ*, see Leuckart, op. cit. Fig. 209, p. 459. Figures of embryos and the history of their migrations are given in the works of Van Beneden and Leuckart referred to.

FIG. 5. Cystic stage in the development of Many-headed Bladder-worm, *Coenurus cerebralis*, after Van Beneden, *l. c.*, Pl. xxvi. Fig. 31.

THE hexacanth embryo, figured at 4, has grown greatly after coming to rest in the organ, ordinarily the brain of a sheep, to which it is carried by the blood-current. The six hooks are observed to be dislocated at *b*, and a number of 'scolices,' the heads of as many future Tapeworms, are developed upon one of the poles of the vesicle. The way in which these heads are formed in the *Taeniae* is detailed on p. 230. There are 300 to 400 heads in *Coenurus*. Each head at first points inwards towards the interior of the parent cyst; but by the contractions of the muscular layers of the cyst, as also by those of the intrinsic muscles of the head itself, it may point either outwards or inwards. For the changes that occur when the cystic animal is swallowed by the host, see p. 230 already quoted.

*a.* Wall of embryonic dilated cyst.

*b.* Hooks of embryo dislocated by its growth.

*c* 1. Scolex fully protruded.

*c* 2. Scolex half protruded.

*d.* Scolex as developed pointing inwards and its tubular body in communication therefore, not with the parent cyst, but with the cavity of the adventitious cyst thrown round the entire organism by the irritated tissues of its host.

For history of *Coenurus cerebralis*, see Van Beneden, *l. c.*, p. 146; Cobbold, Entozoa, 1864, p. 116 seqq.; Id. Parasites, 1879, p. 333; Gamgee, Report on the Parasitic Diseases of Quadrupeds used as Food, Med. Officers' Privy Council Office Report, v. 1862; Thudichum, *ibid.*, vii. 1865.

FIG. 6. *Hydra viridis*, with reproductive organs; after Greene, Manual of Coelenterata, 1861, p. 24.

THE animal is drawn, attached by its 'adhesive' or 'pedal' disc to a

piece of weed with the oral end downwards, a position ordinarily assumed by it during life. It is much enlarged, its natural size being at the greatest, in a fine example, barely  $\frac{3}{4}$  of an inch.

*Hydra* differs from the hydroid form of other *Craspedota* or *Hydromedusae*, (1) in being free and locomotive; (2) in being only temporarily colonial, as the buds formed are eventually set free from the parent and from each other; (3) in being a sexual Hydroid form and not developing a dimorphic sexual zooid or *Medusa*; (4) in being naked, i. e. devoid of a perisarc. The marine and freshwater genus *Protohydra* agrees with *Hydra* in being locomotive and non-colonial.

- a. Tentacle. The tentacles are contracted. They form a single circle: in number they vary from six to ten as a maximum in this species, but the odd numbers, seven and nine, are often met with. They are hollow and their cavities are continuous with the gastric cavity.
- b. Hypostome, or oral cone. It is conical when protruded, and the mouth is situated at its apex.
- c. The line points to the gastric cavity. The outline of this cavity and its extension into the tentacles is dark, owing to the chlorophyl corpuscles contained in the endoderm cells. The ectoderm cells, on the contrary, are transparent, and hence the light outer border both to body and tentacles. The oral and stomachal regions constitute the hydrocephalis. The peduncle is known as the hydrocope.
- d. Testis. The testes are always placed near the base of the tentacular circle, and are, as here, generally more than one in number (8-9). They are formed by the local multiplication of *interstitial* ectoderm cells, which are developed into spermatozoa and raise the covering-cells into a pointed capsule. This capsule dehisces at its apex, setting free its contents into the water.
- e. Ovum. The ovum is as a rule solitary. It is produced by the growth of one out of a mass of cells produced by the division of interstitial ectoderm cells. The outer cells undergo regressive changes, and the products formed serve as food to the growing ovum. The ovum is the only ectoderm cell which forms chlorophyl corpuscles, and it may be noted that these bodies have colourless predecessors. The covering-cells are raised by the ovum and burst. The ovum is then fertilised, and undergoes fission: the superficial cells are completely used up in this species but not in *H. fusca* to form (1) a chitinous coat, (2) a vitelline membrane, and (3) a mucous coat. Thus protected, the ovum drops away from the parent and remains quiescent.
- f. Adhesive or pedal disc. The ectoderm cells of this disc are glandular and secrete a clear tenacious fluid, and they emit pseudopodia, and hence move the animal slowly. *Hydra* swims by creeping up to the surface of the water and exposing its disc; and it creeps by bending

the body and bringing a tentacle into contact with the surface upon which it rests, then detaching the disc, and bringing it up to the tentacle and reattaching it.

*Hydra* rarely occurs hermaphrodite as figured here, but one and the same individual may produce both testes and ovaria at different times. These structures are *organs* in *Hydra*, not zooids. This fact is proved (1) by their development out of interstitial ectoderm cells, as in the organs of many sexual Medusae, and (2) by the absence of any evagination of the endoderm as in the *reduced* sexual zooids known as sporosacs or gonophores. It may be added that if a *Hydra* which is budding actively be starved, the buds dwindle away and sexual organs are evolved.

The ectoderm consists of (1) covering cells, the surface of which is exposed, the body and base irregular, the latter reaching the supporting lamina; (2) epithelial muscle cells, the surface of which is exposed, the base forming a muscle filament, disposed in a longitudinal direction and applied to the supporting lamina; (3) interstitial cells, small, irregular, in masses between the bases of (1); (4) young cnidoblasts placed deeply; (5) fully formed cnidoblasts which are superficial; (6) gland cells, restricted to the pedal disc; (7) ganglion cells with numerous outrunners which are certainly continuous, as in *Eudendrium*, with cnidoblasts and perhaps *inter se* on the tentacles, as also in *Eudendrium*. Sense-cells appear to be wanting. A 'supporting lamina' everywhere separates ecto- from endo-derm save at the edge of the mouth. It is delicate, and contains fibrils emitted from both the ecto- and endo-dermal muscle cells (Jickeli). The endoderm cells are ciliated. They are of three kinds—(1) endodermal cells so called, which contain chlorophyl corpuscles (see on Symbiosis, p. 243), are vacuolated to a certain extent and throw out pseudopodia during digestion (Parker), and also develop in the walls of the gastric cavity muscle-filaments, which appear to run both circularly and longitudinally; (2) small granular gland cells in the hypostome; (3) vacuolated gland cells at the base of the gastric cavity. According to Jickeli cnidoblasts are present in the endoderm both of *Hydra* and *Eudendrium*. The chlorophyl corpuscles are present chiefly in the marginal part of the endoderm cells, only when very plentiful in their bases. They are spherical, and consist of an outer envelope containing chlorophyl, usually entire but sometimes in plates, and central protoplasmic contents. They therefore closely resemble the chlorophyl bodies of plants.

It was formerly asserted that a *Hydra* could be turned inside out, and continue to live in this condition (Trembley). More modern researches have disproved the statement. But it appears that within certain limits the animal can be propagated by artificial division.

*Hydra*. Kleinenberg, Leipzig, 1872; Jickeli, M. J. viii. 1882; *Figures*, Atlas of Practical Elementary Biology, Howes, 1885.

*Tentacle*. Development, Jung, M. J. viii. 1882. *Pedal disc*. Hamann, J. Z. xv. 1882, p. 552.

*Muscle cells*. Korotneff, A. Z. Expt. v. 1876.

*Endodermal pseudopodia*. T. J. Parker, P. R. S. xxx. 1880. *Chlorophyl corpuscles*. Ray Lankester, Q. J. M. xxii. 1882; Id. Nature, xxvii. 1882-83; Hamann Z. W. Z. xxxvii. 1882; Id. Z. A. vi. 1883; Brandt, Z. A. vi. 1883.

*Sexual organs*, Marshall, Studies Biol. Lab. Owen's College, i. 1886.

*Embryology.* Korotneff, Z. W. Z. xxxviii. 1883. (Transl. A. N. H. (5) xi. 1883.)

*Artificial reversal of animal.* Engelmann, Z. A. i. 1878 and Marshall, 'Vital phenomena, &c., and new species of *Hydra viridis*,' Z. W. Z. xxxvii. 1882.

FIG. 7. Portion of tentacle of *Eucopeella campanularia*; from Von Lendenfeld, Z. W. Z. xxxviii. 1883, Pl. xxviii. Fig. 4.

THE tentacle, as in all *Hydrozoa* and *Anthozoa*, consists of ectoderm, supporting lamina and endoderm. The ectoderm consists of three layers, shown in *A* and *B*.

*A.* The superficial stratum of covering cells, fully formed cnidoblasts and sense cells. The covering cells have polygonal outlines, a superficial delicate cuticle, a nucleus centrally placed, and protoplasm much vacuolated, and disposed in a mass round the nucleus with irregular peripheral strands, as seen in three of the more centrally placed cells. These details are omitted in the remaining cells for the sake of clearness, as also is the delicate cilium which each cell carries. Three projections, two on the right and one on the left, are cnidocils (see Fig. 8), and the nematocysts corresponding to them are seen as oval bodies at their base. Both cnidocils and nematocysts are disposed at an angle of  $45^{\circ}$  to the axis of the tentacle. At its tip, however, they are placed at right angles. Sense-cells are not figured (see Fig. 8, *s'*), but they occur principally towards the apex of the tentacle, scattered among the covering or supporting cells.

*B.* Deeper layer of ectoderm, composed of ganglion cells, young cnidoblasts and muscle cells. A flattened ganglion cell, *g*, is figured with its nucleus and outrunners. Von Lendenfeld did not observe any anastomosis of these fibrils in *Eucopeella*. There are ten ganglion cells in the proximal portion of the tentacles in this hydroid, but none in the distal. Between the ganglion cell and the edge of the covering cell-layer is a young cnidoblast. The muscle cells, *m*, form a continuous layer applied to the supporting lamina, and this continuous layer is absent only at the tip of the tentacle. They are here deeply placed, i. e. sub-epithelially, as they are in some other Hydroids (*Plumularia*, *Eudendrium*) not superficially as in *Hydra* and others. Each cell consists of a small quantity of protoplasm surrounding the nucleus, and a long contractile fibre pointed at each end. The pointed ends are shown turned up in the figure. There are many nuclei scattered about, and the filaments are all disposed longitudinally, as is the case in the tentacles of most *Hydrozoa*.

*C.* The supporting lamina between the ectoderm and endoderm, and parts of two endoderm cells. The lamina is very thin: not so the cell-wall of the endoderm cells, which is thick and resistant, and shown in the diagram as dark lines. The cells are arranged in a single linear series

as they generally are in a *solid* tentacle. At the proximal end they abut against the gastric endoderm, from which they are in the first instance derived. Their protoplasm is much vacuolated, and surrounds the nuclei in a little mass, from which radiate towards the cell-walls irregular strands. A very thin layer covers the walls internally. The nuclei are disposed in a linear series in the axis of the tentacle. A large fat globule lies above the nucleus in the figure. This is sometimes broken up into 2-3 smaller drops.

FIG. 8. A portion of the head of a *Guard-polype* from a *Plumularia*, showing a sense-cell, supporting cell, and cnidoblast in relation with a ganglion cell; from Von Lendenfeld, Z. W. Z. xxxviii. 1883, Pl. xviii. Fig. 3 (cf. A. N. H. (5) xii. 1883).

- g.* Ganglion cell, such as have been detected in the ectoderm of many *Hydromedusae* including *Siphonophora*. It has a nucleus, granular protoplasm and outrunners.
- s'*. Sense-cell. The body of the cell is slender, nucleated, and bears at its outer extremity a cilium, and at its inner it is prolonged into a slender filament. The body of the cell is sometimes very granular. The basal process has been traced into continuity with a ganglion cell. Cf. Z. W. Z. vol. cited, Pl. xxix. Fig. 8.
- s.* Covering or supporting cell. It bears a cilium, and its outer extremity is broad. The body of the cell is stouter than in *s'*, but the basal extremity is elongated. In many instances it is broad, and rests on the supporting lamina.
- M.* Muscle cell. The protoplasm with nucleus is on one side, the contractile filament (dark in the diagram) on the other.
- C.* Cnidoblast containing an undischarged nematocyst. The outer extremity of the cell bears on the side opposite the nucleus a pointed process, sensory in nature, the cnidocil. This cnidocil has in some instances been observed to have a complex structure and to contain an axial simple or basally trifold filament. The cell body contains a long oval nematocyst, granular protoplasm, and a nucleus. Its basal portion is attenuated, and is in relation with processes of the ganglion cell. Actual continuity of the two structures has been observed by Jickeli (op. cit. *ante*, under *Hydra*), and by von Lendenfeld in *Cyanea Anaskala* (Z. W. Z. xxxvii. 1882, pp. 480, 513). This connection would explain the voluntary control which many of these animals appear to exert over the discharge of the nematocyst. It does not, however, exist in all instances.

There is some dispute over the nature of the basal process of the cnidoblast. In some instances it is hyaline, and Hamann believes that it is attached to the supporting lamina, and is purely a supporting structure itself. Chun has observed



that in the case of some of the cnidoblasts in *Physalia* it is transversely striated and the protoplasm of the cell itself contains a network of striated filaments. Jickeli (M. J. viii. 1883, p. 393) appears to be of an opinion that the cnidoblasts possess muscular processes. Von Lendenfeld points out, in the paper from which this figure is taken, that the basal processes of cnidoblasts in *Medusae* and *Anthozoa* are granular; that in *Crambessa mosaica* he has observed the discharge of nematocysts contained in cnidoblasts within the jelly when acetic acid was applied to the olfactory epithelium; that in arenicolous *Actiniae* contact of sand will not cause discharge of the nematocysts, but that contact of the prey does so at once. These facts point to some nervous control. The discharge of the thread is therefore brought about through pressure exercised on the sac of the nematocyst, by contraction of the cell body called out in response (1) to direct mechanical or chemical irritation of the cnidocil, or (2) to a nervous impulse generated by the will of the animal set in motion by special stimuli.

Von Lendenfeld has pointed out in the same paper the existence in certain *Guard polypes* of adhesive cells. These cells form a globule, which approaches and finally projects beyond the surface, and retains any body which comes into contact with it. As such cells occur in the same polyp side by side with cnidoblasts, or *replacing these structures* in later stages, Von Lendenfeld believes that there is an homology between the two. Adhesive cells occur to the exclusion of cnidoblasts in *Ctenophora*.

*For the nervous system in Hydroid forms* add to the works of Jickeli and Von Lendenfeld referred to, Chun on Siphonophora, Z. A. vi. 1883.

*For cnidoblasts and nematocysts* see also Chun, Z. A. vi. 1883, and Hamann, J. Z. xv. 1882.

FIG. 9. Two nematocysts, *A*, partially discharged, *B*, undischarged from a *Millepora*; after Moseley, Ph. Tr. 1877, Pl. ii. Fig. 2 *a* and *b*, *a* is slightly reduced in this copy.

THE nematocysts are removed from the cells or cnidoblasts in which they were developed, and where they usually remain until discharged and torn away by the struggles of the prey. The cyst consists of two membranes, an outer thick and an inner thin, both of chitinoid character. The thick membrane apparently does not close over the pole at which the filament is emitted. The thin one, on the contrary, forms a closed sac. The filament is developed as a hollow ingrowth of one pole of this sac, and as growth proceeds and the filament becomes longer than the greater diameter of the sac, it is disposed in coils shown in *B*. When the filament is discharged the discharge takes place by a process of eversion, the inner surface of the hollow ingrowth becoming the outer surface of the hollow filament. This fact can be readily made out in a filament, the discharge of which has been arrested. The sac itself contains a homogeneous fluid, and it is apparently the pressure of the surrounding cell protoplasm on the sac with its fluid contents that causes the eversion of the filament. But after discharge the sac is said to retain its form and dimensions unchanged. The base of the filament as seen in *A* is dilated, and hence the clear rod-like space passing

down the centre of *B*. The dilatation is armed near its distal end with three spines. This form is characteristic of the larger nematocysts of *Hydrozoa*, and is only found in that group. In some *Anthozoa* the basal dilatation is of great extent, and is armed with spines disposed in a spiral.

Nematocysts are found in all *Anthozoa* and *Hydrozoa*, but in no other *Coelenterata*. The trichocysts of *Infusoria* are formed in the same manner, as are the structures found on the dorsal processes of *Aeolidia* among *Mollusca*. In the *Turbellaria* very similar structures are met with in the rhabdocysts or rod-cells.

# THE ANIMAL KINGDOM.

## METAZOA.

MULTICELLULAR animals in which there is an ectoderm (=epi- or hypo-dermis) and an endoderm with tissues of various kinds,—sensory, nervous, muscular, connective and reproductive, derived either solely from them, or, with the exception of the two tissues first-named, from an independent source. A Gastrula stage occurs in the life-history of the individual. There are two subdivisions, the *Coelomata* and *Coelenterata*.

## COELOMATA.

METAZOA, in which an intermediate layer of cells, the mesoblast or mesoderm, developed in different ways (pp. xxviii–ix) intervenes between the epi- and hypo-blast of the embryo. It gives rise to the muscular and connective tissues, to the lymph or blood, to the nephridial (renal) and with perhaps few exceptions to the reproductive cells. A cavity or a system of cavities or channels, known as the coelome, is typically present; it lies within the mesoblast and is not homologous throughout the *Coelomata* (pp. xxix–xxx). In a few instances (most *Turbellaria*, the *Trematoda*, and *Cestoda*), it is represented by intercellular spaces. The principal axis of the Gastrula passing through the blastopore, never persists as the main axis of the body. Bilateral symmetry is always established. A shorter anterior region or head which is preoral, and a longer postoral region, the body, are readily distinguishable in most instances. The *Echinodermata*, however, acquire a secondary radial symmetry. An anus is typically present.

The Coelomata include the phyla *Chordata*, *Mollusca*, *Arthropoda*, *Echinodermata*, together with *Vermes*, as well as a few groups, the zoological position of which is uncertain, e. g. *Brachiopoda* and *Polyzoa*.

## PHYLUM CHORDATA.

BILATERALLY symmetrical coelomate Metazoa, in which the neural surface of the body is dorsal, the haemal ventral, i.e. the surface of locomotion, the reverse of what obtains in the other phyla of this division of Metazoa. The body is segmented, except in *Urochorda*, where segmentation is obscurely indicated in the caudal region alone. The central nervous system is formed typically from a neural (medullary) plate of epiblast which

becomes converted into a neural (medullary) groove, and finally by the meeting and closure of the two edges of the groove, into a neural (medullary) tube. The dorsal wall of the archenteron gives origin to an axial rod of cells—the notochord—which primitively underlies the central nervous system in its whole extent, or, as in *Urochorda*, only in its caudal section. The mouth is anterior, and the stomodaeum on the ventral side of the nervous system, which it does not perforate, as in other Coelomata. The pharynx, or first section of the archenteron, immediately following the stomodaeum, is perforated by one or more pairs of lateral clefts developed as outgrowths of the hypoblast, coming into contact with the epiblast which then thins away and leaves an opening. These clefts are respiratory in function, and vascular channels run in the partitions or septa between them. The anus is a ventrally placed proctodaeum, or, as in some *Amphibia*, *Ceratodus* and *Petromyzon*, a persistent blastopore. The coelome is either a schizocoele or crypt-enterocoele (p. xxx), formed in the two plates of mesoblast lying one on either side the notochord, as in *Vertebrata*, or an enterocoele, as in *Cephalochorda*, derived from two lateral outgrowths of the archenteron which divide from before backwards into a series of pouches, or primitive somites, in open communication for some time with the archenteron.

The phylum includes three sub-phyla—*Vertebrata*, *Cephalochorda*, and *Urochorda* (= *Tunicata*).

The somites of the body are formed in *Vertebrata* as follows. The dorsal section of the primitive coelome becomes separated from the ventral. The latter forms the permanent coelome, whilst the former is divided into a series of masses right and left lying on either side of the notochord. These masses are the somites, formerly known as primitive vertebrae. They give origin to the bodies of the vertebrae in part and to the muscle plates. The muscle plates extend both dorsally and ventrally, and give origin to the muscles of the body-wall, and in *Elasmobranchii*, *Amphibia*, and *Lacertilia*, of the limbs as well. The coelome extends round the archenteron, and its two halves meet ventrally and form a longitudinal septum. Traces of this septum persist as the ventral mesentery seen in a few Fish. The coelome in the region of the head becomes divided into a series of cavities by the formation of the mouth and the gill-slits. In *Amphioxus*, the first coelomic pouch belongs to the head; the remainder form the somites of the body. Their dorsal sections give rise to the muscles.

After the formation of the notochord a small sub-notochordal rod of cells is developed from the dorsal aspect of the archenteron in *Ichthyopsida* among *Vertebrata*. It is doubtfully represented in the Chick. It is an evanescent structure, but is said to form the sub-vertebral ligament of *Acipenser*. It is interesting to note that a rod of cells derived from the neural aspect of the archenteron in *Blatta* and *Clepsine* forms a sheath for the nerve-cord.

The mouth of *Urochorda* is a stomodaeum. In *Amphioxus* it appears as a pore in the centre of an ectodermic disc-like thickening. Two views are taken

as to its nature in *Vertebrata*. It is either a stomodaeum—the view taken later on, as there is certainly an ectodermic invagination—or it represents a modified pair of gill-clefts. In favour of this last-mentioned view, it is urged (1) that the fifth nerve branches over the dorsal angle of the mouth, just as e.g. the glossopharyngeal nerve does over the first branchial cleft; (2) that a branchial sense-organ lies at each dorsal angle from which the Gasserian ganglion is derived like the ganglia of the other segmental cranial nerves; (3) that in some *Teleostei* it appears as a double pit.

The part of the archenteron which occupies the tail in the larval *Urochorda* is metamorphosed partly into muscle-cells, partly into blood corpuscles. There is generally said to be a post-anal section of the archenteron in *Vertebrata* which communicates by a neur-enteric canal with the neural tube. But it is possible that the neural and archenteric tubes both open at the blastopore, as in certain *Amphibia* (*Rana*, *Alytes*, and *Triton*), where the blastopore certainly persists as anus; and that as the tail grows out, the blastopore is gradually shifted to the ventral surface, the neural tube still retaining its connection with it<sup>1</sup>. This view ascribes a neural origin to the post-anal gut, and appears to explain its subsequent disappearance. See Spencer, Q. J. M. xxv: cf. Durham: Miss Johnson: Q. J. M. xxvi.

For the *Hemichordata* of Bateson, see *Enteropneusta* in the *Vermes*.

### SUB-PHYLUM VERTEBRATA.

CHORDATA, which possess the following characters. The integument is composed of an epidermis consisting of several layers of cells, and a dermis chiefly composed of fibrous connective tissue. There is a well-developed endoskeleton, consisting of a cranium with moveable jaws: a backbone with neural and sometimes haemal, arches, and vertebral centra replacing the notochord more or less completely: and two pairs of limbs, pectoral and pelvic. The nerve-cord is enlarged anteriorly, forming the brain which is lodged within a cranium. There are two olfactory pits and two eyes. The lens of the eye is cellular, and developed from epiblast: the retina is cup-shaped, and derived from a vesicle of the brain. A contractile fibro-muscular iris, placed in front of the lens, controls the amount of light entering the eye. There are also two auditory organs arising as involutions of the epiblast which close and usually become highly complicated. A ventrally placed section near the head of the closed blood-vascular system is differentiated into a rhythmically contractile heart. There is a set of haemoglobin-containing blood-corpuscles or haematids, with fixed outlines in addition to the amoeboid corpuscles, or leucocytes. There is a blood-making organ—the spleen—lodged in the mesogastrium and traversed by the blood-current. And there is a system of lymphatic channels communicating with the blood-vascular system. The coelome is large and lodges the heart, the main portion of the alimentary

<sup>1</sup> In the Cyclostome *Petromyzon* the post-anal gut is represented by a solid rod of cells. The blastopore persists as the anus; it is, at first, dorsal, but shifts to the ventral surface in consequence 'of the elongation of the embryo and the formation of the tail.' Shipley, P. R. S. xxxix. 1885.

canal, and genital glands, which are retained in situ by folds of its lining membrane, the peritoneum. The two kidneys lie on its dorsal aspect, behind the peritoneum. They are compact glands though developed segmentally, and open externally, each by a common longitudinal canal. The ova are very generally shed into the coelome, taken up and carried away by two oviducts, and the testes connected to a portion of the kidney through which their products are conveyed to the exterior. The anal, urinary and reproductive apertures are ventral and close together, opening primitively into a common cloaca.

The deeper layers of cells of the epidermis are protoplasmic and form the stratum Malpighii, or rete mucosum: the more superficial layers are modified, and are often converted into flat horny coherent plates—the stratum corneum—which is least developed in aquatic Vertebrata. Certain of the epidermic cells may become glandular, or pigmented, and others modified into sensory nerve-endings (*infra*); and invaginations of epidermic cells into the cutis in higher Vertebrata form glands of various kinds. The dermis, cutis, or corium, consists of fibrous connective tissue, with connective tissue cells often modified into pigment cells. It gives support both to blood-vessels and nerves, as well as attachment to muscles. The spaces in the cutis give origin to the superficial lymphatics. The cutis is connected to underlying parts as a rule by more loosely arranged fibrous tissue—subcutaneous tissue—in which fat-cells, scattered or in masses, may be developed in higher Vertebrata. The integument gives origin in many instances to an exo-skeleton, which may be derived either from the epidermis or the dermis exclusively, or in part from one, in part from the other. An epidermic exo-skeleton is represented by the stratum corneum, and by special developments such as hairs, feathers, scales, tortoise-shell, hoofs, nails, claws, and other structures noticed where they occur. The dermic exo-skeleton consists of bony scutes or plates found in a few Mammals and many Reptiles, and in the scales of some Fish (most *Teleostei*, *Dipnoi*). A mixed exo-skeleton is seen in the various forms of teeth, with enamel derived from the epidermis, and dentine with cement derived from the dermis, and in the tooth-like scales of *Elasmobranchii*, *Ganoidei*, and some *Teleostei*.

The muscular system is well developed. The primitive division into somites or myomeres, with intervening fibrous septa or myocommata, is retained in the body-walls of *Pisces*, in the dorso-lateral parts of the body of perennibranchiate *Amphibia* and *Lacertilia*, and in the tail of all Vertebrata. It is retained in the trunk of the higher forms only in the spinal muscles (and the intercostals?) and more or less in the recti abdominis. In these cases the primitive longitudinal direction of the muscle-fibres persists. In the region of the head, and in the trunk generally, both in *Amphibia* and higher Vertebrata, the primitive arrangement is lost, and the muscle-

fibres take various directions in accordance with the necessities of their position. The muscles of the limbs are derived from the primitive muscle-plates (p. 334) in *Elasmobranchii*, and probably in other orders of Fish as also in *Amphibia* and *Lacertilia*. In higher Vertebrata they arise independently, probably by an abbreviation of development. All the muscles referred to above lie externally to the ribs and the transverse processes of the vertebrae. They are hence termed episkeletal. A superficial portion of this episkeletal system may retain its original independence of the skeleton and forms the 'muscles of the skin.' It is sparingly represented in *Pisces*, in *Amphibia* and *Reptilia*, except where moveable scales are present, as in *Gymnophiona* and *Ophidia*. In *Aves* it is said to form the erectors of the feathers, and in most *Mammalia* it is very well developed. The *Primates*, however, retain but few traces of it (*platysma myoides*). In *Amniota* there is a small system of hyposkeletal, or sub-vertebral muscles, underlying the vertebral column, the origin of which is unknown. It is also uncertain whether or not the fibro-muscular diaphragm of *Mammalia* belongs to this last-named system. Both epi- and hypo-skeletal muscles are striated. On the other hand, the musculature of the viscera with the exception of the heart, is, as a rule, non-striated.

The skeleton, or endo-skeleton, assumes a vast importance in Vertebrata. It consists of an axial and an appendicular portion. The former includes the skull and backbone: the latter the skeleton of the paired limbs and the girdles to which they are attached.

The notochord, which forms the axis of the backbone, extends into the skull as far forwards as the pituitary fossa. It undergoes atrophy, as a rule, in the skull, even though it persists, more or less, in the backbone. Exceptions are *Cyclostomi* and the *Sturgeon* (*Acipenser*). The skull itself is derived from the following elements: (1) two parachordal cartilages which lie one on each side of the anterior end of the notochord; (2) two trabeculae cranii underlying the fore-brain, and in shape resembling more or less lyrifiform rods in contact near their anterior extremity, and diverging posteriorly where they encircle the pituitary fossa and come into contact with the two parachordals<sup>1</sup> with which they are continuous in development in higher types (Bird, Pig), and with which they ultimately unite in all classes. They fuse together anteriorly in the region of the nose except in Eels. They retain in *Ophidia* the form of two rods in the region between the nose and the parachordals. Except in Urodelous *Amphibia* and a few other forms, the membranous floor of the pituitary region chondrifies continuously with the trabeculae, and is perforated only by the carotid arteries. Chondrification extends upwards from the parachordals and trabeculae in the layer of indifferent cells investing the brain. The former constitutes the occipital region. The trabeculae give origin to the basi- and ali-

<sup>1</sup> It is possible that the trabeculae are dissociated portions of the parachordals.

sphenoid, the paired prae- and orbito-sphenoid ; the interorbital septum, when it is present (*Teleostei*, *Lacertilia*, *Aves*) ; the paired lateral or ecto-ethmoids in front of the orbits ; the internasal septum ; and sometimes a prae-nasal rostrum, as in many *Elasmobranchii*, &c. The degree to which the cranial cartilage extends dorsally varies. The part of the chondro-cranium formed as above becomes (1) united with the cartilaginous capsules of the nose, and ear, that of the eye remaining independent, and (2) connected to visceral arches. The capsule of the nose is open externally and coalesces with the ethmoidal region. The capsule of the ear is generally closed, except where the auditory nerve enters it, and when two membranous spots, the fenestrae ovalis and rotunda, are formed on its external face. This capsule makes part of the lateral wall of the chondro-cranium and is wedged in between the occipital and basi-sphenoidal regions. It may even intervene in the floor of the skull between the two. The visceral arches, which are independent of the chondro-cranium, are paired and post-oral. The first is the mandibular or Meckel's arch, the second the hyoidean, the third and succeeding are branchial arches. The hyoidean and branchial arches are united ventrally by basal pieces or copulae, not, however, equal in number, to the arches themselves. Meckel's arch in some *Elasmobranchii* and in *Anura*, among *Amphibia*, bends over the angle of the mouth. The piece bent over lies in front of the mouth, and is cut off, forming the palato-pterygo-quadrate bar, whilst the remaining part of the arch forms the cartilaginous mandible. In other Vertebrata the palato-pterygoid is an independent formation, and Meckel's arch is segmented transversely, forming a small upper segment—the quadrate—or in *Teleostei* and bony *Ganoidei*, the quadrato-metapterygoid, and a large lower segment—the cartilaginous mandible. The hyoidean arch also undergoes transformation. Its upper part is cut off as a hyomandibular-symplectic in *Pisces*, or a stapedial element in *Amphibia* and higher Vertebrata, while the lower part of the arch forms the hyoid proper. This hyoid in the limited sense, proceeding from its dorsal to its ventral end, is broken up typically into stylo-, epi-, and cerato-hyal divisions, to which, in some Fish, is often added a hypohyal. A branchial arch is typically divided in the same manner, but the posterior arches in the series are simpler in structure<sup>1</sup>.

With the addition of a variable number of labial cartilages round the mouth, the above constitutes the cartilaginous skull. When it undergoes a normal ossification the occipital region divides into a basi-, a right and left ex-, and a dorsal supra-, occipital bone. The ear-capsule contains

<sup>1</sup> Dohm has recently investigated the embryos of various *Elasmobranchii*, and has come to the conclusion that (1) the palato-pterygoid, (2) the mandible, (3) the spiracular cartilage, (4) the hyomandibular, and (5) the hyoid represent as many visceral arches. With the exception of the hyoid, these arches remain simple. The hyoid segments and its dorsal element fuses with the hyomandibular in *Selachoides*. The thyroid gland is, according to him, the remnant of the gill clefts between the hyomandibular and hyoid arches. See Mitth. Zool. Stat. Naples, vi. 1885.



at the most five bones, pro-, sphen-, pter-, ep-, and opisth-, otics, but the second and third of the five are frequently absent. A basi- and two ali-, sphenoids appear in front of the ear-capsule, and in front of them in turn a prae- and two orbito-, sphenoids. The nasal septum ossifies as a mesethmoid and the lateral masses each as an ecto-ethmoid bone. A palatine, pterygoid, and sometimes a meso-ptyerygoid appear in the palatopterygoid bar. The quadrate region forms the quadrate bone, and in *Teleostei* and bony *Ganoidei* a meta-ptyerygoid also. The mandible has generally an articular ossification at its proximal end and occasionally an angular. An ossification sometimes found at the distal end of each mandible, and known as Mento-meckelian, is a persistent lower labial cartilage. The hyomandibular element of the hyoid arch has, in *Teleostei* and bony *Ganoidei*, two ossifications—the hyomandibular and the symplectic. It forms the simple stapes of some *Amphibia* and *Reptilia* and the *Mammalia*; the complex chain of stapedial elements (medio-, extra-, infra-stapedials) of Anuran *Amphibia*, the Crocodile, and *Aves*. The other segments of the hyoid ossify separately, but are sometimes more or less represented by ligament. The segments of the branchial arches may be similarly ossified. In adult *Amniota* the first only is represented, and is large in some *Reptilia* and in *Aves*; the rest abort.

To this cartilaginous skull, as above-described, are added a series of bones, developed in the first instance from the skin or mucous membrane of the mouth, but engrafting themselves in higher forms upon the skull or the cranium proper. The principal bones in this series, often spoken of as 'membrane' bones, are paired parietals, frontals, nasals, lacrymals, upon the dorsal aspect of the cranium; a vomer single or double, and except in *Mammalia*, where it is scarcely identifiable, a parasphenoid, on its oral aspect. To the palato-ptyerygoid bar are added praemaxillae, maxillae, jugals, and sometimes quadrato-jugals. To the quadrate region belongs the squamosal; to the mandible a dentary, and in *Sauropsida* a splenial, coronoid, angular, and supra-angular. A tympanic bone underlying the tympanic cavity of the ear appears in *Mammalia*, and in many Fish the opercular flap of integument covering the branchial cavity contains opercular bones: see p. 93.

The backbone is formed by the notochord and its sheath alone, in *Myxinoidei*; with the addition of neural arches in *Petromyzon*, and of haemal arches as well in some *Pisces* (certain *Elasmobranchii*, chondrostean *Ganoidei*). In all other Vertebrata the notochord is constricted by vertebral centra, and except in *Pisces*, some *Amphibia* and *Reptilia*, but slight traces of it persist in the adult in the intervertebral regions. The arches are developed in mesoblast independently of the notochordal sheath in *Ichthyopsida*, in continuity with it in other Vertebrata. The neural arches originate from a continuous right and left ridge in most instances; they

inclose the spinal cord, and in *Elasmobranchii* form a complete cartilaginous investment, which is segmented into neural arches proper, placed vertebally, and intercalary pieces placed intervertebrally. The intervertebral regions are occupied by a fibrous membrane in other *Vertebrata*, and it is only in a few instances that intercalary pieces are rudimentarily present. Haemal arches are well-developed in *Pisces*, where they originate like the neural arches from a continuous right and left ridge. Haemal intercalary pieces are present in the tail of *Elasmobranchii*, but not in the dorsal region. Haemal arches are developed also in the tail of Urodelous *Amphibia*. How far the transverse processes (=di- and parapophyses) of the vertebrae in other *Vertebrata* can be said to represent them is doubtful. The processes in question are continuous both with the centrum and the neural arch, or with one of the two in the adult. They are said to arise independently and then to fuse with the vertebrae in Urodelous *Amphibia*; in other cases they appear to be out-growths from them. Vertebral centra are formed by the growth of the cartilaginous or cellular sheath of the notochord, together with additions from the bases of the arches in *Elasmobranchii*, or from the surrounding mesoblast in *Teleostei*. The centrum is primitively due to a growth of cartilage in the vertebral region, and so it remains in *Pisces* and *Mammalia*, with isolated examples, living or extinct, in other classes. Large intervertebral remnants of notochord persist in *Pisces*; very slight in *Mammalia*. Traces of the vertebral growth may be visible in the development of *Amphibia* and *Sauropsida*, but they are masked by a great growth of cartilage in the intervertebral region. The vertebally placed remnants of notochord are then converted into cartilage and very commonly eventually into bone. The vertebral centrum may be biconcave (amphicoelous), biconvex, concave in front or behind (=pro- and opistho-coelous), or flat. It may remain independent of the arches or fuse with them. It is always ossified, and ossification may spread from it to the arches; or the latter may ossify separately. The centra alone may be connected together (most *Pisces*, a few *Reptilia*) or articulating processes (=zygapophyses) may be developed from the neural arches both from their anterior and posterior aspects, as in *Amphibia* and higher *Vertebrata*. The neural arches are generally provided with a dorsal neural spine (neurapophysis), formed independently or in continuity with them; and the centra may have a ventral outgrowth or spine (=hypapophysis). Each vertebra, consisting of centrum and neural arches, corresponds to a myocomma; the intervertebral region to the centre of a myomere. However in the tail of some *Elasmobranchii* the centra are twice as numerous as the myomeres.

The ribs support the body walls. They coincide with the myocommata<sup>1</sup>

<sup>1</sup> The ribs extend outwards horizontally in the fibrous septum between the dorso-lateral and ventro-lateral muscles in *Elasmobranchii*. It is possible that this position is secondarily acquired. In other *Vertebrata* they lie close to the peritoneum.

and are probably independent formations, but in some *Pisces* they are continuous at an early period of development with the haemal arches. They always ossify independently. At their dorsal extremities they articulate with the haemal arch, or the transverse processes, or with the vertebral centrum, as well as with a transverse process. The double articulation in Urodele *Amphibia* is brought about by the addition to the primitive rib of a dorsal rod which fuses with it and is thus connected to the transverse process of the neural arch. The persistence of this dorsal element, its loss, or the loss of the ventral articulation, is sufficient to explain the variations observable in the way the ribs articulate with the vertebrae in higher Vertebrata. In *Amniota* the ventral ends of the ribs meet in the middle line. A ventral segment is cut off from each rib, and from the elements thus derived the sternum (costal sternum) is formed. The remainder of the rib is generally divided into a vertebral and a sternal section, with an intercalated 'intermediate rib' in some *Reptilia*.

All Vertebrata possess typically two pairs of limbs—the pectoral and pelvic, one or the other, or both of which are sometimes aborted. It is still doubtful however if they were ever developed in the ancestors of the *Cyclostomi*. They appear to have arisen at first as a continuous ridge on each side of the body. A trace of this origin is seen in the ontogeny of *Elasmobranchii*. The primitive position of the limbs is one of horizontal extension, but it is only incompletely retained in *Elasmobranchii* and not at all elsewhere. The skeleton of such a primitive limb appears as a basal bar or plate of cartilage, the outer edge of which segments into radially placed radialia. These are borne upon the rest of the bar which divides into two or three large pieces—pro-, meso-, and meta-ptyerygium, or the two latter only. The radialia are bordered by an integumental fold, supported by fine rays similar to those of the azygos fins. In connection with the horizontal bar of cartilage in each limb is a vertical rod of cartilage possibly derived in the first instance from the horizontal bar. This vertical rod forms the shoulder girdle for the fore-limbs, the pelvic for the hind. The shoulder girdle in *Pisces* becomes connected in most cases with investing bones. It is always divisible into a portion dorsal to the articulation of the limb known as the scapula and a portion ventral to it, the coracoid. A clavicular process grows forwards from the junction of the two regions, or in higher forms from the scapula. The corresponding portions of the pelvic girdle are the ilium (dorsal), the pubes, and ischium (ventral); the pubes perhaps homologous with the clavicle. All these parts ossify independently. A supra-scapula or vertebral border may either remain cartilaginous at the dorsal end of the scapula or ossify separately from it; and an epi-coracoid may be similarly formed from the ventral or sternal edge of the coracoid which is in contact with the costal sternum except in the *Eu-* and *Meta-theria* among *Mammalia*. The

anterior edge of both scapula and coracoid may, when large, be partially converted into membranous spaces with intervening processes, prae- and meso-scapula; prae- and meso-coracoid. The two clavicles in some *Amphibia* and in higher types unite ventrally in the embryo, and from their point of union is differentiated an interclavicle or episternum. This episternum is free in *Reptilia* when it is present. It unites in *Aves* with the costal sternum forming the keel (?). In *Mammalia* except *Prototheria*, where it is large and free, it fuses with the manubrium sterni, and then the clavicular region of this bone either persists, aborts, or is transformed into ligament. The origin of the epipubic cartilage, which often exists projecting forwards from the median anterior edge of the pubes, is unknown. The two pubes and ischia unite ventrally, and the line of union is termed the symphysis.

The limbs articulate with cup-shaped cavities—the glenoid cavity for the fore- and the acetabulum for the hind-limb—in all classes higher than *Pisces*. In the latter tubercles may take the places of cavities. In *Amphibia* and upwards the fore-limb is divisible into a series of segments pre-formed in cartilage, but all ossifying—viz., a humerus, articulating with the shoulder-girdle; a radius and ulna, articulating with the humerus and with each other; followed by a carpus, consisting of (typically) a radiale = scaphoid, intermedium = lunar, and ulnare = cuneiform, constituting a proximal row; a centrale; and then a distal row composed of carpale 1 = trapezium, 2 = trapezoid, 3 = os magnum, carpalia 4 and 5, or 4 + 5 = unciform, to which articulate the digits typically 5 in number, composed each of a proximal metacarpal, and a distal series of phalanges. The corresponding parts in the hind-limb are femur; tibia, and fibula; tarsus composed of tibiale, intermedium, or both together = astragalus, fibulare = calcaneum; centrale = navicular; tarsale 1 = ento-cuneiform, 2 = meso-cuneiform, 3 = ecto-cuneiform, tarsalia 4 and 5, or 4 + 5 = cuboid; and 5 digits each with a meta-tarsal and phalanges. There are great modifications observable in the hand and foot of different groups of *Vertebrata*<sup>1</sup>. In addition to the paired limbs, the *Ichthyopsida* possess a system of azygos fins, either temporarily or permanently. An account of them is given under the general introduction to that division.

In addition to the above-named bones, ossifications appear frequently

<sup>1</sup> The account given in the text is the one ordinarily accepted. In some Urodele *Amphibia* the centrale is double. A digit external to the great toe also occurs in some of them, and some Anuran *Amphibia*. Baur (*Z. A.* viii. 1885) has come to the conclusion that the astragalus of *Mammalia* represent one of the two centralia + the intermedium, the tibiale being represented by a sesamoid, or forming part of the navicular (= the other centrale). The unciform and cuboid represent the fifth carpal and tarsal respectively. Traces of a finger external to the thumb, and of a toe external to the great toe, are found in some Mammals, the sesamoid of the abducens pollicis representing the former, an extra ossicle seen in many *Carnivora* the latter. Cf. *Id.* on *Archegosaurus*, *Z. A.* ix. 1886.

in tendons. Such bones are known as sesamoids. The most familiar example is the patella or knee-pan.

The nervous system is divisible into central and peripheral parts. The former is constituted by the brain and spinal cord; the latter by the nerves and sympathetic system. The brain consists in the embryo of three hollow vesicles—a fore-, mid-, and a hind-brain. The first of these eventually gives origin to the two olfactory lobes (rhinencephala), the two cerebral hemispheres (prosencephala), whilst a remnant of the original vesicle persists as the thalamencephalon or vesicle of the thalami optici, from which arise the two hollow outgrowths converted afterwards into the optic nerves, retina and retinal pigment layer. The pineal gland (epiphysis cerebri) is continuous with the roof of the thalamencephalon. It has been supposed to represent either the region of closure of the neural folds (cf. *Cephalochorda*), or else, an unpaired eye<sup>1</sup>. The floor of the thalamencephalon is prolonged into a hollow infundibulum, to the apex of which is attached the pituitary body (hypophysis cerebri=conarium), derived in part from the ectoderm of the stomodaeum, in part from mesoblast. It is supposed to represent either the sub-neural gland of *Urochorda* (Balfour, Julin) or an abortive pair of gill-clefts (Dohrn). The floor of the mid-brain (mesencephalon) becomes crura cerebri; its roof simple in *Protopterus* and *Siredon* (=Axolotl) forms two hollow optic lobes or corpora bigemina; or in *Mammalia* four solid corpora quadrigemina. The notochord in the embryo extends as far forwards as the mid-brain. At one period the whole fore-brain is bent or deflexed more or less in

<sup>1</sup> In *Cephalochorda* and *Urochorda* the neural folds unite over the groove from behind forwards, and a pore opening into the brain-cavity persists anteriorly for some time. In Vertebrata, however, the folds unite from before backwards. Götte describes in the embryo *Bombinator* a cord of cells uniting the pineal body with the epidermis, and suggests that in this union is to be seen a remnant of the pore alluded to above. A short slit has been found by Van Wijhe in the same position in the embryo Elasmobranch. Recent researches have shown that in *Lacertilia* the apex of the pineal gland is transformed into an azygos eye. According to de Graaf (*Z. A.* ix. 1886), this eye, which is detached from the pineal gland itself, lies below the parietal foramen of the skull, between the membranes of the brain. It is a vesicle with cellular walls. The part of the wall turned towards the foramen is thickened and lens-like; the remaining part is deeply pigmented, and in *Anguis fragilis* has a complex structure, consisting of three tiers of cells. Of these, the one turned towards the cavity of the vesicle has its cells elongate, pigmented and provided with refractile processes. W. B. Spencer (cf. *Nature*, xxxiv. 1886) has confirmed and extended de Graaf's results. He finds that the azygos eye is sometimes embryonic (?), e.g. in *Cyclodus*, sometimes highly developed, e.g. in *Hatteria* and *Iguana*. He finds that it is often connected to a nerve, which may be traced into the pineal gland, and is always accompanied by a blood-vessel; that the pigmented cells are transversely striated, and appear to be connected at their bases with the cells of the two other tiers, the whole forming a complex retina; that the cavity of the vesicle is filled with a coagulable fluid. But he has not observed the refractile processes of de Graaf. Mr. Spencer will publish his results *in extenso* in the *Q. J. M.* Ahlborn came to the conclusion, on various grounds, that the pineal gland represents a rudimentary eye (*Z. W. Z.* xl. 1884), but the view appears to have been also hinted at by Rabl-Rückhard (see, *Z. A.* ix. 1886, p. 405). The extinct *Stegosauria* possess a large parietal foramen, which, as suggested by de Graaf, may possibly indicate the former existence of a pineal gland of great functional importance.

the different Vertebrate classes, and the mid-brain thus forms the anterior extremity of the body. This bend is known as the cranial flexure. The hind-brain is constricted into two lobes—the cerebellum in front, and the medulla oblongata behind. The cerebellum of the adult is the roof, the pons Varolii, the floor of the first lobe. The medulla oblongata is the floor of the second lobe. Its original roof widens and thins away at the same time, and is eventually represented only by an epithelial layer. The two ridges which carry the roots of the nerves are thus widely separated from the middle line. The primitive cavities of the brain-vesicles persist as the ventricles. The ventricles of the olfactory lobes are sometimes obliterated; those of the cerebral hemispheres only in some *Pisces*. The spinal cord extends primitively throughout the whole length of the spinal canal or backbone, and so persists in *Pisces*; but in other Vertebrata it shortens, its terminal portion being represented by a filum terminale.

The original cellular walls of the spinal cord develop into an outer layer of medullated nerve-fibres (=white matter), and an inner mass of ganglion cells and fine fibrils (=grey matter) surrounding a *canalis centralis*, a remnant only of the original cavity of the cord continuous anteriorly with the ventricles of the brain, which is lined by a ciliated epithelium. The grey matter in the thalami optici, mid-brain, and medulla oblongata, forms ganglionic masses; in the cerebellum an outer layer; in the cerebral hemispheres both ganglionic masses (*corpus striatum*) and an outer layer or cortex. The superficial layer of white matter in the cerebellum and hemispheres is exceedingly thin; on the contrary white matter is largely developed internally to the grey layer. In *Amphibia* and higher Vertebrata the hemispheres are united anteriorly by a transverse band of fibres—the anterior commissure. A similar band behind the root of the pineal gland forms the posterior commissure of *Elasmobranchii*, *Sauropsida*, and *Mammalia*. In the last-named class there is a grey or middle commissure uniting the two optic thalami, and two bands, one of transverse fibres—the *corpus callosum*—uniting the hemispheres across the roof of their ventricles, the other of longitudinal fibres—the *fornix*<sup>1</sup>. The brain and spinal cord are invested by three membranes—a pia mater, immediately applied to their surfaces; an arachnoid, covering the pia mater; and a dura mater, which lines the inner surface of the cranium, but in the spinal cord is split into two layers, one lining the spinal canal, the other, or *theca spinalis*, forming a sheath round the cord.

The cranial or cerebral nerves are (1) olfactory, in connection with

<sup>1</sup> The *corpus callosum* appears to be represented in both *Reptilia* and *Amphibia*. The anterior commissure of the brain in these classes is divisible into an upper and lower portion. The latter represents the true anterior commissure; the former represents the *corpus callosum*, 'and contains the fibres of the dorso-medial moiety of the hemispheres.' See Osborn, Z. A. ix. 1886. The *corpus callosum* is also possibly indicated in Fish.

the olfactory lobes of the brain ; (2) optic, which forms a chiasma or union with its fellow, in which fibres cross from one to the other side, except in *Teleostei*, where the two nerves cross one another, the right to the left side, and *vice versa* ; (3) the oculo-motor, which supplies all the muscles of the eye except two ; (4) the trochlear, which supplies the superior oblique muscle of the eye ; (5) the trigeminus, or mixed sensory and motor nerve of the face and jaws ; (6) the abducens, or nerve of the external rectus muscle of the eye ; (7) the facial, chiefly a motor nerve ; (8) the auditory ; (9) the glossopharyngeal ; (10) the vagus ; (11) the spinal accessory ; and (12) the hypoglossus. Of these nerves the optic is derived from the brain, the spinal accessory and hypoglossus apparently from spinal nerves, the trochlear and abducens perhaps belong to the trigeminus and facial respectively. The auditory is supposed by some authorities to be derived from the facial, by others it is supposed to be like the remaining cranial nerves (1 (?) 3, 5, 7, 9, 10, *supra*) segmental<sup>1</sup>. The cranial nerves differ from spinal nerves in having primitively single roots, and in being connected with branchial sense organs (*infra*) from which the olfactory and auditory sensory epithelia are perhaps derived in the first instance. The ganglion of the roots of the oculo-motor, i. e. the ciliary ; of the trigeminus, i. e. the Gasserian ; and of the remaining segmental nerves are supposed to arise in connection with the same sense bodies. Each segmental nerve typically supplies a gill cleft. The main trunk passes down the posterior side of the cleft, a small branch down the anterior side, a third to the pharynx, and a fourth—the so-called dorsal branch—appears in continuity with the branchial sense organ at the upper end of the branchial cleft<sup>2</sup>. This primitive arrangement is very well seen in the case of the glossopharyngeal nerve of many fish. The spinal nerves have two roots—a dorsal sensory root with a ganglion, and an anterior motor root which joins the sensory distally to the ganglion. The two roots have different origins. But all nerves, cranial as well as spinal, are outgrowths continuous with the central nervous system. And the more or less extensive series of sympathetic ganglia, which lies at the side of the backbone, and is connected with the nerves and ganglia of the viscera, take their origin from the spinal nerves, to which they are always united by rami communicantes.

Sensory ectodermic cells are found on the surface of the body in *Ichthyopsida* as branchial sense organs or organs of the lateral line (*infra* under *Ichthyopsida*), and in *Pisces* of end-buds. End-buds in other Vertebrata are restricted to the oral cavity, and in *Mammalia* as 'taste' buds to certain papillae or lamellae on the tongue and on the epiglottis.

<sup>1</sup> For the difficult questions connected with this subject of segmental cranial nerves, and their connections, the student must consult the original authorities cited below (p. 358).

<sup>2</sup> The segmental nature of the olfactory nerve is not universally admitted.

Touch cells, i. e. ganglion cells, terminating a nerve filament, are found in the cutis of Anuran *Amphibia* and higher forms, often united within a common sheath forming touch corpuscles. Finally, in *Sauropsida* and *Mammalia* Pacinian corpuscles or terminal nerve filaments surrounded by greatly developed sheaths are found in the skin, among the muscles, &c. The olfactory mucous membrane in some *Pisces*, e. g. Flying Fish, Pike, and Urodele *Amphibia*, e. g. Newt, appears to consist of end-buds intermingled with non-sensory epithelium, but in most Vertebrata it consists of sensory epithelium mingled with supporting cells. The former are terminated by sensory hairs, except in *Pisces* and *Mammalia*. The nose is originally a depression, but becomes in the *Dipnoi* and higher forms a sac, with an external opening in the face and an internal opening into the mouth. A portion of the nasal cavity becomes separated off from the nose proper. It is known as Jacobson's organ, and is supplied by the fifth nerve as well as by the olfactory. It exists in many *Lacertilia*, *Ophidia*, and *Mammalia*, and is represented in *Amphibia*. The retina of the eye, the retinal epithelium and optic nerve are derived from a vesicle of the brain, originating from the thalamencephalon, i. e. secondarily from the epiblast. The retina is composed, proceeding from within outwards, of an inner layer of nerve-fibres derived from the optic nerve; a layer of ganglion cells; an inner granular, or cell layer; and an outer granular, or cell layer—the cells of which give origin to the visual rods, or rods and cones. The outer free ends of the latter are immersed in a layer of pigment cells, also derived from the optic vesicle. The retinal elements are supported by connective tissue. Capillary blood-vessels enter the retina in *Mammalia*, *Chelonia*, and the Eel. There is a spot lying in the axis of vision known as fovea centralis, or in *Primates* among *Mammalia* from its colour as macula lutea, in which the cones with their cells are alone present, the other layers thinning away. Between the retina and the lens intervenes a jelly-like vitreous humour, into which projects in many *Pisces*, *Reptilia*, and in *Aves* a pigmented vascular process—the pecten, marsupium or processus falciformis. The lens is cellular, and is formed by an involution of the epiblast. There is an adjustable fibromuscular diaphragm, or iris, placed in front of it. The eye is enveloped in two protective coats, an inner vascular pigmented choroid, and an outer fibroid or cartilaginous sclerotic, continuous in front with a transparent cornea, which is in part an epiblastic, in part a mesoblastic, structure. The eye-ball is moved by four recti and two oblique muscles. It is usually protected by an upper and lower eyelid, and, in very many instances, by a third lid or nictitating membrane, which has frequently special muscles of its own. Two glands, a lacrymal in connection with the upper lid, a Harderian with the third lid, are commonly present; and their secretion is carried to the nasal cavity by a special lacrymal duct which arises at



the anterior or inner angle of the eye. The auditory organ commences as an epiblastic involution. It becomes saccular, but the pedicle of invagination persists as the aquaeductus vestibuli, or saccus endolymphaticus, which in some instances, *Lacertilia* especially, becomes much enlarged, and in many *Elasmobranchii* remains open externally. The ear-sac differentiates into two connected vesicles, the utricle and saccule. Three semicircular canals, anterior vertical, posterior vertical, and external horizontal, originate from the utricle; a lagena, or cochlea, from the saccule. The whole constitutes the membranous labyrinth. The auditory nerve is distributed to certain spots, the maculae of the utricle, saccule, and cochlea, the cristae acusticae of the semicircular canals, the epithelium of which consists of sense-cells and supporting cells. The whole apparatus is filled with a liquid, or endolymph. Calcareous otoliths are found in the sensory region of the maculae, except in the cochlea of *Mammalia*. They vary in size and are borne by the sense hairs of the epithelium, and when small are united by a slimy substance. The membranous labyrinth is inclosed in the auditory capsule, but is separated from it by a space filled with perilymph. In *Pisces* this space opens into the arachnoid space of the brain by passages round the auditory nerve and the aquaeductus vestibuli, but by a special duct the aquaeductus cochleae (ductus perilymphaticus) in *Amphibia* and higher Vertebrata. Two membranous spots, the fenestra ovalis and fenestra rotunda, occur on the outer wall of the auditory capsule, where it bounds the perilymphatic space. They are found in most *Amphibia* and all higher Vertebrata. To the first is attached either a single auditory ossicle, or a chain of ossicles, which connect it to the tympanic membrane (*infra*). The single ossicle is the stapes (=hyomandibular of *Pisces*), found in *Amphibia* and *Sauropsida*, where it is often broken up into a series of segments (*supra*, p. 339), and is generally known as columella auris. The chain of ossicles is found in *Mammalia*, and comprises a stapes, articulated to an incus (=quadrate of *Sauropsida*, &c.), and that in turn to a malleus (=articular part of Meckel's arch). These bones are contained in Anuran *Amphibia* and higher Vertebrata in a tympanic cavity, produced by an outgrowth from the pharynx in the position of the first visceral cleft or spiracle, which atrophies almost completely. The part opening into the pharynx is the Eustachian tube. The outer wall of the outgrowth, together with mesoblast and epiblast, forms the tympanic membrane to which one end of the columella auris, or in *Mammalia* the malleus, is attached. An external meatus is formed in higher Vertebrata by the growth of the parts around the tympanic membrane, but a concha of the ear is well developed only in *Mammalia*.

The alimentary tract consists of a stomodaeum, mesenteron (=archenteron), and a proctodaeum, but in some *Amphibia* (Frog, Newt) the blastopore persists as the anus. The stomodaeum forms the major part of

the oral cavity. This cavity becomes divided in *Chelonia*, *Crocodylia*, some *Aves* and all *Mammalia* into an upper nasal portion, and a lower buccal portion by the formation of a hard or, in Mammals, of a hard and soft palate. Teeth and glands are developed in the mouth. The teeth are composed typically of two substances, enamel and dentine. The former is derived from the inner surface of a cellular structure, the enamel organ, which is formed by a downgrowth of the epiblastic rete mucosum, covering an upgrowth of the mesoblast, the dental papilla. The cells on the outer surface of the latter or the odontoblasts give origin to the dentine, whilst the central part of the papilla persists as a vascular pulp supplied also with nerves. The teeth formed in this manner are phylogenetically identical with the exoskeletal spines of certain Fishes (*Elasmobranchii*). A third substance, cement (crusta petrosa), formed by the connective tissue surrounding the base of the tooth, agrees histologically with bone, but is found only on the roots of some teeth when implanted in sockets. The teeth are attached to the underlying jaws either by a fibrous membrane (some Fish) or by bone, i.e. by ankylosis (some Fish, *Amphibia* and *Reptilia*), or are implanted in grooves or sockets (a few Fish, *Reptilia* and all *Mammalia*). Their shape, situation, number, &c., vary immensely. They are found in the pharynx of many Fish, and here the enamel organ is derived from hypoblast and not epiblast as in the stomodaeal region. New teeth in succession to old teeth are either formed without limit of numbers, as in most *Pisces*, *Amphibia*, *Reptilia*, or are restricted to a second set in some *Mammalia*. In other *Mammalia* there are no successional teeth at all. The enamel organ of these successional teeth is typically derived from the pedicle of a pre-existing enamel organ, but in *Teleostei* independently from the rete mucosum. A partial absorption of the old tooth generally occurs when it is replaced. In some *Mammalia* the teeth grow from persistent pulps as fast as their exposed surfaces are worn away, e.g. the incisors of *Rodentia*. Specialised oral glands are found from *Amphibia* onwards. Their structure, number and position vary much, but *Mammalia* are characterised by three well-developed pairs—parotid, sub-maxillary and sublingual, in addition to minor glands. A muscular growth from the floor of the mouth above the basihyal region constitutes the tongue. It is well developed in *Amphibia* and higher forms.

The mesenteron (archenteron) is divisible into two or three regions. The first, fore-gut, extends from the stomodaeum to the point of origin of the liver, and comprises a pharynx, oesophagus, and stomach. The second constitutes the mid-gut or small intestine; the third the hind-gut, large intestine, or colon. The two latter are sometimes difficult to distinguish. Their limits are either indicated by the presence of one or two lateral caeca, by a difference of calibre or of the mucous membrane. A post-anal section of the mesenteron has also been distinguished in the embryo, but some doubt

attaches to its significance. The anterior limit of the oral part of the mesenteron is lost except in *Cyclostomi*, where it is indicated by the velum. The pharynx of Vertebrata represents a portion and a portion only of the primitive respiratory or branchial section of the fore-gut. Its walls are perforated by a series of branchial or visceral clefts. The greatest number of these known in an adult form is eight, of which the first is the spiracle lying between Meckel's arch and the hyoid (cf. note, p. 338), the position in which the Eustachian tube develops in higher Vertebrata. The remainder are branchial clefts, or in *Mammalia* and *Sauropsida* where branchiae do not exist even in the embryo, visceral clefts, limited to four in number. The clefts are formed by hypoblastic outgrowths from the throat reaching to the epiblast which eventually thins away over them, thus leaving an aperture. The septum or wall between each pair of clefts is supported by a branchial arch, and contains an aortic, i.e. a vascular arch. The anterior and posterior walls of the pouches bear vascular processes, branchiae or internal gills in *Pisces*. External gills, such as are found in *Amphibia*, permanently or temporarily, are outgrowths covered with epidermis near the dorsal ends of the branchial arches. There is reason to believe that the branchial clefts were very numerous in the ancestral Vertebrata, and that the true digestive portion of the alimentary canal commenced, as in *Amphioxus*, with the region to which the liver is attached. The oesophagus and stomach are separated by a cardiac constriction little marked in most *Ichthyopsida*. The stomach and mid-gut are marked off by a similar constriction known as the pylorus or pyloric valve, due to great development of the circular muscular coat of the alimentary canal. The rest of the tract varies much in calibre, length, and consequently in the degree to which it is coiled. In *Mammalia* the terminal section of the colon is straight, and is hence termed rectum. The intestine terminates in the embryo in a cloaca, common to it and the urogenital ducts, a condition which persists in some *Pisces*, all *Amphibia*, and *Sauropsida* and the *Prototheria* among Mammals. But the primitive condition is lost in other cases, and the rectum opens separately from the urogenital ducts, as in *Holocephali*, *Teleostei* among *Pisces*, *Eu-* and *Meta-theria* among *Mammalia*; and occasionally the urinary ducts apart from the genital (*Holocephali* and some *Teleostei*, the female Rat and a few other *Mammalia*). The walls of the alimentary canal consist typically from without inwards of a serous coat; of a longitudinal and a circular coat of non-striated muscle-cells; of a sub-mucous connective tissue; and a mucous coat, the two latter often thrown into variously disposed folds in the mid-gut. The sub-mucous coat contains blood-vessels, lymphatic tissue and vessels. The mucous coat is a single layer of epithelial (hypoblast) cells, which form tubular glands in the stomach of all Vertebrata, in the intestine of *Amphibia* and higher classes.

Two glands, a liver and a pancreas, are connected with the commence-

ment of the mesenteron. The former is a ventral outgrowth of hypoblast into the mesoblast, either double or single at first, but always becoming double at last. The gland tubes develop into a network surrounded by a vascular network, and their tubular character, retained in *Amphibia* and *Reptilia*, is lost in *Aves* and *Mammalia* by the growth of the lining epithelium. The number of bile ducts vary, and there is frequently a gall-bladder or caecum attached to one of them. The fully formed gland is typically bilobed, but its external shape is subject to great changes. The pancreas arises as a single, or in *Aves* double, dorsal outgrowth of the mesenteron into the mesoblast. It is eventually closely connected (with few exceptions) to the bile duct near its intestinal opening. It is absent in some *Pisces*.

A diverticulum from the oesophagus, wanting in *Elasmobranchii* and *Holocephali*, becomes the air-bladder of *Pisces*, the lungs of the higher *Vertebrata*. It is primitively ventral in position, dorsal in nearly all *Pisces* in which the original communication with the oesophagus is often lost. It is either single or double, but in the case of the lungs always becomes double, remaining attached by a stalk to the oesophagus. The stalk is the trachea, the two appended caeca the bronchi and lungs. In *Aves* and *Mammalia* the caeca branch repeatedly forming the bronchia<sup>1</sup>, and the ultimate branches—the air-tubes or cells. Certain of the bronchia are prolonged into air-sacs in *Aves*. The hypoblast cells form the epithelium lining the whole structure, the surrounding mesoblast, the supporting and vascular tissues. The trachea, bronchi, and the bronchia when present, are strengthened by cartilaginous rings or pieces most complete in the two structures first named. The first rings of the trachea differentiate into a larynx, with which are connected the fibrous bands or cords which produce the voice. The organ of voice, however, in *Aves* is developed at the junction of the trachea and bronchi, and is known as the syrinx. A valve, the epiglottis, covers the entrance to the larynx in *Mammalia*.

Two other structures, the thyroid and thymus, are closely connected to the fore-part of the alimentary canal. The former develops as a ventral diverticulum of the mouth, lying at the anterior end of the ventral aorta, and is probably homologous with the endostyle of *Urochorda*. It closes off from the mouth, and when fully formed is a solid body either single, bilobed, or broken up into two parts (*Amphibia*) or many masses (*Teleostei*)<sup>2</sup>. The thymus is formed by epithelial growths from the dorsal ends of more or fewer of the branchial (visceral) clefts. These growths fuse together on the right and left sides into a single body. The thymus atrophies in the higher *Vertebrata* as a rule.

<sup>1</sup> The bronchia, which spring from a spot above, i. e. anterior to the point, where the pulmonary artery crosses the bronchus, are known as ep-arterial; those below, or posterior to it, as hyp-arterial.

<sup>2</sup> See a paper by Dohrn on the thyroid in *Petromyzon*, *Amphioxus*, and *Tunicata* (= *Urochorda*), *Mitth. Zool. Stat. Naples*, vi. 1885.

There is a closed circulatory system formed in the mesoblast consisting of a central rhythmically contractile heart, a set of efferent vessels or arteries, and of afferent vessels or veins—the two sets connected by the smallest vessels or capillaries. The heart is primitively a specially developed section of the subintestinal vein in the region of the throat, but in Amniote *Vertebrata* (? *Reptilia*) it is formed by the coalescence of two vessels directly continuous with the vitelline veins. It consists primitively of a sinus venosus, lost in adult *Aves* and *Mammalia*, an auricle and a ventricle separated by valves; a truncus arteriosus divisible into a conus arteriosus, containing many valves and a bulbus arteriosus (or aortae), which is valveless. The auricle lies dorsally to the ventricle and truncus, and anteriorly to the former. It is divided by a septum into a right and left auricle from *Amphibia* upwards. The ventricle is similarly divided in *Aves* and *Mammalia*. The complete division of the ventricle which exists in *Crocodylia* is perhaps not homologous with that of higher *Vertebrata*. The conus is found in all *Ichthyopsida*, except *Teleostei*, in which it aborts; the bulbus only in *Pisces*<sup>1</sup>. The embryonic truncus (i. e. conus + bulbus) is broken up by an internal septum in all *Sauropsida* and *Mammalia* into the roots of the great vessels, i. e. the aorta and pulmonary artery. The roots of these vessels are guarded in *Sauropsida* by two, in *Mammalia* by three, semilunar valves. The heart lies in a special section of the coelome—the pericardium. The part of the coelome dorsal to the pericardium is aborted in *Pisces*. In other *Vertebrata* it enlarges, and the lungs grow out into it. The bulbus is primitively continued forwards as the ventral aorta as far as Meckel's arch, and gives off to the right and left paired aortic arches, which correspond to Meckel's arch, the hyoid and following branchial arches. The mandibular aortic arch is aborted in growth, and is sometimes not developed (*Amphibia*); the hyoidean persists in some *Pisces*. In *Sauropsida* and *Mammalia* only three branchial aortic arches are ever developed, but four at least in most *Ichthyopsida*. Some or all of these aortic branchial arches, and in some instances the hyoidean also, supply the internal or external gills of *Ichthyopsida*, in the former case being resolved into a branchial artery and vein. The dorsal ends of the primitive aortic arches unite on each side into a vessel which gives off forwards to the head one or two branches, the carotid arteries, external as well as internal, and then runs backwards beneath the notochord parallel to its fellow with which however it fuses, sooner or later, to form the subvertebral aorta of the adult. This aorta gives off vessels to the fore-limbs, or the subclavian arteries; a vessel to the yolk sac, the vitelline artery (the persistent mesenteric artery); one or two iliac arteries to the hind-limbs which are connected with the allantois in foetal *Sauropsida* and *Mammalia*, by the umbilical arteries, the remnants

<sup>1</sup> The distal rows of valves of the conus persist in *Teleostei*, the proximal apparently, in *Sauropsida* and *Mammalia*. The *Amphibia* have both a distal and proximal row in their conus.

of which constitute the hypogastric arteries at a later period. The aorta ends in a caudal artery.

The primitive condition of the arterial system is retained in *Pisces*, but in *Amphibia*, and especially in *Amniota*, changes take place, more particularly affecting the aortic arches. The third aortic arch (i. e. 1st branchial arch of Fish) forms the root of the internal carotid, and the stem of the common carotid, the external carotid being continued forwards from its base. The fourth arch, i. e. 2nd branchial, becomes the aorta, the left persisting in *Mammalia*, the right in *Aves*, both left and right in *Reptilia* and *Amphibia*. The fifth arch (= 3rd branchial) becomes the pulmonary artery, the left in *Mammalia* forming both arteries, the right both in *Ophidia*—the left and right persisting in other *Amniota*. The pulmonary artery of *Amphibia*, however, is developed as a rule from a sixth arch (i. e. the 4th branchial), the fifth arch (3rd branchial) either persisting as a rudiment or disappearing altogether (see account of the class). The artery to the lung in *Dipnoi*, or to the swimming bladder in some *Ganoidei*, is derived also from the sixth arch, or 4th branchial.

As to the venous system. A subintestinal vein continued backwards from the heart is formed in all embryo Fish. Its posterior section, present also in higher forms, constitutes the caudal vein which unites with the cardinal veins (*infra*) and loses its connection with the praecaual portion. The praecaual portion persists in the typhlosole of *Petromyzon* and the spiral valve of *Elasmobranchii*. It is lost in other Vertebrata, but gives off during development, (1) the vitelline veins which subsequently become the roots of the portal vein, and also (2) the portal network of vessels as well as that of the hepatic veins in the liver. The part of the vessel (ductus venosus) between the origins of the two networks eventually undergoes atrophy. To the portal system are subsequently connected visceral veins, and sometimes veins from the abdominal wall (= epigastric) and the genitalia. In *Pisces* a right and left venous trunk—the ductus Cuvieri—open into and really form the sinus venosus. The outer ends of these ducts are continued forwards to the head as the anterior, backwards (and dorsal to the Wolffian body) as the posterior, cardinal veins. The former represent the external jugulars to which the subclavian veins (veins of fore-limbs) become connected. The posterior cardinals become united in *Pisces* with the caudal vein and resolved in part into the renal-portal venous system. In other *Vertebrata* they disappear except at their anterior and posterior extremities—the ductus Cuvieri then forming the venae cavae superiores which receive the jugular and subclavian veins. A vena cava inferior is developed in *Amphibia* and higher Vertebrata. It is connected anteriorly with the sinus venosus or, where this is absent, with the right auricle. In *Amphibia* and *Reptilia* it receives the efferent renal veins and the hepatic veins; in *Aves* and *Mammalia* the veins of the hind-limb as well; and in

the latter the caudal vein. A renal-portal circulation or supply of venous blood to the kidneys exists in all *Amphibia*, in *Reptilia* except *Chelonia*, and possibly in *Aves*, in addition to the arterial supply from the aorta. The blood from the hind-limbs passes in *Amphibia* partly through the renal-portal system, and partly through an epigastric vein, as it does in *Crocodylia*, through the renal-portal alone in *Lacertilia*, through an epigastric alone in *Chelonia*. The epigastric vein lying in the ventral wall of the abdomen exists in *Amphibia* and *Reptilia*, and in the embryos of *Aves* and *Mammalia* where it is lost in the adult. Primitively double, it rarely remains so (*Chelonia*, *Crocodylia*), but becomes single by the atrophy of one of the two veins. Its anterior end is connected with the hepatic portal system. Its posterior extremity is variously connected to the renal-portal system and hind-limbs (*supra*), but in the embryos of *Sauropsida* and *Mammalia* to the allantois, a foetal membrane, which is developed as a ventral out-growth of the posterior extremity of the mesenteron. And it may be noted that veins from the allantoid bladder, the homologue of the allantois, fall into the epigastric in *Amphibia*.

The arteries and veins are connected peripherally by the capillary vessels which form networks in the various tissues, some few, e.g. epidermis, epithelium, cartilage, &c. excepted. The capillaries have a simple epithelial wall, the smaller arteries and veins add a coat of transverse, i. e. circularly disposed non-striated muscle cells, to which the larger vessels superadd coats of connective tissue. The larger vessels are formed apparently from solid cords of cells, the central cells being set free and becoming blood corpuscles, the peripheral being converted into the walls of the vessels. Capillaries are formed in many instances by the development of a vacuole in a branched cell, the branches and vacuoles of adjoining cells becoming connected. Certain of the veins in higher Vertebrata possess valves which ensure a flow of blood in a constant direction. The blood consists of a plasma containing in suspension 'white' corpuscles or leucocytes which possess the power of amoeboid motion. The red haemoglobin-containing corpuscles or haematids are oval and nucleated in all Vertebrata except *Mammalia*, where they are circular and non-nucleated. They have a fixed outline. The leucocytes are formed for the most part in the lymphatic system (*infra*).

A spleen—a structure with a lacunar blood-vascular circulation—is found in all Vertebrata in connection with the mesogastrium. It possesses a blood-making function. There is also a lymphatic system of spaces and vessels formed in the mesoblastic tissues. The lymphatic system communicates with the coelome, and with the blood-vessels at certain spots either anteriorly (*Mammalia*) or anteriorly and posteriorly. Contractile lymph hearts are sometimes found close to the points of communication except in *Mammalia*. The lymphatic channels of the intestine and mesentery con-

stitute the absorbent or lacteal system. The larger vessels have well defined and independent walls, and in *Aves* and *Mammalia* valves like the veins. A large lymphatic vessel or reservoir, the ductus thoracicus, lies at the back of the thorax in *Aves* and *Mammalia*. It communicates with the two venae cavae superiores in the former, with the left one only in *Mammalia*. There is a lymph sinus in the same position in *Amphibia* and *Reptilia*. This sinus, like the duct, receives lymph from the hinder extremities, body walls and viscera. A lymphatic tissue, known as adenoid or reticular tissue, consisting of a net-work of cells, which bud and form lymph or white corpuscles, is greatly developed in the submucous coat of the intestine, and as masses or lymphatic glands here and there in the course of the lacteal and lymphatic vessels of higher Vertebrata.

The supra-renal bodies usually found in close apposition with the kidneys or genitalia, appear to consist of a portion (the medulla in higher forms) derived from the sympathetic nervous ganglia: and another portion, the cortex, derived from mesoblast, and in higher forms in immediate connection with the vena cava inferior and cardinal veins. The two parts remain separate in *Elasmobranchii*—the mesoblastic as the inter-renal body, the nervous as a series of paired bodies connected with the intercostal branches of the aorta<sup>1</sup>.

All Vertebrata possess a paired kidney. This organ with its duct has a complex history. The primitive kidney duct is known as the 'segmental duct'; it extends from the anterior region of the coelome to the primitive cloaca, opening into both. This duct in *Ichthyopsida* becomes divided except in *Cyclostomi* (? *Teleostei* and *Ganoidei*; see general account of *Pisces*) into two ducts, a Müllerian duct with a coelomic aperture, and a closed Wolffian duct. In the *Amniota* the two appear to develop partially, or in some cases perhaps wholly, independently of each other. With the fore part of the segmental duct is connected in the embryos or larvae of *Ichthyopsida* except *Elasmobranchii* a pronephros. It has the form of 1-5 tubes produced from the extremity of the segmental duct, inclosed in a special section of the coelome, with a vascular ridge or glomerulus opposed to the apertures of the tubes. It appears to atrophy in all cases. There is a somewhat similar structure in the Chick, connected however with the Müllerian duct and devoid of a glomerulus. A mesonephros, or Wolffian body, is developed in all Vertebrata posteriorly to the pronephros, but it is only an embryonic organ in the *Amniota* with the exception of its genital region in the male (*infra*). It consists of a series of tubules derived from the peritoneum or mesoblast opening into the segmental duct in *Cyclostomi*;

<sup>1</sup> Weldon believes that the supra-renal bodies represent the pronephros in *Cyclostomi*; the pro-plus part of the meso-nephros in *Teleostei*; a part of the mesonephros in secondary connection with the sympathetic ganglia in *Elasmobranchii* and higher *Vertebrata*. P. R. S. xxxvii. 1884; see also Q. J. M. xxiv. 1884.



into the Wolffian or mesonephric duct in other types (*Teleostei* and *Ganoidei*?). These tubules are arranged segmentally, one to each segment in the embryo *Elasmobranch*, and the adult *Myxine*, and *Gymnophiona*, but in other types they are, especially in the posterior segments of the body, more numerous than the segments. Secondary and tertiary tubules are added to those first formed. Each tubule is typically composed of (1) a ciliated funnel or nephrostome opening into the coelome; (2) a Malpighian body, i. e. a dilatation with a tuft of blood-vessels projecting into it; (3) a coiled glandular tube or tubulus uriniferus; and (4) a collecting tube. The nephrostomata persist in *Elasmobranchii* and *Amphibia* in connection with more or fewer of the primary tubules. Present in the embryo in many other instances, they are always aborted at a certain stage of growth. The anterior part of the mesonephros becomes connected with the testis in the male of *Elasmobranchii*, certain *Ganoidei* (? all), all *Amphibia* and *Amniota*. The corresponding portion in the female is modified or nearly aborted in the *Ichthyopsida*, and persists in *Amniota* as a variable rudiment (ep-oophoron of *Mammalia*). The posterior non-sexual part of the mesonephros becomes partially or wholly independent of the fore part in *Elasmobranchii* and communicates with the Wolffian duct by one or more independent ureters, specialised collecting tubes. In *Amphibia* it remains continuous with the sexual region, but is strongly marked off from it in *Urodela*; and its ducts sometimes tend to unite *inter se* before they fall into the Wolffian duct. The permanent kidney of the *Amniota* is a metanephros. It appears to be 'a specially differentiated posterior section of the mesonephros' (Balfour) developing at a later period, comparable to the posterior region of the mesonephros of *Elasmobranchii*. The ureter in this case is an outgrowth of the Wolffian duct, the collecting tubes of the ureter; the gland tubes (tubuli uriniferi) and Malpighian bodies are formed independently (?) out of the mesoblast. There are no nephrostomata. Remnants of the non-sexual part of the mesonephros may persist (par-epididymis, par-oophoron, of *Mammalia*).

The primitive connection of the segmental duct or of its derivatives, the Müllerian and Wolffian ducts, as well as of the ureter in *Amniota* with a cloaca common to both anus, urinary and genital ducts, is retained in *Cyclostomi*, *Elasmobranchii*, and *Dipnoi* among *Pisces*, in all *Amphibia* and *Sauropsida* and in the *Prototheria* among *Mammalia*. The cloaca is divided into an anal section and a urogenital section in all *Ganoidei*, many *Teleostei* and nearly all *Mammalia*. In *Holocephali* and a few *Teleostei* among *Pisces*, and a few female *Mammalia* the anal, genital and urinary apertures are independent. The anal aperture of *Mammalia* is always placed behind the genito-urinary apertures, in front in all the other classes. But in all Vertebrata the urinary aperture is anterior to the genital. The ureters in *Mammalia*, except *Prototheria*, open into a urinary bladder, a persistent

part of the allantois (*infra*). The urinary bladder so called of *Teleostei* and *Ganoidei* is a dilatation or outgrowth of the urinary ducts themselves.

The sexes are distinct in Vertebrata. Hermaphroditism may occur as an abnormality, as a rule only in one Anuran and two Teleosteans. The testis and ovary are alike derived from a thickened ridge of coelomic epithelial cells. They are as a rule retained in the coelome, but in many *Mammalia* the testes shift their position either temporarily or permanently and are lodged in a pouch or caecum of the body wall which includes them and a portion of the coelome, and is known as scrotum. The sperm is shed into the coelome in *Cyclostomi*, in *Dipnoi* (?) and perhaps some *Ganoidei*: but as a rule it is transported to the exterior by a network of tubes derived from and in connection with the anterior region of the mesonephros and thence through the Wolffian duct. This region of the mesonephros persists in the *Amniota* and forms the coni vasculosi and vasa recta, while the Wolffian duct becomes epididymis and vas deferens. Remnants of the Wolffian duct are sometimes found in female *Amniota* (tube of ep-oophoron; duct of Gärtner in *Mammalia*). The ova are typically shed into the coelome and are thence transported outwards by the Müllerian duct, which is known as Fallopian tube or oviduct. It has a wide coelomic aperture, and its walls for part of its course may become richly glandular, secreting albumen and sometimes an egg-shell, whilst its lower section may be dilated and as uterus<sup>1</sup> retain the ovum while it undergoes development. Remnants of the Müllerian duct may be present in the male (hydatid of Morgagni: uterus masculinus, p. 30, *ante*, of *Mammalia*), but it is only in one Toad, *Alytes*, that it is connected directly to the testis and acts as vas deferens. It *may* so act in *Dipnoi* and some *Ganoidei*, but in this case it is not connected to the testis. In the male *Gymnophiona* and *Bufo* it persists and has a glandular function. Exceptions to the typical condition are (1) *Cyclostomi* and the Eels (*Muraenidae*), where sperm and ova are conducted outwards by an abdominal pore or pores (*infra*) as are the ova in a few *Teleostei*, e.g. Salmon: (2) *Lepidosteus* among *Ganoidei* and the *Teleostei*, where there are genital ducts continuous with the glands (see p. 89). Copulatory organs are formed as processes of the pelvic fins in *Elasmobranchii* and *Holocephali*; as organs varying in character attached to the cloaca in *Amniota*. In male *Mammalia*, except *Prototheria*, the organ is traversed by a continuous genito-urinary canal; similar but rudimentary organs are found in the female, and in some female *Mammalia* the clitoris (homologue of the penis) is traversed by the urinary canal (p. 36, *ante*). Accessory glands or diverticula are formed in connection with the male genito-urinary duct in most *Mammalia*, some of which have corresponding structures in the female.

<sup>1</sup> This name is also generally given to the lower section of the oviduct in *Aves*, &c.

All the viscera except the nervous centres are contained in a body cavity or coelome inclosed between the body wall and their outer surfaces. It is lined by an epithelium and a delicate layer of connective tissue known as peritoneum. The viscera are kept in position and are sometimes freely suspended by dorsal folds of this peritoneum, known by special names according to the organ they support,—mesogastrium (stomach), mesentery (intestine), mesorchium (testis), mesovarium (ovary); besides several ligaments, e. g. those of the liver. Properly speaking the coelome is a paired cavity (p. 334), but traces of its paired character, due to the presence of a ventral in addition to a dorsal mesentery, are rarely found, e. g. in *Dipnoi*. A section of the coelome is inclosed to form the pericardium, and in *Mammalia* a thoracic region, including heart and lungs, is separated from an abdominal region containing the remaining viscera, by a fibro-muscular diaphragm. The coelome usually communicates with the lymphatic system. And it may open externally in one of three ways: by posteriorly placed abdominal pores in *Pisces*, with the exceptions of some *Elasmobranchii* and the vast majority of *Teleostei*, or by peritoneal canals in some *Chelonia* and the Alligator: through the nephrostomata when present: and through the Müllerian ducts of the female.

Each ovum in Vertebrata is surrounded during growth in the ovary by one or more layers of abortive ova, the cells of the tunica granulosa, the whole being known as the Graafian follicle. It is impregnated externally to the body in *Cyclostomi*, *Ganoidei*, *Teleostei* and *Dipnoi*, and in *Anura* among *Amphibia*; internally in all other Vertebrata. There are three ovular membranes known, (1) an external or vitelline persistent in *Aves*, (2) a middle striated membrane or zona radiata persistent in *Teleostei* and *Mammalia* and probably *Amphibia*, and (3) a delicate internal membrane present in *Reptilia* and *Mammalia* (? in *Teleostei*). But when ripe the ovum may be devoid of membranes as in *Elasmobranchii*. A single micropyle is present in *Petromyzon*, and many *Teleostei*, several in *Acipenser*. An adventitious coat of albumen is secreted round the ovum in *Elasmobranchii*, *Holocephali*, *Dipnoi* (*Protopterus*), *Amphibia*, *Sauropsida* and some *Mammalia*, to which may be added an egg-shell as in *Elasmobranchii*, *Holocephali*, and *Sauropsida*. The ovum contains much food yolk in *Elasmobranchii*, *Holocephali*, and *Sauropsida*; also in *Teleostei*. It is large in the three first named groups, small in the last named, but segmentation is partial in them all. The ovum is smaller in other groups, and segmentation is either very unequal or, as in *Mammalia*, nearly equal. The gastrula is much modified. In *Petromyzon*, *Acipenser* and *Amphibia* there is a distinct invagination; one less distinct in *Elasmobranchii*; while a trace only of it is preserved in *Sauropsida* and *Mammalia* in the primitive streak which lies at the posterior end of the medullary groove.

There is an external yolk sac opening into the intestine with which its

walls are continuous in *Elasmobranchii*, *Lepidosteus*, *Teleostei*, and *Sauropsida*. It is known as umbilical vesicle in *Mammalia*. The part of it within the coelome frequently persists for a considerable period after birth or permanently as the omphalo-mesenteric duct (ductus vitello-intestinalis), especially in water-birds. The yolk is contained within the alimentary canal itself in other types, so far as is known. The embryo of *Sauropsida* and *Mammalia* is provided with two foetal envelopes, the amnion and the allantois. The former is produced by the upgrowth of a fold of the body wall (somatopleure). The fold surrounds the embryo on all sides and gradually incloses it. Fusion takes place on the dorsal aspect, and the inner limbs of the fold thus form a sac containing the embryo, and filled by a liquor amnii. The outer limbs are dissociated at the same time from the inner, and with the part of the somatopleure beyond the point where the fold first originated, form a second or outer sac, the false amnion or subzonal membrane. The allantois is a ventral diverticulum of the posterior end of the mesenteron. It grows out into the space between the true and false amnion, and eventually comes into contact, except in a few instances, with either the whole or a part of the inner surface of the false amnion. The allantois is essentially a respiratory structure and is supplied with blood by two vessels, the umbilical arteries, derived from the iliac arteries. Its blood is returned at first by two umbilical veins homologues of the epigastric veins (*supra*, p. 353). One of them atrophies subsequently. In most *Mammalia* the 'chorion' formed by the union of the false amnion with the allantois comes into special relations with the uterine blood-vessels forming a 'placenta.' In some *Mammalia* the yolk sac is also in contact and fuses with a portion of the false amnion.

The majority of Vertebrata are oviparous. *Mammalia* except *Prototheria* are viviparous, and instances of viviparity occur among *Lacertilia*, *Ophidia*, Urodele *Amphibia*, *Teleostei* and *Elasmobranchii*.

There are two divisions of Vertebrata, the *Amniota* and the *Anamniota* s. *Ichthyopsida*.

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*Mucous membrane of nose in Pisces and Amphibia*, Blaue, Arch. f. Anat. u. Physiol., Anat. Abth., 1884. *Phylogeny of Vertebrate eye*, Dohrn, Mitth. Zool. Stat. Naples, vi. 1885. *Ear*, Retzius, Gehörorgan der Wirbelthiere, Stockholm, i.

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*Comparative anatomy of Tongue*, Ludwig Ferdinand, Königler Prinz von Bayern, München, 1884.

*Thymus and Thyroid, development*, Fischelis, A. M. A. xxv. 1885; cf. Dohrn, Mitth. Zool. Stat. Naples, vi. 1885.

*Blood corpuscles of Vertebrata*, Gulliver, P. Z. S. 1875.

*Cloaca, &c.*, Spooß, Embryol. u. Vergleich. Anat. der Kloake u. der Urogenital-system bei den höheren Wirbelthieren, Helsingfors, 1883.

*Development of organs in general*, Balfour, Comparative Embryology, ii. 1881, Chapters on Organogeny; Foster and Balfour, 'Embryology of Chick,' ed. 2, by Sedgwick and Heape, London, 1883.

### AMNIOTA s. *Allantoidea* s. *Abranchiata*.

THE embryo is provided with the two foetal envelopes known as the amnion and allantois. Branchiae are never developed.

Three classes are included in this division of Vertebrata, the *Mammalia*, *Aves* and *Reptilia*. The two latter are very closely connected in descent, and may be grouped together as *Sauropsida*.

### CLASS MAMMALIA.

*Air-breathing warm-blooded Vertebrata in which the epidermis develops hairs over a greater or less extent of the surface of the body: which are viviparous with the exception of Prototheria, and always nourish their young for longer or shorter periods after birth with the secretion of lacteal or mammary glands. There are two occipital condyles to the skull and seven cervical vertebrae. The coelome is divided into a thoracic and abdominal portion by a muscular diaphragm. The aorta is single and bends over the left bronchus; and the red corpuscles or haematids are non-nucleated. The rectal and urogenital apertures are typically separate, and the former placed behind the latter.*

The minute structure and the character of the hairs vary much in different Mammals, and on different parts of the body in the same Mammal. The hairy coat is scanty in some instances, e. g. *Sirenia*, *Hippopotamus*; and in *Cetacea* is restricted to the snout, where it may be present only in the foetus. The edges of the eyelids are protected by a single row of hairs—the eye-lashes or cilia: and the snout in most Mammalia has a few stout tactile hairs, or vibrissae, connected with an abundant nerve-supply. Certain hairs, e. g., those of the mane and tail in *Equidae*, the vibrissae, appear to be persistent, but as a rule the coat is shed both before and after the winter season: the winter coat being thicker and sometimes, as in Arctic Mam-

malia, white in colour. Epidermic structures in the shape of nails, claws, or hoofs, protect the terminal joints of the hand and foot, except in *Cetacea* and certain fingers in the *Chiroptera*. Other instances of epidermic skeletal structures are the imbricated scales covering the body and tail in *Manis* among *Edentata*, or the under side of the tail in certain flying Rodents (*Anomalurus*); the flat scales placed edge to edge on the tails of some Rodents, e. g. the Beaver (*Castor*), of certain *Insectivora* (*Ptilocercus*) and *Metatheria*; the spines of some *Insectivora* (the Hedge-hog, *Erinaceus*), *Rodentia* (the Porcupines, *Hystriidae*), and of *Echidna* among *Prototheria*; the horns as opposed to their bony supports, the horn-cores, of hollow-horned *Ruminantia* (Cows, Sheep, Goats, Antelopes); the nasal horns of the *Rhinoceros*; the thickened epidermis of the *callosities*, hair-less patches of skin occurring in different regions of the body, e. g. over the ischial tuberosities in Apes; and the whale-bone plates implanted in the gum of the Baleen Whales. A bony dermal skeleton is found only in the *Dasypodidae* and the extinct *Glyptodontidae* among *Edentata* in the shape of scutes or plates covered by a thickened epidermis. The antlers, or bony frontal outgrowths, of the Deer, which are shed and renewed annually, must be reckoned under the same head. The glands of the integument are the following: sebaceous glands connected with the roots of the hairs; sudoriparous glands opening on the surface of the skin, and rarely wanting, e. g. in *Cetacea*, as well as certain other special glands, e. g. the Meibomian glands of the eyelids, the lacrymal glands; and glands known as sub-orbital, anal, inguinal, &c., according to position. The mammary glands characteristic of the class, which secrete the milk, are probably modified skin-glands. Their ducts open on an area which is usually raised into a more or less prominent papilla—the true teat. In *Ungulata*, however, this area lies at the bottom of a tubular depression produced by the growth of a surrounding wall forming a false teat. The number of teats present varies according to the number of young usually produced at a birth, from two, e. g. in the *Primates*, to twenty-two as a maximum in *Centetes* among *Insectivora*. When numerous they usually extend in two rows from the pectoral to the inguinal region: when few they are restricted to the pectoral, abdominal or inguinal regions. In all Mammalia except the Hare, *Lepus timidus*, a layer of adipose tissue, the *panniculus adiposus*, sometimes attaining great thickness as in the blubber of the *Cetacea* and Seals, is interposed beneath the skin and underlying muscles and bones; and in most instances there is a well developed system of skin-muscles.

The bones of the skull, with the exception of the lower jaw, the auditory ossicles, and hyoid, are united by sutures which persist as a rule. The two occipital condyles are formed by the exoccipital bones, but in some Mammals in part by them, in part by the basi-occipital. The prae-maxillary, maxillary and palatine bones possess palatal plates which con-

stitute the hard palate and separate the narial and buccal cavities. There are distinct lacrymal and tympanic bones, and the latter is often dilated into a tympanic bulla and prolonged outwards as an external bony meatus. The periotic bones anchylose *inter se*, and form a compact periotic mass which is either connected by suture to neighbouring bones or is partially or wholly free. The carotids enter the cranial cavity, either by piercing the periotic mass or passing between it and the base of the skull. The rami of the lower jaw articulate directly with the squamosal bones. Each ramus consists in the adult of a single bone which unites with its fellow at the mental symphysis either by suture or by ankylosis. It is derived in Man from four centres of ossification which correspond respectively to a mento-meckelian, dentary, splenial and coronoid element. There are three auditory ossicles, a malleus, incus and stapes, which represent, the first-named, the articular element of the lower jaw, the second, the quadrate bone, and the third the columella auris of the *Sauropsida* and the hyomandibular of Fish. The cervical vertebrae are reduced to six in the Manatee, in *Choloepus Hoffmanni* among *Edentata*, and increased to nine in *Bradypus tridactylus* in the Order named. Cervical ribs are represented only by centres of ossification often absent. The rib-element is often wanting in the seventh cervical vertebra; it is sometimes present abnormally, however, as a free rib. The cervical is always sharply marked off from the dorso-lumbar series of vertebrae. The latter series varies in number between the extremes of 14 in the Armadillo (*Edentata*) and 30 in *Hyrax*. The number is often constant within the limits of a given group, e. g. to 19 in *Artiodactyla* among *Ungulata*. The dorsals are usually 12 or 13. There may be but a single sacral vertebra as in *Perameles* among *Metatheria*, or more commonly two; and the number is generally increased by the ankylosis of a variable number of anterior caudal vertebrae, more rarely of a posterior lumbar. A sacral region is not defined in *Cetacea* and *Sirenia* where the ilia either fail to reach the backbone, or else are absent. The caudal series may be reduced to 3-5 vertebrae in Man and the higher Apes, but is generally numerous. The largest number known, 46, occurs in *Manis macrura* among *Edentata*. The two first cervical vertebrae articulate one with the other, and with the skull by synovial joints: the remaining vertebrae by fibro-cartilaginous discs, in the axis of which is found a remnant of the notochord, the *nucleus pulposus*. The centra of the vertebrae are usually flat, but in the *Ungulata* those of the cervical region in particular are more or less opisthococelus. The ribs are divided into a vertebral and sternal section, the latter sometimes cartilaginous, sometimes ossified. Some of the posterior ribs may lose their connection with the sternum, and also with the vertebrae, and in the latter case are known as floating ribs, e. g. in *Cetacea*. The sternum undergoes, at a certain stage of growth, transverse segmentation into a series of sternebrae which may or may not

remain separate. It is divisible into three regions—a praesternum or manubrium sterni, with which the clavicles and first pair of ribs articulate; a mesosternum composed of a variable number of sternebrae with a pair of ribs articulating between every two adjoining sternebrae, the last sternebra, however, sometimes, e. g. in Man, giving attachment to more than one pair of ribs; and a xiphisternum, sometimes cartilaginous, sometimes ossified, representing a sternal region in which the original connection with ribs has been aborted. The fore-limbs are never absent; the hind-limbs are wanting in *Cetacea* and *Sirenia*, or reduced to rudiments of a femur, and in the Greenland Whale of a tibia as well. The scapula has the true anterior border or *spine* placed on the external surface of the bone, and the apparent anterior border is a new development. The coracoid is a small process which forms a portion of the glenoid cavity but fails to reach the sternum. The clavicle, originally continuous with the acromion or free extremity of the spine, articulates with the praesternum and may either be represented by ligament at each end, e. g. many *Carnivora* and *Rodentia*, or be absent altogether, e. g. *Ungulata*, *Cetacea*. The interclavicle is fused with the praesternum; it may be partially converted into ligament or atrophied away completely. The ilium slopes downwards and backwards from its articulation with the sacrum. The pubes meet in a ventral symphysis with rare exceptions (e. g. the Mole, *Talpa*); the ischia on the contrary have no symphysis, or only just touch one another. There is a well-developed heel, or os calcis, formed by the growth of the fibular tarsal bone. The digits are limited to three phalanges in addition to the metacarpal and metatarsal bones, except in the hand of some *Cetacea*, where the second and third fingers have a larger number. The bones of Mammalia, with the exception of those of the skull, of the sternebra, and save in a few cases of the carpus and tarsus, possess epiphyses or separate caps of bone to their free extremities or articulating surfaces.

The cerebral hemispheres are the largest part of the brain: their surface is often convoluted, and they are connected by a system of transverse commissural fibres, the corpus callosum, as well as by longitudinal fibres, the fornix. Their ventricles are large and form an anterior and a descending cornu with the addition in the higher *Primates* of a posterior cornu. The olfactory lobes are usually small, and are absent in toothed Whales: the olfactory nerves very numerous, and perforating the ethmoid bone in small bundles so as to give it a sieve-like aspect (the cribriform plate). The anterior commissure is small. The pineal gland has no connection with the dura mater or the skull; is small, and its base alone contains nervous substance. The optic lobes are small, solid, and divided by a transverse fissure into four lobes—the corpora quadragemina. The lateral lobes of the cerebellum are large and connected by a pons Varolii, or set of ventral transverse fibres. The angle, or bend, between the



medulla oblongata and spinal cord is generally considerable. The brain of the gigantic extinct Mammalia from the American Eocene was remarkably small. The cast of it passes with ease through the neural canal of the vertebrae, and is Lacertilian in aspect, with large olfactory and small cerebral lobes. The sympathetic cord accompanies the vagus nerve in the neck, and has never more than three cervical ganglia. There are no sensory hairs to the cells of the olfactory epithelium. The eye is rudimentary in *Platanista* among *Cetacea*: rudimentary or absent in certain burrowing *Rodentia* and *Insectivora*. There is often a tapetum lucidum external to the retina, composed of fine parallel waved connective tissue fibres as in *Ungulata*, or of cells as in *Carnivora*. There is, except in *Primates*, a suspensory or choanoid muscle to the eye internal to the circle of recti muscles; and in *Carnivora* it is broken up into four muscles. The nictitating membrane is present except in *Primates* and *Cetacea*, but has no special muscle. The eyelids are reduced in *Sirenia* to a circular fold which contracts to a point. The *Cetacea* have no lacrymal glands. In the inner ear the cochlea is spirally convoluted. The external aperture of the ear is a simple aperture in most aquatic and burrowing Mammals, but in others it has a well-developed and characteristic pinna. For the ear-bones, see p. 361.

A few Mammals are edentulous as the Ant-eaters (*Myrmecophaga*, *Cyclothurus*, and *Manis*); or there may be transitory teeth which never cut the gum (Baleen Whales). Teeth are limited to the prae-maxillary, maxillary, and mandibular bones. They are implanted in sockets by one or more roots, and are attached to the socket by a fibrous alveolo-dental membrane, and ankylosis is said to occur only with the incisors of certain Shrews (*Insectivora*). The teeth are either simple and alike in shape (homodont), or differ from one another (heterodont), and are then termed in a complete series incisors, canines, praemolars and molars. When their number is limited, as is usually the case, the full dentition includes 44 teeth, that is to say 11 teeth on each side above and below, viz. 3 incisors, 1 canine, 4 praemolars, and 3 molars, as in the Pig among *Ungulata*, and the genera *Gymnura*, *Myogale* and the Mole (*Talpa*) among *Insectivora*. But in living Mammals the number generally falls below this maximum. In homodont dentitions, however, the number is often great, e. g. 100 in *Priodon* among *Edentata*, 200 in *Delphinus* among *Cetacea*. There are two sets of teeth, a milk and a permanent, in the majority of Mammals, hence termed Diphyodonts, as opposed to Monophyodonts, which have but one set. It is probable that the single set of teeth of Monophyodonts corresponds to the permanent set in Diphyodonts. The milk dentition includes incisors, canines, and deciduous (prae)molars which are replaced by corresponding teeth in the permanent set as a whole or in part. The milk dentition is sometimes shed *in utero* (Guinea-pig), absorbed at an early

period without cutting the gum (Seal), or aborted altogether (e. g. Rat and some other Rodents). The teeth are composed of dentine capped above the gum by enamel, partially or completely, and in the root or fang coated with cement. The exposed portion, or crown, varies much in character, and when folded the interval between the folds is often filled with cement. Enamel is entirely absent in *Edentata* and the Dugong among *Sirenia*. Dentine with vascular channels (vaso dentine) makes up the whole tooth in most *Edentata*; and is found in the Manatee (*Sirenia*) and Tapir (*Ungulata*). The pulp sometimes grows throughout life, e. g. incisors of Rodents, teeth of *Edentata*; or up to a certain age, e. g. molars of Horse and some Rodents; and in *Cetacea* it either atrophies or is calcified.

The mouth has soft fleshy lips, except in *Cetacea* and *Prototheria*. The tongue is well developed, is rich in glands, in tactile papillae, and possesses special gustatory bulbs lodged at the sides of certain papillae or folds. There is a soft palate or *velum pendulum palati*. Three pairs of glands—parotid, submaxillary, and sub-lingual—open into the oral cavity. They are wanting in *Cetacea*, and much reduced in Seals. The labial glands are small in size. The stomach is always sharply marked off from the oesophagus, and is generally of complicated structure in vegetable feeders. The small intestine is of considerable length, and is as a rule separated from the large intestine by an ileocaecal valve, rarely wanting as in some *Carnivora*. The caecum is sometimes absent, e. g. some *Carnivora*, and is of great size in most herbivorous Mammals. It is small, and double only in the two-toed Sloth among *Edentata*. The large intestine (colon) is of great relative length: the rectum is very short, and the anus is posterior, i. e. dorsal to the urogenital aperture. The whole tract is remarkably rich in glands, and the small intestine possesses innumerable minute villi. The liver is often complex. The ligamentum teres, or remnant of the umbilical vein, divides it into a right and left lobe. The latter is sometimes subdivided into a central and lateral lobe. The right lobe is usually subdivided in a similar manner, and often has a caudate lobe cut off from the lateral lobe and fitting on the right kidney and a Spigelian lobe projecting behind the entrance of the portal vein. A gall-bladder is rarely absent (Horse, *Cetacea*, some Rodents) and is always a diverticulum of the hepatic duct. The pancreas is usually compact, but is a scattered gland in some Rodents, e. g. Rabbit, Rat, and its duct as a rule unites with the hepatic duct to form a ductus communis choledochus.

The red-blood corpuscles are biconcave discs, circular in outline, elliptical in the Camel and Llama. Their size varies much, and in one and the same group are largest in the larger species. They are largest in the Elephant ( $\frac{1}{2} \frac{1}{4} \frac{1}{5}$ "), some *Cetacea* and *Edentata*, smallest in the *Tragulidae* among *Ungulata* ( $\frac{1}{12} \frac{1}{8} \frac{1}{5}$ "). The heart has two auricles and two ventricles. The right auricle has no sinus venosus, and the auricular septum is marked

by a fossa ovalis, indicating the position of the foramen ovale in the foetus by which blood passed from the right to the left auricle. The right, like the left, auriculo-ventricular valve is membranous, and consists of three flaps (hence tricuspid), one of which, the septal flap, is attached to the septum of the ventricles. The aorta crosses the left bronchus, and the right sub-clavian artery represents the corresponding, i. e. the fourth aortic arch of the right side. The sub-clavians and carotids arise from the aortic arch in various ways. The blood of the left vena cava superior is frequently carried across to the right cava superior by a transverse vein, and the cardiac end of the vessel (= coronary sinus) alone persists receiving the coronary veins of the heart, and sometimes, as in many *Ungulata*, a left azygos vein. The veins of the extremities at least possess valves, structures wanting, however, in *Cetacea*. The lymphatic system is well developed, and there are numerous lymphatic glands. The thoracic duct opens into the left subclavian vein. The lymphatic vessels have valves. The tonsils, masses of adenoid tissue at the entrance to the pharynx, are peculiar to Mammals. For the hibernating gland, see pp. 2 and 4.

The nostrils which lead to the air-passages are double, except in some toothed Whales. The entrance to the trachea is protected by an epiglottis. There is a larynx composed of two arytenoid cartilages, a single thyroid and cricoid cartilage, and provided with well-developed muscles. The cartilage rings of the trachea are incomplete, posteriorly or dorsally. The trachea divides into two principal bronchi. There is but a single bronchia rising *above* the entrance of the pulmonary artery. This eparterial bronchia is present either on both sides or on the right only, e. g. *Primates*, and in some instances it rises on the right side from the trachea, e. g. in *Artiodactyle Ungulata*. It is wanting in the Porcupine (*Hystrix*). There are 9 hyparterial bronchia. The lungs are suspended freely in pleural sacs, and they are frequently lobed, especially on the right side. The respiratory capillaries are distributed on the walls of the lobed air-cells, or alveoli, in which the ultimate branches of the bronchiae terminate.

The kidneys sometimes retain the embryonic lobed character (*Cetacea*, the Seals, Bear, &c., among *Carnivora*), but, as a rule, the lobes fuse completely at their outer extremity, while at their inner they unite to form the Malpighian pyramids, upon which the tubuli uriniferi open. These pyramids project into the dilated upper ends or pelves of the ureters. The blood-vessels of the gland and of the surrounding adipose tissue anastomose, but there is no functional renal-portal system. The ureters enter the dorsal aspect of the urinary bladder, either near its apex or more usually its fundus (=base). This bladder is a remnant of the urachus, or internal portion of the allantois. It has an outlet or urethra which, in the male, unites with the genital ducts to form a well developed uro-genital canal, while in the female the urethra and genital outlet alike fall into a shallow

depression, the vestibule which represents the urogenital canal. In some female *Rodentia*, *Insectivora* and Lemurs, the female urethra perforates the clitoris (*infra*), and is entirely separate from the genital outlet. The testes may be retained within the abdomen, e. g. Elephant, or pass at the breeding season into a temporary scrotum, e. g. some Rodents, or be lodged permanently in a scrotum. The termination of the vasa deferentia are often furnished with vesiculæ seminales. Prostatic and Cowper's glands often open into the urogenital canal which enters an erectile intromittent organ or penis, composed of two corpora cavernosa, and of a corpus spongiosum inclosing the canal and forming a terminal glans. The two former bodies are attached to the ischia, except in the Sloths and Ant-eaters, among *Edentata*, in the *Meta-* and *Proto-theria*, and the latter is absent in the *Edentata* just named. The ovaries are relatively small: the oviducts have wide abdominal apertures, usually fringed (=fimbriate), and are differentiated into an oviducal portion (=Fallopian tube), a muscular uterine portion, and a canal or vagina. But the characters of these parts vary in the three chief divisions of Mammalia. The penis of the male is represented in the female by the clitoris. The ovum is relatively small: the granulosa cells are very numerous, and, during the growth of the Graafian follicle, a liquid—the liquor folliculi—appears in the centre of the follicle, while the granulosa cells occupy the periphery, and bear the ovum within a small projection, or discus proligerus. Segmentation is total, but slightly irregular.

The class Mammalia is divisible into three sub-classes—*Eutheria*, *Metatheria*, and *Prototheria*—which are the equivalents of De Blainville's three groups—*Monodelphia*, *Didelphia*, and *Ornithodelphia*.

'Mammalia,' Flower, Encyclopaedia Brit. (ed. ix.) xv; Giebel and Leche Bronn's Klass. und Ordnungen des Thierreichs vi, Abth. v. (in progress); Huxley, P. Z. S. 1880. *Nails, Claws, Hoofs*, Boas, M. J. ix. 1883; Gegenbaur, M. J. x. 1885. *Types of molar Teeth*, Cope, Journal Acad. Nat. Sc. Philadelphia, viii. 1874–81. *Mammary glands*, Klaatsch, M. J. ix. 1883. *Sublingua*, Gegenbaur, M. J. ix. 1883. *Tongue*, Id. M. J. xi. 1886. *Osteology of Mammalia*, Flower, ed. 3 by Gadow, 1885.

*Mammalian Descent*, W. K. Parker (Hunterian Lectures), London, 1884. *Mammals in relation to primæval Times*, O. Schmidt, Internat. Ser. liv. 1885.

### SUB-CLASS EUTHERIA.

THIS sub-class contains all the orders of existing Mammalia except two. Its general characters are those typical of Mammalia, from which the two other sub-classes deviate in certain respects. The distinctive features of the reproductive system and of development are as follows. The scrotum, when present, is behind the penis. The uteri either remain distinct

throughout their entire length (uterus duplex), e. g. Rabbits; or fuse distally having a common aperture into the vagina, but retaining an internal septum in the fused portion (uterus bipartitus), e. g. most *Rodentia* and many *Chiroptera*; or they fuse throughout the greater part of their whole length having a common cavity, and leaving only the oviducal portions of the tube distinct (uterus bicornis), the commonest form of all (*Ungulata*, *Carnivora*, &c.); or finally the uteri are completely fused (uterus simplex) as in Man and Apes. The vagina is always single, and opens, as a rule, into a vestibule or urogenital sinus common to it and the urethra, except where the clitoris is perforated by the latter. The yolk sac, or umbilical vesicle, is large in *Rodentia*, *Insectivora*, and *Chiroptera*, and fuses with that part of the subzonal membrane left free by the allantois; in other Eutheria it is small, and does not reach the subzonal membrane. The allantois always fuses with a greater or less proportion of the subzonal membrane, and renders it vascular, forming the foetal placenta. This placenta is in relation with the uterine walls which become thickened and more vascular during pregnancy, forming the maternal placenta. The foetal placenta is furnished with vascular villi, which are either simply in contact with corresponding depressions in the maternal placenta, or else fuse with that structure. If at the birth of the young the maternal placenta persists, or only loses epithelium, the placenta is said to be non-deciduate; if vascular parts of it come away also, the placenta is said to be deciduate. The non-deciduate placenta is either diffuse when the villi are scattered (most *Ungulata*, except *Ruminantia*; *Sirenia*, *Cetacea*, *Lemuridae*, among *Primates*); or cotyledonary, when they are aggregated into patches corresponding with maternal patches (true *Ruminantia*). The deciduate placenta is either discoidal when the villi are developed over a circular area and form with the maternal structures a cake-like mass (*Rodentia*, *Insectivora*, *Chiroptera*); metadiscoidal when the villi, at first scattered, are restricted to a limited area, as in the placenta of Man and *Simiidae*; or zonary when the villi are restricted to a partial or complete girdle surrounding the embryo (*Hyrax*, *Elephant*, *Carnivora*). The *Edentata* have different types of placenta: it is non-deciduate and diffuse in *Manis*; deciduate and zonary in *Orycteropus*, and *Dasypus novem-cinctus*, or discoidal in the remainder. In Man and *Simiidae* the ovum sinks at an early stage into the maternal mucous membrane, which completely surrounds it, or is reflected over it. Traces of a similar reflection are observable in some zonary placentae.

The nine orders of living Eutheria are separated from one another by subordinate characters. They are (1) the *Edentata* (Sloths, Ant-eaters, Armadillos in America, Cape Ant-eater in South Africa, Pangolins (*Manis*) in Africa and the Oriental region); (2) the *Sirenia*,—Manatee from the rivers flowing into the Atlantic in Africa and South America: Dugong (*Halicore*) from the Red Sea, East of

Africa, Ceylon, Bay of Bengal, Indo-Malayan Archipelago, North coast of Australia; (3) the *Cetacea*, including toothed and whale-bone Whales; (4) the *Insectivora*, a group of small inconspicuous Mammals with a wide distribution; (5) the *Chiroptera* or Bats; (6) the *Rodentia*, an order widely and evenly distributed with a large number of families; (7) the *Ungulata*, an order comprising a large number of dissimilar groups, including the *Hyracoidea*, *Proboscidea* (Elephants), the *Perissodactyla* (Horse, Rhinoceros, Tapir), the *Artiodactyla*, subdivisible into the *Ruminantia* (Cows, Sheep, Goats, Antelopes, Deer, Camels, Giraffe), and the *non-Ruminantia*, i. e. the Hippopotamus and *Suidae*; (8) the *Carnivora*, including a sub-order *Fissipedia* with the groups *Aeluroidea* (Cat-group), *Cynoidea* (Dogs), and *Arctoidea* (Bears, Weasels, &c.), as well as a sub-order *Pinnipedia*, or the Seals; (9) the *Primates*, which includes the *Lemuridae*, *Simiidae* (Monkeys and Apes), and the *Hominidae* (*Anthropidae*) or Man.

There are many extinct groups, especially groups allied to *Ungulata*. For these, see Marsh's papers in the American Journal of Science; his *Deinocerata* in the United States Geological Survey, x. 1884; Cope, 'Vertebrata of Tertiary formations of the West,' Report of U. S. Geological Survey of Territories, iii. 1885; his papers in the American Naturalist for the last few years; Flower, 'Mammalia' (*supra*); Wallace, 'Distribution of Animals,' 1876, caps. vi. vii. viii; Schlosser, 'Stammesgeschichte der Huftthiere,' &c. M. J. xii. (1), 1886. *Tritylodon longaevis*, a Triassic South African Mammal of doubtful affinities, Owen, Journal Geol. Soc. 40, 1884.

### SUB-CLASS METATHERIA.

THIS sub-class contains the single order *Marsupialia* with a large number of families, one the *Didelphidae*, confined to America, the remainder to the Australian and Austro-Malayan sub-regions. The auditory bulla is formed by a process of the alisphenoid and the tympanic is a loose semiring. The carotid canals pierce the basi-sphenoid as in *Cetacea*, among Eutheria, and as in Sauropsida. The palate often has unossified vacuities and the angle of the lower jaw is inflected except in *Tarsipes*. The median inferior piece of the atlas vertebra may remain unanchylosed (*Thylacinus*), or be absent altogether (*Phascalomys*, *Macropus*, &c.). There are as a rule two epipubic or 'marsupial' bones. In the brain the corpus callosum is small and the anterior commissure large. The retinal cones contain coloured oil globules. The crowns of the teeth conform to very different patterns according to the habit of life, i. e. carnivorous, insectivorous, rodent, &c. There may be more than three incisors on each side in the upper, rarely in the lower, jaw, and the number in the upper and lower is equal only in *Phascalomys*, which has two above and below. There are three praemolars and four molars above and below on each side, reversing the numbers usual in Eutheria. The last praemolar alone has a milk predecessor, and it is not certain that this is the case in all forms. The dentinal tubes are frequently continued on into the enamel. The character of the stomach varies much with the food. The anus opens in the female, except

in Kangaroos, just within the sinus urogenitalis, forming a rudimentary cloaca, and both orifices are in all cases surrounded by a common sphincter. The fossa ovalis is absent in the heart, and the muscoli papillares arise in the right ventricle only from the septum. The testes are suspended in a scrotum in front of the penis. The glans penis is bifurcate except in Kangaroos, and the crura of the corpora cavernosa are either free altogether from the ischia, as in most instances, or are attached to the symphysis pubis by ligamentous fibres (*Macropus*, *Hypsiprymnus*), or have the usual connection as in a *Phascogale* (Sack). The left ovary is sometimes the larger of the two, and the ripe Graafian follicles project from the surface of the ovary to a degree rarely observable in Eutheria. The oviducts are differentiated into oviducal, uterine and vaginal sections which are typically separate throughout their whole extent, and open separately into the urogenital sinus which is of considerable length. But in some instances the proximal portions of the vaginae fuse and develop a median caecum extending towards the urogenital sinus. The cavity of this caecum is divided by a complete septum, each half being continuous with the vagina of its own side in the Wombat (*Phascalomys*). The septum may be lost, and in a few instances (e.g. *Macropus Bennetti*) the caecum opens direct into the urogenital sinus. The yolk sac, or umbilical vesicle, is large, fused to a limited area of the subzonal membrane, and is variously stated to be vascular (Osborne) or non-vascular (Caldwell). The allantois is small and vascular, but it is doubtful whether it always fuses to the subzonal membrane: if so, union occurs at a late period. The subzonal membrane is attached to the uterine walls either by villi or by villiform pseudopodial processes of the external cells (Caldwell) which are developed only from the region covered by the yolk sac. The uterine glands enlarge during pregnancy, and perhaps secrete a nutritive fluid. Intra-uterine life is brief, extending from 2 weeks (Opossum) to 38 days (*Macropus major*). The number of teats which are abdominal in position vary from 4 to a larger number in multiparous forms, e.g. 13 in the Virginian Opossum. In this case they are grouped round a central teat and not extended in lines. The marsupial pouch for the young enclosing the teats is rudimentary, or absent in some Opossums (*Didelphidae*). Its aperture is generally directed forwards, but backwards in *Thylacinus*, *Perameles*, and *Choeropus*. In the Kangaroo milk is forced down the throat of the young animal by the contraction of the cremaster muscle covering the mammary gland.

The Mammalian remains, consisting chiefly of isolated teeth and lower jaws, small in size, from Triassic and Jurassic strata in England and America, are generally referred to this sub-class. Cf. Owen, 'British Fossil Mammals and Birds,' 1846, and Palaeontographical Society's Publications, 1871; Marsh, American Journal of Science, xx. 1880, p. 235. Fossil post-tertiary *Marsupialia*, some gigantic in size, occur in Australia. Cf. Owen's Memoirs in Ph. Tr., republished in two vols. 1877.

*Paratherium*, an extinct genus of *Didelphidae*, occurs in European Eocene and upper Miocene strata.

Waterhouse, *Marsupialia*, 'Natural History of Mammalia,' i. London, 1846; Gould, 'Mammals of Australia,' 3 vols. London, 1845-63.

*Corpus callosum*, Flower, Ph. Tr. 155, 1865. *Tongue of Marsupialia*, Poulton, P. Z. S. 1883, and Q. J. M. xxiii. 1883. *Union of crura penis to pelvis*, Sack, Z. A. ix. 1886. *Female genitalia*, Brass, Inaugural Dissertation, Leipzig, 1880, cf. Zeitschr. f. ges. Naturw. liii. 1880, p. 672. *Ovum*, Poulton, Q. J. M. xxiv. 1884. *Foetal membranes*, Osborne, Q. J. M. xxiii. 1883; Caldwell, *Ibid.* xxiv. 1884.

### SUB-CLASS PROTOTHERIA.

THIS sub-class is represented by the single order *Monotremata* with two families *Ornithorhynchidae* and *Echidnidae*. The former contains the single genus *Ornithorhynchus* found in the rivers of Australia and Tasmania, the latter the genus *Echidna* found in the same places, as well as in New Guinea, and the genus *Pro-echidna* from the last-named locality. *Ornithorhynchus* feeds on soft organisms inhabiting mud, &c.: its jaws are shaped like a Duck's bill and covered by thickened epidermis, in which are lodged peculiar tactile organs. The *Echidnidae* have spines mingled with the hairs. They feed on Ants, &c., which they catch with their long extensile tongue. The sub-maxillary gland is of unusual size in this family.

The cranial sutures close, and the surface of the cranium is polished as in Aves. The rami of the lower jaw do not form a symphysis, and have no ascending portion. The cervical ribs are distinct up to a certain age at least: the odontoid process of the axis is long, and not fused to the centrum of that vertebra. There are no epiphyses to the centra of the vertebrae as in *Sirenia* among Eutheria. There are intermediate ribs as in many Reptilia. The spine of the scapula forms the anterior border of that bone: the coracoids reach the praesternum, and there are large distinct ossified and overlapping epicoracoids and a T-shaped interclavicle. The axis of the ilia is more vertical than usual among Mammals, and the ischia meet in a ventral symphysis of great extent in *Ornithorhynchus*. The centre of the acetabulum is fibrous in *Echidna* as in Aves. There are epipubic bones. The fibula has a process homologous with the olecranon. The os calcis is feebly developed, and the males have a curved spur perforated by the duct of a gland, and borne by an accessory ossicle on the inner side of the tarsus. The spur is present also in the female, but remains rudimentary, and is lost in aged specimens.

The brain has a small corpus callosum and a large anterior commissure. The olfactory nerve quits the skull in *Ornithorhynchus* as in lower Vertebrata, in a single strand, and there is no lamina cribrosa. The cochlea is curved, not spirally twisted. *Ornithorhynchus* has eight horny epidermic teeth: the *Echidnidae* are edentulous. The right auriculo-ventricular valve has no septal flap, or sometimes in *Ornithorhynchus* a rudimentary one.



There are no chordae tendineae, and the muscoli papillares are attached to the membrane of the valve, and in *Ornithorhynchus* even invade its substance, and extend to the auriculo-ventricular ring; and in this animal a transverse section of the ventricles is remarkably Avian in character<sup>1</sup>. The thyroid cartilage in the larynx is formed of two separate cartilages, and the cricoid shows traces of its origin from a number of tracheal rings. The rectal and urogenital canals unite in a common cloaca which is closed by a sphincter muscle. The ureters open below the neck of the bladder into the urogenital canal itself. The testes are retained within the abdomen: the left ovary is larger than the right. The vasa deferentia open separately into the urogenital canal, as do the oviducts. The latter have non-fimbriate abdominal apertures, and are dilated towards their lower extremities with a thickened mucous membrane. There is no thickened muscular uterus. The oviducal aperture opens *above* that of the ureter on a common papilla. The penis is attached to the ventral wall of the cloaca: and consists of two corpora cavernosa. It is perforated by a canal which can be brought into temporary connection with the openings of the vasa deferentia. The clitoris is large. The mammary glands are two in number, and their ducts open on an area of the skin which is depressed in *Echidna*, flat in *Ornithorhynchus*. The ova are large and meroblastic, and the tunica granulosa of the Graafian follicle consists, as in Sauropsida, of but a single layer of cells. *Ornithorhynchus* lays its eggs on a rough kind of nest at the bottom of a burrow: *Echidna* carries them in a marsupial pouch which appears to be developed at stated periods, and to arise in the first instance as two folds, each inclosing a mammary area. The young animal has a knob or caruncle, as in some Aves, on the snout, which probably assists in perforating the tough egg-shell.

The temperature of the body in *Echidna* is said to be 28°C., in *Ornithorhynchus* 24.8°C., by Miklucho-Maclay, *Nature*, xxxi. 1884-85, p. 809. That of other Mammals, according to J. Davy, is 38.4°C.

Goold, 'Mammals of Australia,' 3 vols. 1845-63. *Echidna*, Oldfield Thomas, P. Z. S. 1885. *Corpus callosum of Echidna*, Flower, Ph. Tr. 155, 1865. *Eye of Ornithorhynchus*, Gunn, *Journal of Anat. and Physiol.* xviii. 1884. *Cochlea of same*, Pritchard, Ph. Tr. 172, 1881. *Tongue of Ornithorhynchus*, Poulton, Q. J. M. xxiii. 1883; *sense organs of bill in do.*, Id. *Proc. Physiol. Soc. in Journal of Physiology*, 1884, p. xv. *Heart*, Ray Lankester, P. Z. S. 1882; 1883. *Reproductive organs*, Martin Saint-Ange, *Études de l'appareil reproducteur*, Paris, 1854. *Ovum*, Poulton, Q. J. M. xxiv. 1884; *of Echidna*, Beddard, *Proc. Roy. Phys. Soc. Edinburgh*, viii. 1885; Ramsay, A. N. H. (5) xvi. 1885; *Do. and oviparity*, Baldwin Spencer, *Nature*, xxxi. 1884-85. *Marsupial ovum, pouch and mammary glands of Echidna*, Haacke, P. R. S. xxxviii. 1884-85, cf. von Lendenfeld, Z. A. ix. 1886.

<sup>1</sup> An anterior abdominal or epigastric vein, arising from the bladder and distributed to the left lobe of the liver, has been found in a female *Echidna*. It may not be a constant structure. Beddard, P. Z. S. 1884.

## SAUROPSIDA.

AIR-BREATHING Vertebrata, with a skin remarkably deficient in glands and an epidermic skeleton in the shape of feathers, scales, or scutes. The skull articulates with the vertebral column by means of a single occipital condyle into which the basi- and ex-occipital bones enter in varying proportions. The pro-, epi-, and opisth-otic bones either remain separate *inter se*, and fuse with adjoining bones, or else fuse with adjoining bones and then with each other about the same time (Birds). There is an interorbital septum and the carotids pierce the basisphenoid, entering the cranial cavity at the pituitary fossa. The mandible is always complex: each ramus consisting of one cartilage bone, the articular, and five membrane bones, the dentary, splenial, coronoid, angular and surangular. It articulates with the skull by the intermediation of the upper part of Meckel's arch, the quadrate bone, which is free or fixed. There are well-developed cervical ribs, and the neck passes insensibly into the thorax. The sternal elements of the ribs unite on each side in the embryo to form a broad plate on the right and left side of the body, which are always in contact and with rare exceptions fuse in the middle line: and either remain as cartilage more or less ossified, or are eventually replaced by membrane bone. When the pelvis is present, the true axis of the ilium trends forwards and downwards. There are as in all lower Vertebrata no epiphyses to the bones. There is no corpus callosum. The olfactory nerve forms a single strand invariably. The cervical sympathetic cord is generally double. The ciliary muscle of the eye is transversely striated and the cones of the retina contain clear and variously coloured oil globules except in *Ophidia*, the Crocodile and Geckoes. There is a cloaca (= proctodaeum) common to the rectum and urino-genital ducts. The heart has two auricles and either one or two ventricles, but the single ventricle is *physiologically* divisible into two. The haematids are oval and nucleated and smaller than in Ichthyopsida. The urine is semisolid and contains urates and not urea. The ova have a single layer of cells in the tunica granulosa of the Graafian follicles: they are large and projecting from the ovary when ripe. The oviduct has entire edges as in all lower Vertebrata to its abdominal aperture, and is divisible into a narrower conducting portion, a glandular portion in which albumen is secreted, and a lower muscular or uterine portion in which the ovum stays while the shell is formed. Accessory glands to the reproductive organs are nearly invariably absent. The egg-shell is more or less calcareous. All are oviparous with rare exceptions among the Reptilia. The ovum is telolecithal and segmentation consequently partial.

There are two classes, *Aves* and *Reptilia*.

## CLASS AVES.

Warm-blooded Sauropsida in which the epidermis develops feathers clothing the head, neck, body, fore-limbs and the upper part of the hind-limbs (cf. pp. 51-2). The fore-limbs are modified into wings. The sacral series of vertebrae is long and includes 1-3 dorsal, all the lumbar, the two true sacral and a variable number of caudal (= urosacral) vertebrae, all ankylosed together. The bones of the pelvis are ankylosed: the ilium of great antero-posterior extent: and the pubes (postpubes) and ischia do not meet in a ventral symphysis. There is a carpo-metacarpus; a tibio-tarsus and tarso-metatarsus formed by the union of both proximal and distal tarsalia to the tibia and metatarsals respectively. The jaws are covered by a horny epidermic sheath, and there is a more or less muscular gizzard in the digestive tract. The heart is quadrilocular and the right auriculo-ventricular valve muscular, consisting of two flaps. The aorta is single and crosses the right bronchus. The lungs are firmly fixed to the back of the thorax, and there are air-sacs developed from the ends of certain of the bronchia. The right ovary is atrophied.

Epidermic scales are found covering the tarso-metatarsus and the toes, but these parts may in exceptional cases be feathered. There are claws on the last phalanges of the toes, frequently on the thumb and first finger. A thickened epidermis covers the upper and lower jaw. It is subject to a partial moult and renewal every year in the Puffin; see Zoologist, 1878, p. 233. There is no dermal exo-skeleton unless the bony spur on the metacarpus in a few birds, e.g. *Megapodius*, the Mound-bird, and on the posterior aspect of the tibio-tarsus in many *Gallinae* (= *Alectoromorphae*) is to be considered a dermal structure. The corium or derm is remarkably thin, very vascular, rich in Pacinian bodies, and contains numerous bundles of non-striated muscle fibres connected to the follicles of the feathers. There is but one skin-gland, the uropygial or oil gland, situated on the dorsal aspect of the tail.

The leading features of the skeleton are as follows<sup>1</sup>. The surface of the skull is polished, and the sutures between the bones obliterated at an early period; the interorbital septum well ossified. The praemaxillae are very large and the maxillae small, their palatal plates variably developed. The parasphenoid is very large in the embryo and ossifies as an anterior azygos bone, the rostrum, and posterior paired bones, the basi-temporals. The quadrate is free, and usually articulates by two heads, both with the cranium and the lower jaw: it is connected to the maxillae by jugo-quadrato-jugal bones, the rami of the lower jaw are ankylosed at the symphysis at an early period, and the constituent bones are also ankylosed. The hyoid arch is rudimentary, but the first branchial well-developed. The

<sup>1</sup> For detailed description see Preparation ii. pp. 58-67.

neck is long and mobile, and contains a variable number of vertebrae. The centra of the praesacral vertebrae are procoelous, cylindrical and saddle-shaped posteriorly. They articulate by synovial joints with a cartilaginous meniscus interposed between successive centra. Certain of the dorsal vertebrae are opisthocelous in the Penguins and Auks, and all the vertebrae are amphicoelous in the extinct *Archaeopteryx* and *Ichthyornis*. Some of the dorsal vertebrae are occasionally ankylosed and they always possess strong spines and ligaments. The terminal 4-6 caudals fuse as a rule and form a ploughshare bone or pygostyle. The cervical ribs are small, provided with double articulations, and ankylosed to the vertebrae with the exception of the 2-3 last which are large and free. The dorsal ribs are divided into a vertebral and sternal section, both well ossified. The posterior ribs fail to reach the sternum. Ossified plates or 'processus uncinati' are attached to the posterior edges of certain of the vertebral sections of the dorsal ribs. The sternum is very large, convex ventrally, and the original cartilage replaced by membrane bone. It has in the majority of living birds, in *Archaeopteryx* and *Ichthyornis*, a prominent ventral keel, probably derived from the posterior part of the interclavicle: hence *Carinatae*. In a few living birds and the extinct *Hesperornis* this keel is absent and the sternum smooth and raft-shaped: hence *Ratitae*. The scapula is thin, narrow, sabre-shaped, either ankylosed to the coracoid (*Ratitae*) or united to it by ligament (*Carinatae*). The ventral ends of the coracoids are received into grooves of the ventral surface of the sternum. The clavicles are rarely absent (most *Ratitae*) and are generally fused at their lower extremities, forming the furcula. The interclavicle is present apparently in development: its anterior end either becoming entirely fibrous, or else partially ossified as hypocleidium and fused to the furcula, and its posterior either remaining fibrous (*Ratitae*) or ossified as the keel of the sternum (*Carinatae*). The pubes form a ventral symphysis in the Ostrich (*Struthio*), and the ischia a dorsal symphysis in *Rhea*. The conformation of the limb-bones is characteristic. The fibula has a pointed lower extremity and is shorter in the adult than the tibia. The scaphoid is present in the carpus; the lunar and cuneiform fused. The hand has but three digits, first, second, and third, with fused metacarpals (except in *Archaeopteryx*): the foot, four digits, the fifth toe being always absent. In *Struthio* the third and fourth are alone present, but the tarso-metatarsus retains a trace of the articulation for the second toe. In *Aves* as in *Lacertilia* the phalanges of the toes increase typically in number from the first to the fourth toe in the series 2, 3, 4, 5.

The cerebral hemispheres are large and made up chiefly of corpus striatum. They touch the cerebellum posteriorly, and the two solid optic lobes are thus thrust aside laterally. The olfactory lobes are small. The cerebellum has a median foliate lobe, showing in longitudinal section an

*arbor vitae* as in Mammalia, and two small floccular lobes. The extinct Cretaceous birds had large olfactory lobes, and small hemispheres, their brain resembling to a certain extent that of the Alligator. The spinal cord has a lumbar swelling with the posterior fissure widely open and filled by gelatinous tissue. The cervical sympathetic is double, one part accompanying the common carotids, the other running in the vertebrarterial canal. The fore-part of the sclerotic is obtusely conical, and contains a ring of bones; the hind-part spheroidal, and there is in some birds a bony plate in it near the entrance of the optic nerve. A vascular pigmented process, the pecten or marsupium, projects into the vitreous humour in the line of the choroidal fissure and is absent only in *Apteryx*. The muscular fibres of the iris are striated, and the radial portion of the striated ciliary muscle, known as Crampton's muscle, large, a bird having apparently exceptional powers of accommodation. The movements of the third eyelid are governed by two special muscles, the quadratus and pyramidalis, and its gland, the Harderian gland, is large. The stapes or columella auris is well-developed, provided with processes at its outer end, and it has an epihyal element added to it. The posterior and the horizontal semicircular canals unite where they cross, and the cochlea contains no otoliths, but has a cuticular membrane, the homologue of the membrana Corti of the Mammal. The tympanic cavity is continued into the lower jaw by a membranous or bony canal, the siphonium. A nasal gland, lying on the nasal bone or extending to the frontals above the orbit, pours its secretion into the nose.

All living birds are edentulous. But in some-embryo Parrots there are dental papillae attached to the periosteum of the jaws, supplied by vessels and nerves, and capped by cells of the rete mucosum. These cells become cornified, and contain air. Three such papillae are found on the maxillae, and ten in shallow alveoli on the mandibles of *Melopsittacus*. They are however hidden in every instance beneath the horny covering of the bill. In the *Lamellirostres* (= *Chenomorphae*) the edges of the bill are raised into oblique lamellae, and in the Mergansers the edges of the bill are produced into pointed processes, supported by corresponding bony processes. In *Odontopteryx* from the London Clay there are similar bony processes, large and small intermingled. *Hesperornis* and *Ichthyornis* from the Cretaceous strata possess numerous true teeth, composed of dentine and enamel with large pulp cavities. In the former the praemaxillae are edentulous, and the teeth lodged in grooves of the maxillae and mandibles. They have fangs composed of osteodentine. The succession is lateral as in *Mosasauros* and the Crocodile among Reptilia. The teeth of *Ichthyornis* are implanted in sockets, and the succession is vertical as in *Deinosauria*. *Archaeopteryx* from the Solenhofen slates also has teeth which probably resemble those of *Hesperornis*. The tongue is well-developed, especially in

Accipitrine birds and in the Parrots where it is thick and fleshy. Its anterior extremity may be forked (Humming Birds, *Trochilidae*), or terminate in a brush of delicate papillae (*Trichoglossinae* among Parrots): and it is of great length and extensile in Woodpeckers (*Picidae*) and Humming Birds. It has a horny surface and is often covered by recurved papillae. There are numerous glands in and around the tongue as well as palatal glands, and an especially large gland opening at the angle of the mouth<sup>1</sup>. In the oesophagus the circular muscle layer is external to the longitudinal, thus reversing the relations usual in Vertebrata. The oesophagus itself is of uniform calibre in omnivorous, frugivorous and insectivorous birds. In birds which swallow large masses of food at once, e.g. fish-eating birds, its calibre is large: and in birds of prey, and especially grain-eating birds, it is provided with a dilatation or crop in which the food is stored. In grain-eating birds such as *Gallinae*, Pigeons, &c., the walls of the crop are generally said to be glandular, and the secretion of the glands to act upon the food (but see p. 53), whilst in other birds the walls are non-glandular. The stomach is divisible in all birds into a glandular stomach or proventriculus, and a muscular stomach and gizzard, connected by a narrow tube or lower oesophagus. The proventriculus varies much in size: its glands are simple or compound and are disposed in various ways. The gizzard is saccular, or more or less angular in outline. Its walls show two tendinous spots between which radiate muscle fibres. The degree to which these fibres are developed varies much with the food, least in flesh- and fruit-eating birds, most of all in grain-eating birds and *Lamellirostres*. The character of the secretion poured out by the glands varies in the same direction: and it either forms a tenacious coat, or a thick horny coat, which is continually worn away by the action of the food and of the stones swallowed with it to assist in trituration, and as continually secreted anew. The two apertures, one leading into the gizzard the other from it, are close together. The pyloric aperture is often guarded by a raised fold to prevent stones, &c. passing on into the intestine: and, in a few birds, there is a small so-called 'pyloric stomach' intervening between the gizzard and the pylorus, e.g. in the Heron. The duodenum is, as a rule, wide and long. The length of the small intestine varies much, as does also the mode in which it is coiled, a point which has been utilised for classificatory purposes. The large intestine is usually straight and short: in the Ostrich alone it is of great length and disposed in coils. It opens into the anterior end of the cloaca, which is large in *Ratitae* and Accipitrine birds, but in others usually small. The urinary and genital ducts ordinarily open separately on its dorsal wall, but there may be a more or less distinct urogenital section of the cloaca. The

<sup>1</sup> The edible bird's nest produced by a Swift is composed of a substance closely akin to mucin, secreted by two glands lying one on either side of the tongue. These glands are said to enlarge at the nesting season. See Green, *Nature*, xxxiv. 1886: *Journal of Physiol.* vi. 1885.

liver ordinarily consists of two lobes into the fissure between which the apex of the heart is received. There are always two, and sometimes three bile-ducts: they open separately into the duodenal region of the intestine, and on one of them a gall-bladder is usually developed. It is absent in many Pigeons, some Parrots, &c. A large and compact pancreas with two or three ducts is always to be found in the concavity of the duodenal loop. A ductus vitello-intestinalis, the duct of the yolk-sac of embryonic, and of early life subsequent to the hatching, is often to be found on the small intestine, especially in aquatic birds and waders. In *Ratitae* remains of the yolk may be found in it for a long time or during life. Two caeca, rarely absent, e. g. some Parrots, are appended to the intestine at the junction of the ilium with the large intestine. The Herons have but one. Their size varies much, and they are largest in grain-eating birds, *Lamellirostres* and *Ratitae*. In the Ostrich they are very large and contain a spiral valve. In all young birds, and in some adults, a Bursa Fabricii opens on the dorsal aspect of the cloaca close to its external aperture. This bursa is produced originally as a solid growth which subsequently acquires a cavity. It usually atrophies away: its function is unknown, but its walls contain a rich vascular supply, and numerous follicles derived from the epithelium of the intestine and surrounded by adenoid (reticular) tissue (see pp. 54-5).

In addition to the points already noted in the heart, the right auricle is larger than the left: the left ventricle is of great size, with strong muscular walls, whilst the right has thin walls and embraces the left: the left auriculo-ventricular valve consists of two membranous flaps with attached chordae tendineae and muscoli papillares. The fourth aortic arch on the left side is converted into the innominate artery, instead of forming a second or left systemic aorta as in Reptilia, though its homology with this latter vessel is shown in many birds, especially Accipitrine, by the retention of a compact fibrous prolongation onwards to the dorsal aorta. The aorta appears to divide close to its origin into three great trunks, as it gives off two sub-equal innominate arteries. In birds of powerful flight these arteries are often of larger calibre than the aorta itself. The two carotids run up the ventral aspect of the neck and are sometimes united for a portion of their course, or the aortic origin of one of the two may be lost. There are various arterial plexuses, and one especially is notable on the surface of the abdomen which enlarges during the period of incubation. There are as a rule two superior venae cavae, but the cardiac extremity of the left is sometimes much reduced or even obliterated. They open separately from each other and from the vena cava inferior into the right auricle, the sinus venosus of Reptilia having disappeared by absorption into the auricle. The two jugular veins are united under the base of the skull by an anastomotic vein. The vena cava inferior is formed by the confluence of the iliac veins. These veins are in their turn formed by the union

of the femoral veins with the two efferent renal veins (see p. 56). Lymphatic glands are present, few however in number. A pair of lymph-hearts with striated muscle fibres in their walls are found in the pelvic region of the Ostrich, Goose, Swan, and Stork, and also in the embryo chick in which they subsequently disappear. The valves of the lymphatics are not so numerous as in Mammalia.

The nostrils lie at the tip of the beak in *Apteryx*: in other birds at its base in front of the orbits. In the Gannets (*Sula*) they are closed. The larynx consists of two arytenoid cartilages and a cricoid ring. The trachea is always of considerable length: its cartilaginous rings are usually perfect and at least partially ossified: it is often tortuous, forming convolutions beneath the skin and sometimes lodged in the keel of the sternum, e.g. in the Swan: it may be dilated at intervals and its cavity is divided by a longitudinal septum in *Aptenodytes* and *Procellaria* (a Penguin and a Petrel). In most birds including the *Ratitae* (see p. 55) a lower larynx or syrinx is developed at the junction of the trachea with the bronchi. It is produced by modifications of some of the lower tracheal rings only (some American *Passeres* = *Coracomorphae*), of the upper bronchial rings only (*Steatornis* among *Caprimulgidae* or Goatsuckers, and *Crotophaga*, a Cuckoo, both from S. America), or, as most usual, of both tracheal and bronchial rings. It has often a complicated structure, and in many singing birds six intrinsic pairs of muscles. The voice is caused by the varying tensions of an internal and external tympaniform membrane developed, the former on the inner aspect of the incomplete upper bronchial rings, the latter between two of the same rings. In the males of many Ducks the lower tracheal rings are dilated asymmetrically into a resonant cavity with walls partly membranous, partly ossified. The bronchi lose their cartilaginous rings to a great extent when they enter the lung. There are four eparterial bronchia, and usually nine hyparterial. Of the former, the first winds round the trachea and branches in a dorsal and ventral direction: the fourth is rudimentary: but the second and third run towards the inner border of the lungs parallel to one another. The hyparterial bronchia branch on the outer aspect of the lungs dorsally and ventrally. The lungs are fixed to the back of the thorax and are deeply indented by the ribs but not otherwise lobed. The pleura cover only their ventral surfaces on to which pass from the ribs small muscular bundles. The ultimate branches of the bronchia are tubes more or less hexagonal, and containing transverse and longitudinal ridges upon which the respiratory capillaries are distributed. Certain of the chief bronchia traverse the lungs and open at their surface into air-sacs. Of these there are nine (see pp. 55-6). Processes are prolonged from the anterior and posterior air-sacs into the bones, with the exception of those of the head, which are supplied with air from the nasal fossae and the tympanic cavity. The bones of the



head are sometimes, as in Mammalia, the only pneumatic bones: the vertebrae, sternum and humerus come next; whilst in a few birds, e.g. the Toucan, all the bones of the body are stated to be pneumatic. The bones of the fore-arm, of the lower leg, of the hand and foot often retain their medulla. In some instances processes of the air-sacs are prolonged between the muscles and under the skin, e.g. in the Gannet (*Sula*). The ciliated epithelium of the air passages is replaced by pavement epithelium in the air-sacs and their extensions.

The kidneys are divided into three lobes which fit into the fossae of the ilia. The glands often meet and even fuse posteriorly, and their ventral surface is often marked by the intestines. The ureter arises from the ventral surface, is dilated at its origin, and opens into the cloaca on a papilla placed to the inner side and a little in front of the genital papilla.

The sexes differ much externally in colour, development of peculiar feathers, &c., and in Accipitrine birds the females, as is so commonly the case in Arthropoda, are larger than the males. The testes are always retained within the abdomen, and lie anteriorly on the kidneys. They undergo a periodical enlargement at the breeding season and the left is occasionally the larger of the two. The vasa deferentia lie to the outer side of the ureters, and when filled with spermatozoa are disposed in short wavy folds. They are slightly dilated at their cloacal terminations. The right ovary and oviduct are usually atrophied, and when the ovary is persistent, as in some *Accipitres* (= *Aetomorphae*), its ova do not come to maturity. The oviducal aperture is very wide in correlation with the large size of the ova. The length of the duct and the number of its coils increase with the breeding season. It is divisible into three sections: the first narrow, the second glandular and secreting the albumen, the third muscular and glandular. This last part is often termed 'uterus,' as the egg stays in it for some time whilst the calcareous shell and its colouring matter, if any, are secreted by the glands. There are no accessory glands appended to the generative ducts in either sex. The Ostrich has a solid grooved intromittent organ similar to that of *Chelonia* and *Crocodylia*: the Duck and other aquatic birds, the remaining *Ratitae* and a few others, an eversible grooved organ attached to the front wall of the cloaca. The organ is represented in the female. The egg is impregnated in the upper part of the oviduct or on the ovary. It is incubated by the female, in rare instances by the male as well or exclusively, and is generally laid in a special nest or shelter constructed for the purpose. Development lasts for a time dependent on the size of the bird, e.g. about 11 days in smaller birds to 7 weeks in the Ostrich. During the growth of the young bird an air space is formed and gradually increases in size at the obtuse end of the egg. Many young birds are provided with a hard knob on the upper surface of the bill for breaking through the shell when ready for hatching. When the food-yolk is large, the young

are hatched well-clothed with downy feathers, able to run or swim and provide for themselves, e. g. gallinaceous birds, waders, *Lamellirostres*, *Ratitae*. Such birds are termed *Praecoces* or *Autophagi*. But when the food-yolk is small in amount, the young are hatched, either naked or with little down, unable to run or swim, and requiring to be fed by the parents and to be brooded on by the female: e. g. Accipitrine birds, *Passeres*, and many others. Such birds are termed *Altrices* or *Insessores*. Most of them are monogamous and have few young, while many of the *Praecoces* are polygamous and their young numerous.

The classification of Birds presents great difficulties, and many arrangements have been proposed which it is impossible to discuss in a short compass. Three chief divisions are generally recognised—*Saururae*, *Ratitae*, and *Carinatae*. The first contains the Jurassic *Archaeopteryx*, the second a few living Birds mostly of large size, such as the Ostrich, Cassowary, Emu, &c., incapable of flight and devoid of a keel to the sternum; the third all Birds capable of flight and with a keel to the sternum. Prof. Damès in a recent memoir (Palaeont. Abhandl. Berlin, ii. part 3, 1884) has proposed to classify *Archaeopteryx* in the group of *Carinatae*. His views have been criticised by Paulow in the Bulletin de la Soc. Imp. des Naturalistes de Moscou, 60, p. 100, 1884, who has pointed out that in several respects *Archaeopteryx* can hardly be considered as within the line of descent of *Carinatae*. Retaining the *Saururae* as a separate group but following Damès in other points, the classification given below may be adopted as showing the main outlines. For subordinate divisions and discussions on the various systems proposed, the student must refer to an article on 'Ornithology' by Prof. Newton in the Encyclopaedia Britannica (ed. ix.) xviii. 1885.

I. *Saururae*. Vertebrae biconcave; sternum broad (? a keel), well ossified; abdominal ribs; tail long with separate caudal vertebrae (i. e. no ploughshare bone); three fingers with separate metacarpals, all clawed; pelvic bones separate; fibula complete, its distal end in front of tibia; metatarsals united but not to the degree observable in living birds. *Archaeopteryx* from the Solenhofen Slates.

II. *Ratitae*. Feathers of the adult with free barbs; an after-shaft to those of the body; sternum devoid of keel; anterior limb shortened or rudimentary; incapable of flight; teeth when present lodged in a groove (*Hesperornis*).

- (1) Imperfectly known order—*Laopteryx* from Jurassic strata in America.
- (2) *Odontolcae* (Marsh). Rami of lower jaw separate; wing with only a humerus. Vertebrae with typical avian centra; no ploughshare bone. *Hesperornis* from American Cretaceous strata.
- (3) Post-cretaceous *Ratitae*. Edentulous; rami of lower with anchylosed symphysis. Vertebral centra typical; wings rudimentary but with humerus, fore-arm and rudimentary hand. Tertiary, Diluvial and living: includes the living *Apteryx*, Cassowary, Emu, Ostrich and *Rhea*, and the fossil *Aepyornis* from Madagascar, *Dinornis* (Moa) and *Palapteryx* from New Zealand.

III. *Carinatae*. Contour feathers in the adult; sternum with a keel; anterior limb well developed; capable of flight; teeth, when present, lodged in sockets (*Ichthyornis*).

- (1) *Odontotormae* (Marsh). Vertebrae biconcave; rami of lower jaw not ankylosed; tail short; some of the vertebrae fused. *Ichthyornis* from American Cretaceous strata.
- (2) Post-cretaceous *Carinatae*. Adult edentulous, but the fossil *Argillornis longipennis* has dental alveoli; rami of lower jaw ankylosed; vertebral centra typical; tail short; a ploughshare bone. Tertiary, Diluvial and living.

For the literature of Fossil Birds, see p. 66, *ante*.

*Teeth in Parrots*, Fraisse, Verhandl. Phys. Med. Gesellsch. Wurzburg, xv. 1881, SB. p. iii.

*Classification*, Newton, 'Ornithology,' Encyclopaedia Britannica (ed. ix.) xviii. 1885; cf. Huxley, P. Z. S. 1867-1868; Sclater, The Ibis, 1880; and collected papers of Garrod and Forbes.

### CLASS REPTILIA.

*Cold-blooded Sauropsida with epidermal scales, sometimes combined with underlying dermal bones and then forming scutes; and not developed as are hairs and feathers in saccular involutions of the integument. The characters of the skeleton vary much but the vertebral centra never possess the typical Avian shape. The sacral vertebrae are usually two, provided with large ribs expanded distally. The interclavicle, when present, never fuses with the sternum which is usually rhomboidal, cartilaginous and more or less ossified but not, as in birds, replaced by membrane bone (? Pterodactyles). The ilia vary much in the degree to which they extend forwards, and in existing Reptilia usually extend backwards more than in the opposite direction: the ischia form a ventral symphysis as do the pubes except in certain of the extinct Deinosauria. The pelvic bones and metatarsalia remain separate except in the extinct Ceratosaurus in which they ankylose. There are always two aortae (right and left), and the ventricle is either single, or double as in Crocodilia where however the venous and arterial blood currents communicate at the base of the aortae: there are only two semilunar valves at the bases of the aortae and pulmonary artery.*

The outer layer of epidermic cells is cornified and its cells often contain air. It is thrown off and renewed periodically in *Lacertilia* and *Ophidia*. The integument appears to have been smooth in the extinct *Plesiosauria* and *Ichthyosauria*, and in the *Amphisbaenoidea* among Lizards it is divided into rectangular areae disposed in transverse rows. Scales are formed as duplicatures of the integument. The corium (derm) is composed of horizontal and vertical bundles of fibres as in the lower Vertebrata. Pigment is not usually found in the epidermis but in special pigment cells of the corium and in many *Lacertilia* (e.g. *Anolis*, *Chamaeleon*) there is a change of colour apparently connected with psychical changes. Dermal bony plates occur in many *Lacertilia* (e.g. many *Scincoidea*), often of microscopic size as in the Geckoes (*Ascalabota*). In the *Crocodilia* these dermal plates

are of large size and form scutes placed on the neck, back and sometimes on the ventral surface, or, as in the extinct *Teleosaurus*, covering the body completely. In the Triassic *Aetosaurus* they overlap one another. Among the *Deinosauria* the *Stegosauria* have large bony plates with spines. The dermal skeleton of the thorax and abdomen is largely developed in the *Chelonia* and forms a firm carapace and plastron within which the head and neck, the tail and limbs can be withdrawn in many instances for shelter. The carapace consists of a median series of eight ossifications which, with the exception of the first and two last, unite each with the dorsal spines of thoracic vertebra; of a lateral series of *costal* plates united with the ribs, and a *marginal* series sometimes absent (e.g. in *Chelone midas*) into which the ends of the ribs are received. The plastron is imbedded in the corium and consists of a median anterior entoplastron, and four pairs of plates (hyo-, hypo-, xipho-plastra) placed one behind the other. These plates cover the ventral surface more or less completely. In many *Chelonia* the carapace and plastron unite firmly at their lateral edges, e.g. land Tortoises. The abdominal walls are covered by a system of dermal bones in the *Plesiosauria* and *Ichthyosauria*, arranged in transverse rows; each row consists of a median bone pointed at both ends and at least three overlapping bones on either side. Most Reptilia possess claws. The integument is poor in glands. Scent-glands are present beneath the mandibles, opening on the neck, or at the sides of the plastron in *Chelonia*. The *Ophidia* have a pair of cloacal scent-glands, and the Crocodile similarly placed gland follicles. Among *Lacertilia*, *Hatteria* has a pair of cloacal glands, and in the majority there is a row of ventrally placed femoral glands, the secretion of which appears to have a copulatory function.

The conformation of the cranial bones varies much in the different groups. The cartilage cranium is much reduced. The occipital region, basisphenoid and alisphenoid are ossified; but the presphenoid and orbitosphenoid are cartilaginous or imperfectly ossified and the ethmoidal region is always unossified. There is an interorbital (ethmo-presphenoid) septum present except in *Ophidia*. The pro-otic is usually free: the epi- and opisth-otic fused with the supra- and ex-occipitals respectively: but in *Chelonia* and *Ichthyosauria* the last-named remains free. The palatopterygoid region is well ossified and large in *Chelonia* and *Crocodylia*. The series of bones developed in membrane is very complete. There are frequently prae- and post-frontals present in front of and behind the orbits respectively. The nasal bones are absent in post-cretaceous *Chelonia*. In *Lacertilia* the quadrato-jugal is represented by ligament: it is ossified however in *Hatteria*. The parasphenoid is very large in *Ophidia*, and the trabeculae cranii remain as two rods on either side of it in front of the basisphenoid and behind the ethmoid. The vomers are double in *Lacertilia* and *Ophidia*. The quadrate is immoveably united to the skull in *Chelonia*,

*Crocodylia*, in *Hatteria* and Chamaeleons among *Lacertilia*, and in the extinct *Ichthyosauria* and *Plesiosauria*. The bones of the lower jaw usually retain their sutures: but in *Ophidia* the articular, coronoid, angular and surangular are anchylosed. The rami are anchylosed at the symphysis in *Chelonia*; connected by a distensible ligament in *Ophidia*, or united by suture, or cartilage. *Iguanodon*, *Hypsilophodon* and *Diclonius* among *Deinosauria*, possess a prae-symphysial or mento-meckelian bone in front of the symphysis. The stapes (columella auris) is a simple rod-like bone. The hyoid arch is well-developed and the *Chelonia* have a large remnant of the first branchial arch.

Amphicoelous vertebrae are found in the existing *Hatteria* and Geckoes among *Lacertilia*: in the prae-cretaceous *Crocodylia*, e.g. *Teleosaurus*: in *Ichthyosauria*, *Plesiosauria* and many *Deinosauria*. In these the notochord is enlarged intervertebrally. In other Reptilia it is enlarged intra-vertebrally and constricted inter-vertebrally and eventually lost. The centra are usually procoelous and are connected by synovial joints, or in the *Crocodylia* by intervertebral discs. Opisthocoelian or biconvex centra are found in exceptional instances, concavo-convex in many *Deinosauria*; and the mobility of the neck in *Chelonia* is insured by a great variety in the shapes of the centra of the cervical vertebrae. The neural arches are united to the centra by anchylosis in *Ophidia*, *Lacertilia* and most *Chelonia*: by suture in a few *Chelonia*, *Crocodylia*, the extinct *Plesiosauria*; and by interposed cartilage in the *Ichthyosauria*. In the last named order, the vertebrae articulate only by their centra; in the remaining orders by the usual articulating processes, and in *Ophidia*, as well as in the *Iguanidae* among *Lacertilia* by a zygosphene and zygantrum in addition (see p. 73). In *Ophidia*, in *Amphisbaenoidea* among *Lacertilia* and the *Ichthyosauria* the vertebral column is divisible into a praecaual and caudal series (see p. 72): in other orders into a cervical, dorsal, lumbar, sacral, and caudal regions, but the lumbar region is absent in *Chelonia*. The number of vertebrae in each region varies much in the different orders. There are in living Reptilia two sacrals, but the number may be greater among extinct forms, e.g. 3-6 in Pterodactyles, 4-6 in some *Deinosauria*. In the *Ichthyosauria* the atlas and axis resemble the remaining vertebrae in their general form. They are often anchylosed in *Plesiosauria* and in Cretaceous Pterodactyles. The atlas in most Reptilia consists of a ventral body and two supero-lateral arches, to which is added in the *Crocodylia* a superior or dorsal membrane bone: and the axis has a well-developed odontoid process united to it by cartilage, by suture in *Crocodylia*, or by anchylosis as in *Lacertilia*. The caudal vertebrae in many *Lacertilia* have a transverse unossified septum through which the tail is apt to split.

Ribs are always present. Their proximal ends though possessing two articular surfaces may be simple, e.g. *Ophidia*, *Lacertilia*, or deeply divided,

e. g. *Crocodylia*. The cervical ribs of *Chelonia* are simple nodules which are either fused to the vertebrae, or united to them by suture. Their dorsal ribs are attached between the centra of adjoining vertebrae. The dorsal ribs when a sternum is present may be divided into a vertebral, intermediate, and sternal section, e. g. *Crocodylia*, many *Lacertilia*; or into vertebral and sternal only: or, when the sternum is either absent (*Ophidia*, some serpentiform *Lacertilia*, *Chelonia*, *Plesiosauria*, *Ichthyosauria*) or rudimentary, they remain undivided. In the Chamaeleons and Gecko, some of the post-sternal dorsal ribs are continuous ventrally. The sacral ribs are usually massive and expanded distally, the caudal anchylosed to the vertebrae. So-called abdominal ribs are found as ossifications of the intermuscular septa (*Crocodylia*) or of the subcutaneous fibrous tissue (*Hatteria*). The sternum is present but is very small and rudimentary in some serpentiform *Lacertilia*: in some other *Lacertilia*, e. g. *Acontias meleagris*, its right and left halves are stated to remain separate: in others again its bilateral origin is evidenced by a median fontanelle, and by the prolongation backwards, as occurs also in *Crocodylia*, of two xiphisternal horns with which a certain number of ribs articulate. It is generally more or less rhomboidal in shape, cartilaginous and partially ossified in substance. In many *Deinosauria*, e. g. *Brontosaurus*, *Iguanodon*, there are two sternal bones which were either joined by cartilage or had each a separate cartilaginous border. The sternum of Pterodactyles is well ossified, the cartilage probably replaced by membrane bone, and there is a median keel to the ventral surface.

The shoulder-girdle and fore-limb are absent in *Ophidia*, but in serpentiform *Lacertilia* the former is present when the limb is absent. There is a scapula and coracoid, the latter articulating with the sternum. The scapula generally possesses a dorsal cartilaginous but partially ossified suprascapula, the coracoid a similar but ventral epicoracoid. In many *Lacertilia*, where the bones are broad, there are membranous tracts forming fenestrae, especially in the coracoids: and the epicoracoids overlap one another anteriorly. The scapula and coracoid are anchylosed in the gigantic *Pteranodontia* among Pterodactyles, and the scapula articulates with the neural spines of several anchylosed vertebrae, a unique feature among Vertebrata. The clavicle is absent in *Chelonia*, *Crocodylia*, Chamaeleons, &c., in some *Deinosauria*, if not in all, and in Pterodactyles. It is continuous with the scapula in *Chelonia*, forming a large stout bone: separated from the scapula and slender in other groups. There is an interclavicle or episternum in *Crocodylia*: it is large and T-shaped in *Lacertilia* and *Ichthyosauria*, and the two clavicles are closely connected with its anterior border. There is no trace of a pelvis nor of hind-limb in the majority of *Ophidia*, but the *Typhlopidae*, *Tortricidae* and *Pythonidae* have both a rudimentary ischio-pubis and limb. In the serpentiform *Lacertilia* there

is a rudimentary ilium. Other Reptilia have a pelvis composed of ilium, pubis and ischium. The iliac axis slopes forwards and downwards, and the bone usually extends backwards, i. e. behind its point of union with the sacral ribs, but in the *Crocodylia*, and especially in many *Deinosauria*, e. g. *Iguanodon*, *Stegosaurus*, it has a forward extension indicated in many *Lacertilia* by a process (processus acetabularis). The acetabulum is formed by the three bones jointly, except in the *Crocodylia* where the pubis is excluded from it. The centre of this cavity is fibrous in *Crocodylia* and many *Deinosauria*. As a rule, there is a pubic and ischial symphysis, but the former is wanting in many *Deinosauria*, e. g. *Iguanodon*. The pubis varies in shape and size. In the *Stegosauria* and *Ornithopoda* among *Deinosauria* it has a peculiar shape; one portion, the post-pubis, being long and slender and parallel to the ischium which, in these two groups, is strongly inclined backwards as in Aves; the other, the praepubis, projecting downwards and forwards. The latter is probably the homologue of the pectineal tubercle. There is no evidence that the two portions represent two distinct bones (see p. 65). There is a large obturator foramen between the pubis and ischium of the same side, but the obturator nerve either perforates the pubis itself (*Lacertilia*) or the fibrous membrane closing the foramen. In land and fresh-water *Chelonia*, the pubes and ischia touch one another in the median line; but in the marine *Chelonia*, in the *Crocodylia* and *Lacertilia*, the two obturator foramina are only separated medianly by a strong fibrous band extending from the former to the latter. There is a small epipubic cartilage in many *Lacertilia* and *Chelonia*, and in many of the former an *os cloacae* extends backwards from the ischial symphysis below the cloaca.

The *Ophidia* with a few exceptions (*supra*) are limbless. Certain *Lacertilia* (most *Amphisbaenoidea*, some *Brevilinguia*, e. g. *Anguis*) are in the same condition. Others possess rudimentary limbs with or without a reduced number of toes. In other Reptilia limbs are well developed. They are short and paddle-like in *Plesiosauria* and *Ichthyosauria*, and in the latter the digits often bifurcate, and there are rows of extra ossicles at their margins. The *Ornithopoda* among *Deinosauria* appear to have walked erect, and their fore-limbs are short. The Pterodactyles have the fifth finger elongated to support the wing membrane, and the fore-limb is large and powerful in them. But as a rule, the limbs are small in comparison with the body. There is much variety in the conformation of the carpus and tarsus, of the digits and their phalanges, but the following points may be noted. The carpus of some *Chelonia* possesses all the typical ossicles separate. In the tarsus the ankle-joint comes to lie between the proximal and distal tarsals in many *Chelonia*, the *Lacertilia*, the *Ornithopoda* among *Deinosauria*: and in the *Ornithopoda* the astragalus has an ascending process more or less developed and at least *applied* to, or in some instances perhaps

fused with the tibia, thus approximating to Aves. The Crocodile has a well-developed calcaneal process. There is said to be an indication of a sixth digit in *Chelonia* and *Lacertilia*.

The cerebral hemispheres are smaller relatively to the rest of the brain, and to the spinal cord than in Aves, and the Deinosaurian *Stegosaurus* appears to have had a brain far smaller than the lumbar swelling in its own spinal cord, and smallest relatively to the bulk of the body among terrestrial Vertebrata. The olfactory lobes are well developed: the cerebral hemispheres are largest in the *Crocodylia* and some *Lacertilia*, and have a conspicuous corpus striatum. They are connected by an anterior commissure, and in the Crocodile there appears to be an indication of a fornix. The thalami optici are usually hidden by the cerebral hemispheres and optic lobes: the pineal gland is composed of non-nervous tissue and often attached to the dura mater. The optic lobes are hollow and the optic tracts often meet behind them dorsally. The cerebellum is either a mere transverse lamella, or of fair size and folded on itself. There is generally a bend between the medulla oblongata and the spinal cord. The ventricles of the brain are large. The spinal accessory nerve is not differentiated in *Ophidia*, and in most Reptilia the cervical sympathetic is double on both sides. The nostrils lie usually at the apex of the snout, but just in front of the orbits in *Plesiosauria* and *Ichthyosauria*, or near them in *Iguanodon*. Many *Lacertilia* and the *Ophidia* have a nasal gland. The eyes are very small in some *Ophidia* (*Typhlopidae*, *Uropeltidae*) and *Typhline* among *Lacertilia*. In the *Ophidia*, the Geckoes, the *Amphisbaenoidea*, and some of the *Scincoidea* among *Lacertilia*, the eyelids are transparent and united together forming a lacrymal chamber in front of the cornea. Other *Scincoidea* have the lower lid partially transparent. The third lid is present in many *Lacertilia*, in all *Chelonia* and the *Crocodylia*: and in the first-named is moved by a bursalis muscle attached to the orbit; but in the two other orders by a pyramidalis springing from the back of the eyeball itself. The *Ophidia* possess only the Harderian lacrymal gland. The sclerotic contains a ring of bones in the *Ichthyosauria*, *Chelonia* and in many *Lacertilia*. There is a pecten homologous with the similar structure seen in Aves in many *Lacertilia*: traces of it are said to be found in many *Ophidia* and the *Crocodylia*, but it is absent in *Hatteria* among *Lacertilia* and in *Chelonia*, an order in which the circular portion of the ciliary muscle only is developed. A tympanic cavity is present except in *Ophidia*, *Amphisbaenoidea* and *Hatteria*. There are three Eustachian tubes in the Crocodile. The stapes is a rod-like bone, and when there is no tympanic cavity lies among the muscles. The tympanic membrane is exposed except in some *Chelonia*, the *Ophidia*, *Hatteria* and Chamaeleons, and is covered by a moveable flap in *Crocodylia*. The cochlea has the commencement of a spiral turn in *Hatteria*.



The *Chelonia*, the Cretaceous genus *Pteranodon* among Pterodactyls, and *Oudenodon* among the *Dicynodontia*, are edentulous<sup>1</sup>. The fore-part of both jaws is devoid of teeth in some *Deinosauria*, e.g. *Iguanodon*, and in some species of *Rhamphorhynchus* among Pterodactyls. A thickened epidermic sheath probably covered these parts as in the living *Chelonia*. Teeth are generally confined to the praemaxilla, maxilla and dentary, but in the *Ophidia* and some *Lacertilia* the palatine and pterygoid are dentigerous also. They are anchylosed either to the edge of the jaw, e.g. *Ophidia*, many *Lacertilia*, or by their sides to a groove, e.g. *Iguana*; or are lodged in alveoli, e.g. *Crocodilia*, many *Deinosauria*; or in a shallow groove scarcely divided into alveoli as in *Ichthyosauria*. These forms of dentition are known respectively as acrodont, pleurodont, and thecodont. They are ranged usually in a single row, but there are exceptions as in some *Ophidia*. Anchylosis takes place by true bone, and, in *Hatteria*, when the teeth are worn away, the dense bone at the edge of the jaws forms an efficient substitute. The enamel is often ridged and sometimes plicated at the base of the tooth in *Lacertilia*. Succession is vertical in *Crocodilia*, many *Deinosauria*; or the new tooth may take a lateral position as in the poison fangs of Ophidians. The two tusks of the extinct *Dicynodon* grew from permanent pulps, whilst the rest of the jaw was probably covered by thickened epidermis. The form of the teeth is very variable. The extinct *Theriodontia* have teeth resembling incisors, canines, and molars. Grooved teeth occur in *Ophidia*, and in poisonous serpents the groove is well-developed in one tooth on each side and utilised to convey the secretion of the poison gland into the wound made by it. Somewhat similar but less specialised teeth occur in the poisonous lizard, *Heloderma* (Nature, xxvii. 1882-83: xxviii. 1883). A single large tooth implanted on the praemaxillae serves to rupture the egg-shell in *Lacerta* and *Anguis* (*Lacertilia*) and in *Tropidonotus* (*Ophidia*). Salivary glands are absent in marine *Chelonia*, and the Alligator: they are confined to the tongue in the Crocodile, but, as a rule, there are not only lingual glands, but also sublingual, palatal, and labial. A differentiation of one of the upper labials forms the poison gland of *Ophidia*. The tongue may be spatula-shaped and immobile, as in *Chelonia* and *Crocodilia* and some *Lacertilia*, or bifid, protrusible and more or less elongated as in other Reptilia. The oesophagus is wide and sometimes, as in *Ophidia*, not clearly marked off from the stomach. In marine *Chelonia* there are large papillae with points directed backwards towards the stomach. The cardiac portion of the latter is enlarged in the *Crocodilia* and shows on its flattened dorsal and ventral surfaces a tendinous spot whence the muscle fibres radiate; it is followed by a small pyloric enlargement. The small intestine is disposed in numerous coils in the *Chelonia* and *Crocodilia*. In the

<sup>1</sup> *Trionyx* (Chelonian) is stated by Wiedersheim to have embryonic teeth.

latter and in the *Lacertilia* it is non-glandular like the rest of the tract. The large intestine is short and straight, and it often has a small caecum close to the ileo-colic valve. It opens into a cloaca which has generally a dorsal enlargement, into which the urino-genital ducts open. The *Chelonia* have a pair of lateral bursae anales appended to the cloaca. And in the same group and the *Lacertilia* but in no other Reptilia a urinary bladder opens into it ventrally and anteriorly. The liver is bilobed as a rule. It is lengthened out and unilobed in the *Ophidia* and the *Amphisbaenoidea*. There is always a gall-bladder which lies removed at some distance from the liver in the two groups just named. The pancreas has several ducts in some *Chelonia* and the *Crocodylia*.

The larynx consists of two arytenoid cartilages borne upon a cricoid ring composed of several united tracheal rings. The trachea is long, and in some Crocodiles and *Chelonia* forms a bend or loop. It and the two bronchi into which it divides are supported by cartilaginous rings, sometimes imperfect, and often united to one another by processes. The lungs are either simply saccular with ridges (primary, secondary, &c.) on the walls, upon which the capillaries are distributed, as in *Ophidia* and most *Lacertilia*: or the bronchus enters the inner side of the lung, traverses it, retaining cartilaginous semi-rings for a greater or less distance, and giving off eparterial and hyparterial bronchia which divide further as in some of the larger lizards, e. g. *Regenia*, and in *Chelonia* and *Crocodylia*. In some of the serpentiform lizards, e. g. *Anguis*, the left lung is shorter than the right. This is the case also in the larger *Ophidia*, but in the majority of that order the left lung is a mere rudiment; and the posterior part of the right lung is thin and membranous and supplied by blood from the dorsal aorta. In the Chamaeleons and some Geckoes delicate saccular prolongations arise from the inner side and posterior extremity of the lungs and lie among the viscera, foreshadowing the air-sacs of birds. Indeed in the Deinosaurian family *Coeluridae* the bones of the skeleton are pneumatic to a greater degree than in the majority of birds. The lungs of the *Chelonia* lie at the back of the thorax and are invested by peritoneum on their ventral surface only. Strong muscular fibres spread into this investment and originate from the ribs. The *Crocodylia* possess pleural sacs.

There is a sinus venosus in the heart which opens by a bivalved aperture into the right auricle and receives the vena cava inferior and the two cava superiores, except in the *Ophidia* where the left cava superior opens separately into the auricle. The septum between the auricles is complete, and the left receives only arterial blood from the lungs. There is a complete ventricular septum in the *Crocodylia*, and the pulmonary artery and left aorta arise from the right or venous ventricle, while the right aorta is derived from the left or arterial ventricle. The two aortae communicate, however, at their roots by the foramen Panizzae. In other Reptilia there

is no complete ventricular septum, but a strong muscular ridge projects from the ventral wall of the ventricle, and is attached anteriorly between the roots of the pulmonary artery and left aorta. When the heart contracts this ridge or septum pulmonale cuts off a cavum pulmonale which contains purely venous blood from the rest of the ventricle which contains mixed blood or on its left side arterial blood. The pulmonary artery rising from the cavum pulmonale is thus filled entirely by venous blood, whilst the roots of the two aortae are so disposed that the left aorta rising rather on the right contains more venous than arterial blood, and the right aorta, vice versa, more arterial. The apex of the ventricle is attached by a fibrous band to the pericardium. The whole heart is broad and flattened dorso-ventrally in *Chelonia*. The roots of the two aortae and pulmonary artery are closely united in *Lacertilia*, *Chelonia* and *Crocodylia*. In many *Lacertilia*, e. g. *Lacerta*, the third or carotid aortic arch is complete and falls into the fourth or aortic arch: in other *Lacertilia* and Reptilia there is no connection between the two. The right aortic arch gives off the carotids, except in the *Lacertilia* first mentioned, and the subclavian arteries which are absent in *Ophidia*, and then unites with the left aorta to form the subvertebral aorta. The left aorta gives off the caeliac artery before it unites with the right, and in *Chelonia* and *Crocodylia* the artery in question is of so large a size that it appears to be the continuation of the arch. In the *Crocodylia* the left aorta arising from the right ventricle carries only venous blood to the viscera, whilst in other Reptilia it carries a mixture of arterial and venous. There are always two venae cavae superiores. The cava inferior is formed by the union of the two efferent renal veins. There is a renal-portal circulation except in *Chelonia*. The caudal vein divides into two branches, each of which goes to the kidney of its own side in *Ophidia*; so too in the *Lacertilia*, but here each branch receives on the way the veins of the corresponding hinder extremity. In the *Crocodylia* the afferent kidney veins are derived from a transverse vessel uniting the two branches of the caudal. These are continued on into the two epigastric veins, remnants of the foetal umbilical veins, which receive the veins of the hinder extremity and conduct the blood to the liver, anastomosing with the hepatic portal system. The two branches of the caudal vein are connected to the epigastrics in *Chelonia*. There is a single epigastric in *Lacertilia* which receives blood from the abdominal walls and the bladder and is distributed to the liver. The corresponding vein in *Ophidia* is resolved into a plexus, ramifying in the fat body\* (see p. 69) and receiving veins also from the abdominal walls. Anastomoses exist, however, between the renal-portal veins and the rootlets of the hepatic portal system. The lymphatic vessels take the shape of loose sheaths or plexuses surrounding the large arteries, and communicate, as in Amphibia, with the superior cavae anteriorly and the ischiadic veins posteriorly. At their

junction with the latter veins, contractile 'lymph-hearts' are developed. The Crocodile alone has a lymph gland which is situated in the mesentery. There are no valves to the lymph-vessels.

The kidneys are usually more or less lobed and placed posteriorly in the body cavity, especially in the *Lacertilia*, an order in which the two glands are sometimes united at their hinder ends. In serpentiform genera, e. g. *Anguis*, the right gland is in advance of the left, an arrangement more marked in the *Ophidia*. The glands are also elongated, and in *Ophidia* the separation into a series of lobes one behind the other is often carried so far that the lobes become independent, and are connected only by their union with a common ureter. There is a cortical as distinct from a medullary region in the Crocodile. The two ureters open on the dorsal wall of the cloaca. Remains of the Wolffian body ('golden yellow body') and its duct are to be found in many *Lacertilia* and *Ophidia*: they have also been found in *Chelonia*. The testes and ovaries are bilaterally symmetrical glands, but in *Lacertilia* the right organ, especially the ovary, is rather larger than the left and is placed slightly in advance of it. The differences of size and in position are greater in *Ophidia*. In both *Lacertilia* and *Ophidia* the glands are placed anteriorly to the kidney. A continual formation of new ovisacs takes place during life. The oviducts have simple apertures: the right is generally longer than the left. The convolutions vary from time to time and are more developed during the breeding season. The vasa deferentia open with the ureters. There are two distinct types of copulatory organs. The *Lacertilia* and *Ophidia* have a pair of eversible sacs opening into the cloaca, and when in repose lying under the skin of the tail. The surface of these sacs is covered with spiny processes. Their homologues are to be found in the female. The *Chelonia* and *Crocodylia* have two fibrous cavernous bodies closely united into a penis but traversed by a furrow and situated on the dorsal wall of the cloaca. In the *Chelonia* and *Crocodylia* two peritoneal canals or extensions of the coelome enter the penis. They have been observed to open on papillae at the base of the glans in the *Chelonia*: by pores at the base of the penis (or clitoris) in the Alligator, but in the Crocodile the two papillae in the same position are imperforate (Bridge). These canals are possibly the homologues of the abdominal pores found in *Elasmobranchii* and other fish. Accessory glands appear to be generally absent. Glands opening into the cloaca have been found in Geckoes (female) and in *Lacerta*. The albumen of the egg, and the more or less calcareous shell are secreted by the glands of the oviduct.

Most Reptilia are oviparous. Some are viviparous, e. g. *Zootoca vivipara*, the Blindworm (*Anguis fragilis*), *Seps*, Chilian Iguanas, among Lizards: many Chilian snakes, the Viper (*Pelias berus*), among *Ophidia*. Other viperine snakes and even a *Boa Constrictor* have produced living

young in confinement, but it is doubtful whether they do so under natural conditions. The female *Python* disposes herself in coils round her eggs and incubates them for a prolonged period. During this process the temperature has been observed to rise as high as 96° F. within the coils<sup>1</sup>.

Many Lizards possess the power of casting off and of reproducing portions of the tail. The Reptilia pass into a lethargic condition in winter, where the cold reaches a sufficient degree of intensity. The aquatic Reptilia do the same in the dry season of hot countries.

All living Reptilia belong to one of four orders. The majority are inhabitants of the warmer parts of the world.

I. *Chelonia* (Turtles and Tortoises). Body compressed in shape; the jaws covered by a thickened epidermis and devoid of teeth; dermal skeleton well developed; its dorsal portion or *carapace* uniting with the neural spines and ribs of the dorsal vertebrae, which are therefore immoveably fixed; its ventral or *plastron* covering the abdomen more or less completely. Head, neck, tail, and limbs often retractile within the protection of the dermal skeleton. A urinary bladder and solid grooved copulatory organ present. Marine, freshwater, and terrestrial; occur in fossil state from the Kimmeridge Clay onwards.

II. *Lacertilia* (Lizards, Blindworm, &c.). Body covered by scales; as a rule two pairs of limbs, but one or other, or sometimes both pairs lost; eyelids moveable, rarely soldered and transparent; tympanic cavity seldom absent; jaws united firmly at symphysis; shoulder-girdle present when fore-limb is aborted; cloacal aperture transverse; a urinary bladder and double copulatory organ. Terrestrial; one marine form, *Oreocephalus (Amblyrhynchus) cristatus*, from the Galapagos Islands. *Iguana* and *Lacerta* have been found fossil in Tertiary European strata. There are several fossil groups; see Huxley, *Anatomy of Vertebrated Animals*, 1871.

III. *Ophidia*. Body covered with scales; in the majority a special series of ventral ambulatory scales. Fore-limb, with shoulder-girdle always absent; hind-limb and pelvis represented in a few. Body elongated; symphysis menti ligamentous and extensible; eyelids transparent and always united; no tympanic cavity; a transverse cloacal aperture and double copulatory organ. Terrestrial, freshwater, or marine; fossil only in Tertiary strata (London Clay, &c.).

IV. *Crocodylia*. Body covered by scales and partially by scutes; a long swimming tail; teeth implanted in sockets in the praemaxillae, maxillae, and dentary bones; longitudinal cloacal aperture and solid grooved copulatory organ. Freshwater. The largest living Reptilia. The Gavials are found in the Ganges, and the rivers of Borneo and N. Australia; the Crocodiles in Africa, India, and as far east

<sup>1</sup> Martin-Saint-Ange states (p. 89, *Études de l'Appareil reproducteur*, Paris, 1854) that Geoffroy St. Hilaire and Florent Prévost succeeded in making the Common Grass Snake viviparous by depriving it of water and maintaining a suitable surrounding temperature. On the Incubation of the Python, see Forbes, *P. Z. S.* 1881.

as N. Australia, in Cuba and S. America; the Alligators are confined to S. America and southern part of N. America. All existing Crocodiles have procoelus vertebrae, and appear first in the Greensand; the extinct *Teleosauria* with amphicoelous or partly opisthocelous (*Steneosaurus*) vertebrae come from the Lias, Kimmeridge Clay, Inferior and Bath Oolite. The genus *Belodon* is Triassic.

In addition to the four groups of living Reptilia, there are a number of extinct groups. The *Plesiosauria* and *Ichthyosauria* are marine forms ranging, the former from the Trias, the latter from the Lias, to the Chalk. Their skin appears to have been naked. *Ichthyosaurus* is believed to have had a vertical tail fin, its intestine had a spiral valve, and some of the species were viviparous (Brit. Ass. Reports, 1880, p. 68). The neck is long in the former group; in the latter short. Both have the limbs modified into paddles. The *Deinosauria* are strictly terrestrial, but some of them, e.g. *Iguanodon*, appear to have frequented marshy ground or swamps. The group (sub-class, Marsh) comprises a large assemblage of herbivorous and carnivorous forms. Two of the sub-divisions (*Stegosauria* and *Ornithopoda*) show ornithic characters especially in the hind-limb. The group extends from Triassic strata to the Chalk (Maestricht beds in Europe). Some of the genera are gigantic in size. A very large number have been discovered in America. The *Anomodontia* are terrestrial forms, found in rocks of Triassic age in S. Africa, India, and the Ural Mountains. A portion of a skull has recently been obtained from a New Red Sandstone quarry near Elgin. *Dicynodon* and the *Theriodontia* (Owen, Journal Geol. Soc. 1876), &c., belong to this group.

Finally, there is a remarkable order of Flying Reptilia—the *Pterodactyla*, *Pterosauria*, or *Ornithosauria*, found in strata from the Lias to the Chalk inclusively. The fifth finger is immensely elongated, and supports the wing membrane. The toothless American genus *Pteranodon* is of immense size, fifteen feet from the tip of one wing to the tip of the other. Accounts of the anatomy of the *Plesiosauria*, *Ichthyosauria*, *Ornithoscelida* (= *Deinosauria* in part), *Dicynodontia* (*Anomodontia* in part), and the *Pterosauria* will be found in Huxley, Anatomy of Vertebrated Animals, 1871, or in Quenstedt's Handbuch der Petrefactenkunde, ed. 3, 1882-83. Some additional memoirs are noted below.

*Reptilia*, Hoffmann, Bronn's Klass. und Ordn. des Thierreichs, vi. Abth. 3 (in progress).

*Chelonia*, Strauch. Mém. de l'Acad. Imp. St. Pétersbourg (7), viii. 1865. *Development of Green Turtle*, W. K. Parker, Challenger Reports, i. 1880. *Carapace*, &c.; *cervical ribs*, &c., Hoffmann, Niederländ. Archiv f. Zool. iv. 1877-78; v. 1879-82. *Peritoneal canals*, see Bridge, cited p. 279, ante.

*Lacertilia*. *Anatomy of Lizard*, T. J. Parker, Zootomy, London, 1884. *Skull*, W. K. Parker, Ph. Tr. 170, 1879. *Chamaeleon*; *skull*, Id. Tr. Z. S. xi; *changes of colour in do.*, Krukenberg, Vergleich. Physiol. Studien, i. Abth. 3, 1880. *Amphisbaena*, Bedriaga, A. N. 50. 1, 1884; Smalian, Z. W. Z. xlii. 1885.

*Ophidia*, see p. 72 and 73, ante.

*Crocodylia*, Strauch. Mém. de l'Acad. Imp. St. Pétersbourg (7), x. 1866. *Skull, development of*, W. K. Parker, Tr. Z. S. xi.

The fossil groups are treated principally in the following. *Plesiosauria* and *Ichthyosauria*, Owen, Fossil Reptiles of Liassic Formations, Palaeontographical Society; Id. Palaeontology, ed. 2, Edinburgh, 1861; *limbs*, see Baur, Z. A. ix. 1886. *Anomodontia*, Owen, Catalogue of S. African fossils in British Museum,

1876; *Theriodontia*, Journal Geol. Soc. xxxii. 1876; *Dicynodon*, Id. Trans. Geol. Soc. vii. 1845-56, and Ph. Tr. 1862; in *Elgin*, Judd, P. R. S. xxxix. 1885. *Deinosauria*, Marsh, Nature, xxxi. 1884-85; Papers in American Journal of Science and Art by same; and by Cope in Proc. Philadelphia Academy, &c. For *Iguanodon*, Dollo, Bull. Mus. Royale d'Hist. Nat. Belgique, ii. and iii.; Moseley, Nature, xxviii. 1883. *Pterosauria* or *Ornithosauria*, Seeley, J. L. S. xiii. 1878; H. von Meyer, Fauna der Vorwelt, 1860; Zittel in H. von Meyer's Palaeontographica, xxix. 1882-83; Marsh, American Journal of Science, xxiii. 1882. *Fossil Crocodiles*, see Nature, xxxiii. 1885-86, p. 331.

Figures of many Reptilian bones will be found in Phillips' Geology of Oxford and the Thames Valley, Oxford, 1871.

ICHTHYOPSIDA s. *Anamniota* s. *Anallantoidea*.

THE amnion is absent altogether, and the allantois, when represented, never extends beyond the body-walls as a foetal membrane. Other important characters are the following.

The epidermic exoskeleton is either absent, or takes the form of enamel coating a subjacent dermic exoskeleton of bone. The cells of the epidermis are connected by protoplasmic processes to one another. The cutis is composed of vertical and horizontal connective tissue bundles as in *Reptilia*. There is a series of epidermic sense-bodies or nerve-eminences forming 'the system of the lateral line'—which may be aborted in the adult. The integument forms a median fold extending along the back, round the tail, and as far forwards as the anus, very rarely in front of it. This fold is the azygos fin. It may persist as a continuous fold; be broken up into sections, the dorsal, caudal and anal fins; or else be aborted. The chondrocranium is often large. The basisphenoid bone is either absent or inconspicuous. Of the investing bones the parasphenoid, when present, is large. There are at least four pairs of branchial arches present in development, and the number may be greater. They are either retained throughout life, or considerable remnants are generally to be found in the adult. The notochord may or may not persist wholly or in part. There is no costal sternum, i. e. one formed from the ventral ends of the primitive ribs. The spinal accessory nerve is a branch of the vagus: the hypoglossal represented by the first, or first and second spinal nerves. The digestive tract either ends in a cloaca, or the anus opens in front of the urino-genital apertures. The heart consists of a sinus venosus, one or two auricles, a ventricle and a conus arteriosus—the last-named being aborted in Teleostean Fish. A pair of aortic arches at least persists: and of the others present in development all or a certain number are temporarily or permanently connected with gills. The haematids are large, oval and nucleated. Branchiae external or internal are present either throughout life or during its first stages. The ova are generally numerous.

There are three classes, *Amphibia*, *Pisces* and *Cyclostomi*.

The organs of the lateral line consist of (1) pyriform sense-cells terminated at their outer ends by a single sense-hair, at their inner by a nerve-fibre; (2) of supporting cells either surrounding or mixed with (1). The sense-cells are shorter than the supporting-cells, and in this point nerve-eminences differ from the terminal buds of the skin of *Teleostei* where the two kinds of cells are of equal length. The nerve-eminences are circular, oval, or ridge-like, and the ridges may be almost continuous with one another. They are either freely exposed, and then their surface is protected by a delicate cuticle perforated by the sense-hairs: or they are surrounded by a delicate hyaline tube as in *Amphibia* and some adult *Teleostei*: or they are sunk in furrows or canals which have apertures leading upwards from spot to spot, as in some *Pisces*. When thus sunk, the dermal skeleton generally comes into relation with them. In the region of the head they are supplied by the fifth nerve (and by the seventh in the Skate): on the body by a branch of the vagus, the lateral line nerve.

They appear to be segmentally arranged in the embryo in many instances, and it has been recently pointed out that a single eminence is seated at the dorsal end of each branchial cleft, and of the mouth at an early period. Hence the name 'branchial sense-organ' applied to them in this region. It is possible that the olfactory mucous membrane is derived from such an organ. The eminences multiply by division. In a few instances they are found scattered over the whole body, e.g. *Mugil* (see p. 85), a condition perhaps to be regarded as primitive.

*Nerve-eminences, &c.*, Merkel, *Endigungen der Sensibeln Nerven in der Haut der Wirbelthiere*, Rostock, 1880; Leydig, *Festschrift zur Feier des 100-jährigen Bestehens der Natf. Gesellsch. in Halle*, 1879. *Branchial sense-organs*, Beard, Q. J. M. xxvi.

On the origin of azygos fins, see p. 101, under interspinal bones.

## CLASS AMPHIBIA.

*Ichthyopsida with an integument rich in glands or glandular cells and devoid of an epidermic exo-skeleton. The azygos system of fins is always present in the larva and in the adult of certain sub-groups, and is never supported by fin-rays. The limbs are borne by well-developed shoulder- and pelvic-girdles, and the latter is connected to a sacral vertebra: they consist as contrasted with the limbs of Pisces of an upper and lower limb, with a hand and foot, thus agreeing with those of higher Vertebrata. The alimentary canal always terminates with a cloaca common to the rectum and urogenital ducts, to which is appended ventrally an allantoid bladder.*

The epidermis in the young larva is ciliated. In older larvae it consists of only two layers of cells, an outer with a striated cuticular border, and an inner, in which mucous cells (=Leydig cells) are to be found scattered. In the adult the outer layer is cornified and is cast off periodically in the *Anura* and the *Urodela*; but the inner layer forms a thick stratum mucosum, and certain of its cells are enlarged and flask-shaped, and are supposed to yield a secretion which facilitates the moult of the cornified layer. Some of the cells contain pigment. The surface of the epidermis



is often rough, and the roughness is due in part to processes and ridges of the corneous cells, in part to local thickenings of the epidermis itself. The lower layers of the corium are loose in texture and contain lymph-spaces continuous with the subcutaneous spaces so largely developed in this class. Smooth muscle cells are found mixed with the fibrous tissue, and chromatophores or pigment cells in abundance. The colours of the pigment are various, black, white, orange, metallic or iridescent: its state of concentration in the cells depends on the activity of the nervous system, and nerve fibres have been traced into direct continuity with the cells. The glands are round or tubular. The former vary much in size; the small are scattered, the large are found chiefly on the head, neck and flanks. Masses of them, known as 'Parotids,' are found on the neck in *Bufo* and *Salamandra*. The tubular glands occur chiefly on the hand and foot, and on the head in many tropical Salamanders. The gland-secretion is milk-white and poisonous. The young larva or tadpole of the *Anura* has two collections of unicellular glands beneath the head. Their secretion is sticky and serves to attach the larva to foreign objects. Variations from the ordinary structure are seen in the development of epidermic nails in the Japanese Salamander *Onychodactylus* and the Toad *Dactylethra capensis*. Calcareous concretions are found in the dermis of the dorsum and dorsal aspect of the limbs in the common Toad *Bufo vulgaris* and *B. japonicus*. Bony dorsal plates are developed in certain species of *Ceratophrys* and *Ephippifer* (= *Brachycephalus*) among *Anura*. The *Gymnophiona* (*Caecilia* and its allies) have semicircular cutaneous lamellae in which are imbedded, except in *Siphonops annulatus*, cycloid dermal scales containing calcareous concretions. This dermal skeleton is well developed and ossified in the extinct *Stegocephali* (= *Labyrinthontia*, &c.). It generally consists of a median anterior thoracic plate, rhomboidal in shape, with the addition of two antero-lateral pieces in some instances, and of a series of ventral scales usually arranged in oblique lines which meet one another ventrally at an angle pointing forwards. These scales, as a rule, only cover the abdominal surface. Sometimes, however, the back, tail and limbs are also protected, but by scales which differ much in shape, &c., from the ventral, e.g. in the *Hylonomidae*. The organs of the lateral line are not known to exist in any *Gymnophiona*, except the larval *Epicrium glutinosum*, but are found in the larvae of every other order. They are persistent in all *Urodela* which lead an aquatic life, e.g. *Proteus*, *Triton*, but are lost in those which are terrestrial when adult, e.g. *Salamandra*, as well as in all adult *Anura*. On the head it is generally possible to distinguish the supra- and infra-orbital lines of organs: the mandibular is generally broken up into an anterior and a posterior part, and the commissure across the supra-occipital region occurs only in *Menopoma*. But in some instances the number of organs is great, and it is difficult to trace the typical arrangement.

There are three lateral lines ; a median which extends to the tip of the tail ; a dorsal which always unites near the tip of the tail with the median line, sometimes also anteriorly ; and a ventro-lateral which extends only between the fore- and hind-limbs. Each organ has a protective hyaline tube in the larva, and there is at first one organ to each somite, but the number increases subsequently by division.

Cartilage persists largely in the chondrocranium of *Anura* : to a much less extent in other Amphibia, especially in *Gymnophiona*. There is a large basicranial and superior cranial fontanelle in *Urodela*, a sub-frontal and two small sub-parietal fontanelles in *Anura*. The occipital region contains two large exoccipitals which form each a cranial condyle<sup>1</sup> : a small supra- and basi-occipital have been detected in some *Anura*. The ear capsule of *Anura* contains a pro-, or a pro-sphen-, otic bone, to which is added in *Urodela* an opisth-pter-otic. *Proteus* and one or two others have an epiotic ossification as well. The middle trabecular region is ossified by a sphen-ethmoid. The olfactory capsules do not unite with the ethmonasal cartilages in *Siren*, *Proteus*, *Menopoma*, and some Salamanders. The chondrocranium is invested by paired parietals, frontals, prefrontals, nasals (absent in *Siren* and *Proteus*), paired vomers and a parasphenoid. The *Anura* have a paired fronto-parietal, sometimes united medianly, nasals, vomers and a parasphenoid. The vomer is single in *Dactylethra*, absent in *Pipa* and *Hylaplesia*. The palato-ptyergoid of *Urodela* appears as a continuous membrane-bone subsequently divided, except in *Proteus* and *Menobranchus*, into palatine and pterygoid bones—the former becoming continuous with the vomer of its side. The latter is absent in *Siren*. The cartilage element appears later : the palatal element from the ethmoid, the pterygoidal from the quadrate. The palato-ptyergoid of *Anura* arises in continuity with Meckel's arch, fuses with the ethmoid anteriorly and remains in continuity with the quadrate posteriorly. Ossification takes place from the perichondrium. The palatine is sometimes absent, sometimes subdivided. Two praemaxillae are always present, fused into one, however in some *Salamandrina*. Maxillae are absent in *Proteus*, very rudimentary in *Siren* and *Menobranchus*. A quadrato-jugal, absent in all *Urodela*, unites them to the quadrate or suspensorium in *Anura* with few exceptions. The quadrate is more or less ossified in *Urodela*, and united to the cranium by three processes. It is as a rule cartilaginous in *Anura* and is united to the auditory capsule by an otic process, and articulated to it by a pedicle. A squamosal lies on its external aspect. The lower jaw is a persistent Meckel's arch. In *Urodela* it is invested by a dentary, splenial and articular bone. A splenial is absent in *Anura*, most of which have a pair of ossified lower labials (= Mento-Meckelians) at the symphysis. The extent of the gape of the mouth depends on the inclination of the

<sup>1</sup> Cope states that the Permian *Trimerorhachis* has but one condyle (American Naturalist, xviii. 1884).

quadrate which is forwards and downwards in *Proteus* and the lower *Urodela*, backwards and outwards in *Anura*. The hyoid of *Urodela* consists of a ceratohyal and generally a hypohyal element: it is united to the quadrate and stapes by ligament. In *Anura* it generally resembles that of the Frog (p. 81), and is continuous with the floor of the tympanum. The *Urodela* have four branchial arches, the two posterior rudimentary and in adult Salamanders lost. There is in them a basi-hyo-branchial as well as a basi-branchial copula. The larval *Anura* have four branchial arches represented by four rudimentary cerato-branchial elements, but there are also four large extra-branchial cartilages united at their dorsal extremities and lying subcutaneously.

The skull in *Gymnophiona* is remarkable for the large size of its bones, and for the very complete case they make. *Epicrium* has a ring of orbital bones like the *Stegocephali*. The mandible articulates with the quadrate by a *concave* surface as in Fish. The skull of the extinct *Stegocephali* is similarly complete. It has remarkably large epiotics and paired supra-occipitals (not homologous probably with the supra-occipital generally so-called). There are prae- and post-frontals, post-orbitals, and a supra-temporal which lies externally to the squamosal. A jugal and quadrato-jugal are nearly always present. The dorsal surface of the skull is often polished and sculptured as in many Ganoid fish, and in this respect it is approached by a few living *Anura*, e.g. *Pelobates*<sup>1</sup>. Remains of two branchial arches have been discovered, and there is reason to believe that they persisted in some adults, e.g. *Branchiosaurus*, whilst they are lost in others, e.g. *Melanerpeton*.

The vertebral column contains a large number of vertebrae in *Ichthyoidea* and *Gymnophiona* (250 or more); a more restricted number in Salamanders; and in living *Anura* only eight praesacral vertebrae and one sacral with a coccygeal style. It is divisible into a cervical, thoracic, sacral and caudal series in *Urodela*. A single more or less ring-like cervical vertebra devoid of ribs is found in all Amphibia. In most *Urodela* it carries a well-marked 'odontoid' process, traces of which are sometimes seen in *Anura*, and which points to the loss, partial or complete, of an anterior vertebra. The remaining vertebrae carry in *Urodela* double transverse processes, the upper, feebly marked in *Gymnophiona*, an outgrowth of the arch, the lower of the centrum. They become rudimentary in the tail. These processes are single in *Anura*. Articulating processes are well developed. The neural arches are in living *Amphibia* ankylosed to the centrum. The neural spines are almost obsolete in *Anura*, but in *Urodela* they are prominent, sometimes forked terminally and articulating one with another; or, in Salamanders, flattened sideways, lamelliform and comb-like, a condition which obtains in some *Stegocephali* (*Nectridea*), where the

<sup>1</sup> The significance of the channels, sometimes termed 'mucous-canals,' on the face in certain genera of *Stegocephali* is not known.

inferior arches of the tail are similarly conformed. These latter arches are present also in *Urodela*, and are homologous with the neural arches and similarly developed. The centra of the vertebrae are formed by ossification of the cellular sheath of the notochord. They constrict the notochord *intra*-vertebrally, while it is also constricted *inter*-vertebrally by a growth of cartilage. If the inter-vertebral cartilage is little developed the vertebrae are biconcave, as in *Ichthyoidea* or extinct *Stegocephali*, and some Salamanders. But in the majority of the latter the cartilage is large in amount and the inter-vertebral constriction great; and in the highest forms, e.g. *Triton*, it is segmented, forming opisthocoelous vertebrae, whilst the intra-vertebral chorda is replaced by marrow. The inter-vertebral cartilage grows rapidly in *Anura*, and the chorda persists for a long time intra-vertebrally; the centra are as a rule procoelous, but in a few, e.g. *Pipa*, *Discoglossus*, opisthocoelous, or even variable, as in *Pelobates*. In these exceptional instances the centra are formed for the most part *above* the notochord, not round it, i.e. are epichordal as opposed to perichordal. The vertebral column terminates in many *Urodela* with an imperfectly segmented cartilaginous rod. In some *Stegocephali* a vertebral centrum, devoid of neural arch and transverse processes, is intercalated between every two vertebrae formed on the ordinary type. In others the centra are stated to consist of a ventral piece (inter- or hypo-centrum) and two lateral pieces (pleuro-centrum or centrum proper). These two forms have been distinguished as embolomere and rhachitome. They occur, however, apparently in the vertebral column of one and the same animal, the former in the tail, the latter in the thorax, and therefore are not of classificatory value. And it is not certain that the hypo- and pleuro-centra belong to the same vertebra (Fritsch). The neural arches of some *Stegocephali* are complex (*Branchiosaurus*). Ribs are present except on the cervical vertebrae and posterior caudal. In *Anura* they are very small, united to the transverse processes, and traces of a suture are rarely observable, e.g. *Discoglossus*. They are bifurcated proximally in *Urodela*, a process articulating with both upper and lower transverse processes, and are developed by the union of a short dorsal and longer ventral rod. They do not surround the body, and in the genus *Spelerpes*, among *Salamandrina*, are absent on two posterior thoracic vertebrae, hence truly lumbar. The extreme shortness of the ribs in living Amphibia is perhaps due to atrophy. They are long in some *Stegocephali*, but there is no evidence of a ventral union.

The sternum or hyposternum (see p. 82) in *Urodela* consists of a shovel-shaped plate of cartilage formed by the union of two cartilaginous rods lying in tendinous intersections of the recti abdominis muscles, with cartilage derived from the coracoid. It is deeply grooved on either side for the reception of the epicoracoidal edges of the coracoid. It has a somewhat similar structure and origin in some *Anura*, e.g. *Bombinator*, but in the

majority it has an ossified base bearing a cartilaginous expansion, and, as in the Frog, is applied to the posterior edge of the united coracoids. It is doubtfully homologous with the sternum of higher Vertebrata.

The limbs with their respective girdles are absent in *Gymnophiona*, and the *Aistopoda* among *Stegocephali*; the pelvic limb and girdle in *Siren lacertina* among *Ichthyoidea*. The shoulder-girdle in *Urodela* has broad scapular, coracoidal and large clavicular processes. The latter projects somewhat forwards, and is free distally except in *Menopoma*, where it fuses with the coracoid as in all *Anura*, inclosing a fenestra. Ossification takes place in the glenoidal regions of both scapula and coracoid, and in the base of the clavicular process. The amount of ossification varies, and is greatest in the *Anura*. The clavicular ossification is in this order purely perichondrial. Many of the *Anura* possess an anterior prolongation of the interclavicular region (see pp. 81-2). The ventral ends of the coracoids overlap in the *Urodela* and a few *Anura*, but in others of the last-named order are connected by intervening interclavicular cartilage. Bony scapulae, coracoids, and clavicles are found in most *Stegocephali*, but there was evidently also a large amount of cartilage.

Each half of the pelvis consists of a continuous cartilage in *Urodela*. The ilium is partially ossified, as is the ischium, but the pubic region is more or less permanently cartilaginous. In *Salamandra perspicillata* there is, however, a continuously bony ischio-pubic region, and some *Stegocephali* have well-formed and separate pubic and ischiadic bones. There is a median ventral symphysis. The obturator nerve perforates the pubic region, but neither in *Urodela* nor in other Amphibia does an obturator, i. e. thyroid, foramen exist. The ilium of the *Anura* is of remarkable length, inclined backwards, and the distal ends of the two ilia, together with the ischio-pubic region, form a thin vertical plate. The acetabulum is a deep depression in this plate. There is an ischium, but a pubic bone is generally suppressed and its region ossified apparently by the ilium. It has, however, been found in *Dactylethra capensis*, a Toad which also possesses a simple epipubic cartilage. This cartilage, which projects forwards medianly from the symphysis pubis, is absent in other *Anura*, but large in *Urodela*, where it is Y-shaped.

The limbs consist of the same parts as in higher Vertebrata. They are relatively small as compared with the bulk of the body in the lower *Urodela* and the *Stegocephali*, but are large and long, especially the hind extremities, in *Anura*. The humerus, radius, and ulna are cylindrical bones with cartilaginous ends in *Urodela*, and the same is true of the corresponding sections of the hind-limb. The cartilage contains much calcareous deposit in *Anura*, in which also the radius is fused with the ulna, the tibia with the fibula. The bones of the carpus and tarsus are usually cartilaginous in *Urodela*, ossified in *Anura*. There are many differences observable in the carpal and

tarsal bones, but in *Anura* the astragalus and calcaneum are always lengthened like the other bones of the limb, and are united at each end. A double centrale is often present in adult *Urodela*. In this order there are generally four, in *Anura* five toes to the fore-foot, in both five toes to the hind-foot. But reduction of the numbers occurs in *Urodela*. Indications of a sixth ulnar digit and a sixth tibial digit are found in both *Urodela* and *Anura*, and in the latter the sixth toe may be well developed. The toes are webbed in *Anura*. The carpus and tarsus appear to have been cartilaginous with rare exceptions in *Stegocephali*.

The olfactory lobes are sessile, and in *Anura* connected at their bases (see p. 75). The cerebral hemispheres are relatively large, largest of all in *Gymnophiona*, and are usually elongated. They are connected by an anterior commissure. The thalami optici and the paired optic lobes are not so clearly marked off from one another in *Urodela* as in *Anura*, where the latter are large, and contain ventricles of considerable size. The cerebellum is always a transverse bridge of variable breadth. The pineal gland is saccular in the young Anuran, perforates the roof of the skull, and is attached anteriorly to the skin. In the adult the cavity of the sac is obliterated, and its walls become fibrous. The gland does not perforate the cranium in *Urodela*, but its apex is attached to the cranial roof. The infundibulum is of great length in *Epicrium*. All the parts of the brain lie in the same plane. The most notable features in the cranial nerves are the following. The roots of the olfactory nerves unite only distally in *Pipa*, and not at all in *Gymnophiona*, where the dorsal and ventral bundles pierce the ethmoid separately. The Gasserian ganglion of the trigeminus and the ganglion of the seventh nerve remain distinct in *Urodela*, though united by a nerve: they are closely approximated in a few *Anura*, but fused in the majority. The auditory and facial have a common root. The ganglia of the glossopharyngeus and vagus are united, and the nerves generally pass out through the same foramen in the exoccipital. There is no spinal accessory nerve, and the area supplied by the hypoglossal is supplied by the first spinal nerve in the majority: by the first and second (*Salamandra*): by the second (*Pipa*) or the second and third (*Menobranthus*). There is a cutaneous branch of the trigeminus to the dorsal aspect of the head in some *Urodela*, and in the tadpole of the Frog. Cutaneous branches of the vagus exist also, taking a lateral course along the body. There are three such nerves in the perennibranchiate *Urodela*, in *Derotremata*, and even in *Triton*, but they are lost in Salamanders (? all) and *Anura*. In the latter, however, a branch accompanies the pulmo-cutaneous artery. The membranes of the brain and spinal cord have an abundance of pigment cells in their visceral laminae, and deposits of crystalline calcium carbonate are observable on the exterior of these membranes, and especially of their prolongations upon the spinal nerves (p. 76). The nasal capsules are supported by a solid

(*Siren*) or fenestrate (*Proteus*, *Menobranchnus*) cartilage tube: they open internally within the lip in front of the ethmopalatine, there being no maxillae. The mucous membrane, as in Fish, is disposed in radial folds. In other Amphibia there are as a rule cartilaginous turbinal ridges, and the internal nares lie between the maxillae and vomers. The *Urodela* possess an internasal gland opening into the mouth and lodged in the septum of the nose. It lies more anteriorly under the praemaxillae in *Anura*. Other glands open into the narial chambers, and in *Anura* on the oral mucous membrane as well. In the *Gymnophiona* the cartilaginous ridges are replaced by bony ridges developed on the bones surrounding the narial chamber. The *tentacles* are structures peculiar to this group. They are essentially fibrous sacs lying in the cavity of the orbit, and opening anteriorly in front of it. They contain large glands and a retractor muscle, which is attached anteriorly close to the external aperture. At this spot there is a ridge or papilla which can be protruded and retracted. A gland lying in the nasal cavity opens into the sac near its external aperture. The eye is small in comparison with that of Fish, but as in that class, the lens is spheroidal, and the cornea, except in the Land Salamander (*S. terrestris*), flat. The eye is hidden beneath the integument in *Proteus* and *Gymnophiona*. An upper and lower lid is usually developed in *Urodela*: the latter in *Anura* forms a large nictitating membrane, connected at its angles with the retractor bulbi muscle. The lacrymal gland is absent, but there is a Harderian gland in *Anura*. A lacrymal duct leads to the narial chamber, except in *Gymnophiona*. The ciliary muscle is feebly indicated. Colourless or faintly yellow oil globules are found in the cones of *Anura*. There is no tympanic cavity in *Urodela*, and the same is true of some *Anura*, but a simple stapes is present, attached to the membrane of the fenestra ovalis. Other *Anura* have a tympanic membrane attached to a tympanic annulus, the homologue of the spiracular cartilage of *Elasmobranchii*, a tympanic cavity, and a well-formed and complex stapes or columella auris (*supra*, p. 339), and a fenestra rotunda in addition to the f. ovalis. In the aglossal *Anura* (*Pipa*, *Dactylethra*) the two Eustachian tubes have a single median pharyngeal orifice. The semicircular canals are well curved in *Anura*, flattish in *Urodela*. The sacculus is large in *Urodela*, but becomes reduced with the increase in the size of the cochlea in *Anura*. The internal ear is very rudimentary in *Siphonops annulatus*, and probably in all other *Gymnophiona*, and contains no sensory nerve-endings.

Amphibia are sometimes edentulous, e. g. *Pipa* and the *Bufo*nidae. The Tadpole of the *Anura* has the jaws covered by a horny sheath. The same is the case with the praemaxillae and dentary bones of *Siren lacertina* with the addition, however, of true teeth on the vomero-palatines and splenials. The adult *Anura* rarely have teeth on the dentaries, and those structures are confined in them to the praemaxillae, maxillae and vomers. On the

latter, however, they are sometimes wanting. In *Urodela* teeth occur on the praemaxillae, maxillae, vomero-palatines, rarely on the parasphenoid, as in *Spelerpes rubra* and *Batrachoseps*, and in the lower jaw on the dentary and splenial. They usually form a single or nearly single row on the praemaxillae, maxillae, and bones of the mandible, but the vomerine, palatine, and parasphenoidal teeth are numerous and thick set. The points of the teeth only just protrude above the mucous membrane. In the *Anura* and Salamandrine *Urodela* they are double pointed, one point external, the other internal. The bulk of the tooth consists of tubular dentine surrounding a pulp-cavity, and coated with a thin layer of enamel in the Frog, or capped by enamel in the Newt, &c. The teeth are affixed to the jaws by pillars of true bone. In *Ceratophrys* (*Anura*) the dentine at the base of the teeth is folded (as in some Lizards, e.g. *Varanus*). So too in many *Stegocephali*, and in the genus *Labyrinthodon* the folds are deep, of great extent, secondarily folded, and the intervals between them are filled with cement. The *Stegocephali* have teeth on the praemaxillae, maxillae, vomers, palatines, on the dentary, and apparently sometimes on the splenial, and they are lodged in shallow depressions. The tongue is rudimentary in the lower *Urodela*. It is wanting in the *Aglossa* (= *Pipa*, *Dactylethra*) among *Anura*, but in this order, and in Salamanders it is of fair size, fleshy, attached anteriorly, but with a free thickened posterior border which is thrown forward in the act of protrusion. In the Anuran *Rhinophrynus* it is free anteriorly, and in the Urodele *Spelerpes* it is fungiform and can be protruded to a great distance. As in higher Vertebrata the tongue has a musculature of its own; it contains numerous glands and has special sense-cells interspersed in the epithelium. The alimentary canal takes a direct antero-posterior course, and the division into stomach, intestine and rectum is scarcely marked externally in *Proteus*. It is marked in other *Urodela* where there is a distinct pylorus, and the intestine (= mid-gut) is thrown into more or fewer coils except in *Gymnophiona*. The rectum is dilated. The *Anura* are characterised by the form of the stomach, which has its cardiac end dilated on the left side and its pyloric end conical and contracted. The convolutions of the intestine are numerous, and lie almost entirely on the right side. In the vegetable-feeding Anuran Tadpole the intestine is of great length and spirally coiled. The rectum opens into the anterior end of a cloaca. The mouth, pharynx, oesophagus, stomach in part, and in *Triton* the rectum are ciliated. The intestinal epithelium has a striated border and there are many glands. The liver is two lobed in *Urodela*, elongated in the lower forms and in *Gymnophiona*, broader in the higher. In the *Anura* the left lobe is subdivided into two more or less completely, and in the *Aglossa* the three lobes thus formed are united only by peritoneum. A gall bladder is always present. The pancreas is flattened and lobed (? absent in *Siren* and *Proteus*).



The heart lies anteriorly, as in Fishes, except in *Gymnophiona*. It consists of a sinus venosus divided into a larger right moiety, receiving the venae cavae, and a smaller left moiety receiving the pulmonary veins: of two auricles separated by a septum, which is complete in *Anura* but often much fenestrated in *Urodela*, e.g. *Proteus*, *Caecilia*, *Triton*; and of a single ventricle. There is always a contractile conus arteriosus, as in *Dipnoi* and *Elasmobranchii*, the muscles of which are striated. It is separated usually by a row of three valves from the ventricle and of four from the truncus aortae. One of the anterior valves is of great length and takes a spiral course in the conus corresponding to the typical spiral twist of that structure. This twist is sometimes lost. The number of valves may be increased. In *Caecilia* (*Gymnophiona*) the conus is very short, and there is but one row of valves, probably the distal. The truncus aortae is short, especially in the *Anura*. A longitudinal septum crosses it from side to side in such a way that it cuts off a ventral cavity, from which the first or carotid arch, and the second or aortic arise, and a dorsal, from which the third and fourth arches arise. These vessels are all closely united at their origins. In the Tadpoles of both *Urodela* and *Anura* there are four vascular arches. There is a direct anastomosis between the three first branchial arteries and veins in *Urodela*, but a connection through the branchial capillaries only in *Anura*. The fourth arch never supplies a gill, but gives off the pulmonary artery. The first arch gives off the internal and external carotids before it unites with the remaining three. At the metamorphosis the first arch either retains its connection with the second as in *Triton* and *Derotremata*, or loses it, as in *Salamandra* and *Anura*. The second enlarges and becomes the aorta: the third dwindles, and is either lost in *Triton*, *Derotremata* and *Anura*, or persists irregularly in Salamanders. The fourth arch enlarges and supplies the lungs: and in *Anura* a large pulmo-cutaneous vessel arises close to the place where the third arch was connected with it. The *Perennibranchiata* retain the condition necessary to branchial respiration as seen in *Urodela*, but *Menobranchus* and *Proteus* have no trace of the fourth arch except its anastomosis with the third, which serves as the origin of the pulmonary artery, and *Siren* has but a small rudiment of it springing from the third arch. There is a carotid gland, so-called in *Anura*, *Salamandrina*, and in *Amphiuma* alone among *Derotremata*. It is absent in *Perennibranchiata* and *Gymnophiona*. It is produced, as in the Frog, by the development of anastomoses between the external carotid, i.e. lingual artery, and the first branchial artery. The aortae unite below the backbone. In *Anura* the left arch gives off the caeliaco-mesenteric artery before uniting with the right. Two superior venae cavae, an inferior cava, epigastric vein and renal-portal system are always present, as in the Frog (see pp. 76-7). There are subcutaneous lymph-spaces, of great size and distinctness in *Anura*; lymph-vessels in the skin, &c.; a lymph

sinus between the two lamellae of the mesentery, which is connected with the lymph vessels and spaces of the stomach and viscera, and with a large subvertebral lymph space (cisterna lymphatica magna). The *Anura* have an anterior and posterior pair of lymph hearts; the *Urodela*, like the *Reptilia*, only a posterior pair<sup>1</sup>. They connect the lymph system with the vascular.

All Amphibia, with the exception of some *Gymnophiona* (?), pass through a branchiate condition. The Tadpole possesses three pairs of external ciliated gills attached near the dorsal ends of the three first branchial arches. The most anterior of these gills is the largest: their form varies. In the perennibranch *Urodela* they are retained, and are either lobed (*Menobranchnus*), dendriform (*Proteus*, *Siren*), or fringed. In the larvae of other Amphibia which lose the gills, they are more or less lobed, or dendriform, as a rule. In the Anuran *Notodelphys* they are bladder-like, as in *Caecilia compressicauda* among *Gymnophiona*. *Epicrium glutinosum* in the same order has three pairs of dendriform gills<sup>2</sup>. There are four branchial slits, reduced to three in *Siren*, or to two between the first, second and third branchial arches in *Proteus* and *Menobranchnus*. The adjacent edges of the arches in *Urodela* are furnished with interlocking tooth-like processes, as in Fish, which become very much complicated in the Anuran Tadpole. The external gills are soon lost in *Anura* and replaced by internal foliate gills. The gill-slits are also covered, as in the larvae of Salamanders, by a membranous opercular fold, which reduces the external apertures. They are eventually closed. In one group of *Ichthyoidea*, the *Derotremata*, the slit between the third and fourth branchial arches is retained permanently after the shedding of the branchiae. This event does not always take place at the same date in the life of the larva.

The inlet from the pharynx to the lungs is guarded by two arytenoid cartilages in *Urodela*, to which are added a circular cricoid cartilage in *Anura*. There are both constrictor and dilator muscles acting on these cartilages. There is a trachea of considerable length in *Menopoma*, *Amphiuma* and *Gymnophiona*, and bronchi in *Pipa* and *Dactylethra*: the cartilage supports of these tubes do not form rings. In other Amphibia the air passages are only rudimentarily represented. There are two lungs, ellipsoidal sacs in *Anura*, more or less cylindrical in Salamanders. As to *Perennibranchiata* they are short in *Menopoma*, long in the others, and much contracted for part of their length in *Proteus*. The left lung is rudimentary in the snake-like *Gymnophiona*. The inner surface of the lungs is areolated, but in *Menobranchnus* and *Proteus* it is smooth. A peritoneal fold suspends

<sup>1</sup> Many contractile lymph-hearts have lately been discovered in *Salamandra maculosa* and *Siredon* (Axolotl); Weliky, Z. A. vii. 1884. So too in the Frog's tadpole, Id. Z. A. ix, 1886.

<sup>2</sup> External gills are not known to exist in other *Gymnophiona*. The young *Epicrium glutinosum*, after losing its gills on hatching, has two gill slits. *Caecilia oxyura* when young has a single pair of slits; *C. recurvirostra* has none.

each lung in the two last-named Amphibians and in *Menopoma* to the dorsal wall of the coelome.

A pronephros connected with the anterior end of the segmental duct forms the excretory apparatus of the Tadpole. It atrophies after a time, and the segmental duct becomes split into the Wolffian duct of the mesonephros, and the Müllerian duct. The mesonephros in the young *Caecilia* (*Gymnophiona*) consists of a segmental tube with a nephrostome and Malpighian body corresponding to each myomere. At a later period the posterior tubes become compound, while the anterior retain their primitive arrangement, and the mesonephros forms a narrow band of great length. In the *Urodela* the mesonephros is divisible into a narrower anterior sexual region and a broader posterior or excretory region. In the lower forms the distinction is not so marked as in the higher, in which the anterior section may exceptionally be cut off (*Salamandra perspicillata*). There appears to be in development more than one segmental tube to each myomere, the number increasing posteriorly, but while in the sexual region the tubes are single and open independently into the Wolffian duct, they are compound in the posterior region. There are a number of separate collecting tubes to the posterior region of the mesonephros in *Urodela* which open into the Wolffian duct as a rule only near its cloacal extremity. The number of nephrostomes is great, and two may open in the posterior region into the same tube or a single nephrostome lead into a canal which divides. These abnormal relations become the rule in *Anura* where the nephrostomes are connected in the adult with the renal-portal capillaries (?). In the *Anura* the mesonephros is broad and a segmental arrangement of its tubes is not traceable. The Wolffian duct is dilated in the male, where it becomes free from the gland. This dilatation acts as a vesicula seminalis (see p. 78). The kidneys are covered by peritoneum only on their ventral surface, to which the nephrostomes are confined, in *Anura* and *Urodela*, on both dorsal and ventral in *Gymnophiona*. The Wolffian ducts open separately on the dorsal wall of the cloaca. An allantoid bladder, or ventral outgrowth of the cloaca, is invariably present. It has an anterior and posterior horn in some *Gymnophiona*, and is bifurcated anteriorly, in all *Anura* and the *Urodela* with a few exceptions (some Salamanders and the lower forms).

The sexual organs, male and female, lie near the inner border of the kidneys, suspended by peritoneal folds: in *Gymnophiona*, however, to their outer or ventral sides. The testes in *Gymnophiona* consist of a series of more or less oval bodies one behind the other, traversed and connected by a common collecting tube. The tubuli seminiferi open into this tube, from which transverse canals, arising one between each testicular body, pass to a longitudinal canal lying near the inner border of the kidney. From this in turn a series of transverse canals arise which are connected each to a

Malpighian body. In other Amphibia the testes are compact bodies. The *Urodela* have an internal collecting tube for the seminal tubes, which is wanting in *Anura*, where there is generally an *intratesticular* network of vessels. The collecting tube of *Urodela* is connected by a variable number of transverse canals to a longitudinal canal (*supra*), and this in its turn by other transverse vessels to the Malpighian bodies of the sexual region of the mesonephros. The longitudinal canal is sometimes absent (*Spelerpes*) and a direct connection then occurs between testis and kidney. The longitudinal canal is present in many *Anura*, but in *Bufo* only do the transverse canals become connected with Malpighian bodies. For *Rana*, see p. 78. In *Bombinator* most of the transverse vessels end blindly, and the anterior are connected directly to the Wolffian duct. In *Discoglossus* a few vessels connect the testis to the same duct, but in *Alytes obstetricans* the *extra-testicular* network is connected to the Müllerian duct, which ends blindly anteriorly, and opens posteriorly into the Wolffian duct. The Müllerian duct always exists in the male. In *Gymnophiona* it may retain its abdominal opening; it is extremely glandular posteriorly, as in *Bufo*, and each duct opens into the cloaca separately. In *Bufo* the two ducts unite first and then open into the cloaca. It always loses in *Urodela* its cloacal connection; it sometimes preserves, sometimes loses, both its abdominal opening and its cavity. In *Anura*, except *Bufo*, it is reduced to a solid cellular cord. Some male Toads, e. g. *Bufo cinereus*, have a rudimentary ovary. The ovary in *Gymnophiona* is a long thin band; in *Urodela* a cylindrical sac, and in *Anura* a sac subdivided by complete partitions into a series of more or fewer compartments. The ova are shed into the coelome, whence they are taken up by the abdominal apertures of the Müllerian ducts, which are close to the anterior ends of the kidneys in *Gymnophiona*, at the roots of the lungs in other Amphibia. They are straight in *Gymnophiona*, somewhat convoluted in *Urodela*, and especially so in *Anura* at the breeding season. In viviparous Salamanders their distal portion is dilated and functions as uterus. It is also dilated and acts as a reservoir for the albumen-coated ova in *Anura*. The two ducts open separately on the dorsal wall of the cloaca, except in *Alytes* and *Bufo*, where they unite and open by a common aperture. In both male and female Toads (*Bufo*) an undeveloped and cellular remnant of the genital rudiment lies at the anterior end of the sexual glands, and is known as Bidder's organ<sup>1</sup>. 'Fat bodies' of unknown function are found in all Amphibia, laterally placed to the sexual glands in *Gymnophiona*: between them in *Urodela* and at their anterior ends in *Anura*. The cloaca is partially eversible in the male

<sup>1</sup> For an account of this remarkable organ, see Knappe, M. J. xi. 1886. It tends to disappear in the female sooner or later. Its cells closely resemble ova and are inclosed by follicle cells, but isolated cells here and there have been observed to form spermatozoa. It occurs in hermaphrodite individuals.

*Gymnophiona*, and is probably used as an intromittent organ. Specialised copulatory organs are not present.

*Caecilia compressicauda* among *Gymnophiona* is viviparous, as are *Salamandra maculosa* and *S. atra*. Other Amphibia are oviparous, and the ova are generally laid in water, either in floating masses (*Anura*) or affixed to water-plants (*Triton*, *Axolotl* among *Urodela*). Certain exceptional cases may be noted among *Anura*. The ova are stored in a dorsal sac opening above the cloaca in *Notodelphys* and *Nototrema*: in cavities one for each ovum, formed by hypertrophy of the dorsal skin in *Pipa*, the male spreading them on the backs of the female. They are affixed to leaves of plants in one or two instances, e.g. by *Hylodes martinicensis*: are carried by the male *Alytes obstetricans* twisted round the hind-limbs until the Tadpoles are ready to escape, and by the male *Rhinoderma Darwinii* in the enlarged croaking sacs<sup>1</sup>. Impregnation is external in *Anura*. The male Urodele, so far as is known, deposits a spermatophore, formed by the cloacal and pelvic glands (?), which is taken up by the female and therefore impregnation is internal, as it must be in *Gymnophiona*. There is a sexual congress in *Anura*, and in one Urodele at least (*Glossoliga Hagenmülleri*). The ova are enveloped in albumen secreted by the oviduct. They are usually small. Segmentation is as a rule complete, but in some instances there is a large amount of yolk and a yolk sac, as in Teleostean fish, e.g. *Epicrium glutinosum*, *Pipa*, *Alytes*. Segmentation is unequal. The epiblast consists of two strata, an epidermic and a nervous, from the first in *Anura*, a condition attained at a later period in the Newt. There is a metamorphosis, the degree of which varies. The larva has usually a fish-like aspect: the head not well marked off from the body: a long tail with azygos fin: three pairs of external gills: no limbs except mere indication of the forelimbs in the Newt: adhesive organs in the *Anura*, and a pair of supporting processes below the neck in the Newt. The young *Caecilia compressicauda*, *Salamandra atra*, *Pipa* and *Hylodes martinicensis* have the adult form when they come into the world. The two first named have an intra-uterine development, the latter of the two having long gills, which are lost if the young are transferred to water, a new and shorter set being developed. *Pipa* passes through its metamorphosis in the cavity of the skin in which the ovum lies. *Hylodes* has an intra-ovular metamorphosis, and in two species of *Nototrema* the young quit the dorsal pouch in a perfect state. *Epicrium glutinosum* loses its external gills before it is hatched, and the larva wanders from the spot in the earth where the eggs are laid and leads an aquatic life for a time. It swims by means of its tail, which is provided with a fin. The tail is lost in the adult as in other *Gymnophiona*. The Anuran Tadpole also loses its tail by absorption. The changes which take place in the metamorphosis are profound in the *Anura* and higher *Urodela*,

<sup>1</sup> See remarks and a table by Boulenger to a paper by von Ihering in A. N. H. (5) xvii. 1886.

and have been indicated in part above. For details larger works must be consulted.

The Alpine *Triton alpestris*, one of the *Salamandrina*, has been observed to attain sexual maturity, indicated by external signs and by maturation of ova and spermatozoa, at a time when the branchiae are still in functional activity, and the characters of the skeleton show the animal to be really in a larval state. The Axolotl (*Siredon pisciformis*) has long been known to be competent to sexual functions whilst in a perennibranch condition, a condition in which many individuals remain. Other individuals undergo a change into the Salamandrine *Amblystoma mexicanum*. This change takes place in its natural habitat, and has been also induced artificially.

Some Amphibia, but not *Anura*, show great power of repairing injuries and of reproducing destroyed or amputated organs. Many of them possess protective coloration which is intensified by the state of distribution of pigment controlled by the nervous system. The Anuran larva feeds on vegetable matters. The adult is carnivorous in all instances, insects, worms, snails, &c., and even higher animals forming the prey. The Amphibia are absent from nearly all oceanic islands. The *Anura* are widely distributed: the *Urodela* are limited to the temperate parts of the northern hemisphere, and are especially numerous in North America. No fossil *Gymnophiona* are known. *Anura* and *Urodela* occur in Miocene strata. The extinct *Stegocephali* are found in the older Mesozoic strata (Trias) and in the more recent Palaeozoic (Permian, Carboniferous).

The class Amphibia may be divided into orders as follows:

I. *Gymnophiona*. Snake-like in form and subterranean in habit; no limbs nor tail; dermic scales imbedded in the integument. *Cacilia* is found in West Africa, Malabar, and South America; *Siphonops* in Brazil and Mexico; *Epicrium* in Ceylon and the Khasya Mountains; and *Rhinatrema*, which has no tentaculiferous fossa in Cayenne. There are certain resemblances between this group and the family *Aistopoda* among *Stegocephali*; see Fritsch (*infra*).

II. *Urodela*. Body elongated; as a rule four short extremities and persistent tail with azygos fin.

1. *Ichthyoidea*. Eyes small, with or without a circular eyelid-like fold; with biconcave vertebrae and large remnant of notochord. Aquatic in habit.

(a) *Perennibranchiata*. Three pairs of persistent gills. *Siren*, with forelimbs only, comes from South-east States of North America; *Proteus* from caves in Carniola and Dalmatia; *Menobanchus* from East States of North America (said to change into *Batrachoseps*); the Axolotl, *Siredon*, from Central America; it changes sometimes into *Amblystoma Mexicanum*. (β) *Derotremata*. Gills caducous; as a rule a persistent gill cleft. *Amphiuma* (= *Muraenopsis*) comes from south part of North America; *Menopoma* (= *Protonopsis*) from Ohio and Alleghany Rivers; and *Sieboldia* (= *Cryptobranchus*) from Japan.

2. *Salamandrina*. Branchiae caducous; gill clefts closed in adult; eyelids;

opisthocoelous vertebrae in higher forms. *Spelerpes*, *Amblystoma*, *Triton*, *Lisso-triton*, *Salamandra*, &c.

III. *Anura*. Body compressed; tail and branchiae lost; hind-limbs of great length, and used for leaping. *Rana*, *Bufo*, &c.

IV. *Stegocephali* (= *Labyrinthodontia*, *Ganocephala*, and *Microsauria*, Auctorum). A tail; paired supra-occipital bones, supra-temporals, and post-orbitals present; generally also both pre- and post-frontals and orbital ring of bones; pubes well ossified; extinct. Extend from the Permian to the Trias.

*Gymnophiona*, Wiedersheim, 'Anatomie der Gymnophionen,' Jena, 1879. Leydig, Z. W. Z. xviii. 1867-69. *Development of Caecilia*, Peters, Monatsberichte Akad. Berlin, 1874-1875; of *Epicrionum*, Sarasin, P. B. and E. F., Arb. Zool. Zoot. Inst. Wurzburg, vii. 1885.

*Urodela*. *Anatomy of Salamandra perspicillata* and *Geotriton fuscus*, Wiedersheim, Annali del Museo Civico di Storia Naturale di Genova, vii. 1875. *Amblystoma punctatum*, Id. Z. W. Z. xxxii. 1879. *Pleurodeles Waltlii*, Fraisse, Arb. Zool. Zoot. Inst. Wurzburg, v. 1882; *skeleton*, Wiedersheim, J. Z. xiv. 1880. 'Molche der Wurtembergischen Fauna,' Leydig, A. N. 33, 1867 (sep. Berlin, 1868). *Lateral line*, Malbranc, Z. W. Z. xxvi. 1875; Merkel, Endigungen der sensibeln Nerven in der Haut der Wirbelthiere, Rostock, 1880. *Skull*, W. K. Parker, Ph. Tr. 167, 1877; Tr. L. S. (2), 1882; Tr. Z. S. xi.; Wiedersheim, M. J. iii. 1877; Stöhr, Z. W. Z. xxxiii. 1880. *Cartilage end of back-bone*, Fraisse, Z. A. iii. 1880. *Cloacal and pelvic glands*, Blanchard, Z. A. iv. 1881. *Impregnation of Axolotl*, &c. Gasco, Z. A. iv. 1881. *Change of same into Amblystoma*, (1) *natural*, Velasco, Biol. Centralbl. ii. 1882-83; (2) *artificial*, M. von Chauvin, Z. W. Z. xli. 1885, and xxvii. 1876; cf. von Siebold, *ibid.* vol. cited last; cf. Weismann, *Studies in Theory of Descent* (transl. by Meldola), pt. 3, 1882. *Sexual Urodele larvae*, Von Siebold, Z. W. Z. xxviii. 1877. *Larva of Salamandra atra*, M. von Chauvin, Z. W. Z. xxix. 1877. *Regeneration of lost parts*, Götte, Über Entwicklung und Regeneration des Gliedmassenskelets der Molche, Leipzig, 1879; Fraisse, Tagesblatt der 52 Versamml. Deutsch. Naturf. Baden-Baden, 1879, p. 223; Id. Biol. Centralb. iii. 1883-84; cf. Wiedersheim, M. J. ii. 1876.

*Anura*. See p. 78-9, 82-3. *Organs of adhesion of larva*, Stöhr, SB. Phys. Med. Gesellsch. Wurzburg, 1881, p. 118; Niemiec, 'Les ventouses,' &c.; Recueil Zool. Suisse, ii. (1), 1885.

*Stegocephali*, Fritsch, Fauna der Gaskohle und der Kalksteine der Permformation Böhmens, Prague, i. 1883; ii. pt. 1, 1885; pt. 2, 1886; cf. *Labyrinthodontia*, Brit. Association Reports, 1873, p. 225; 1874, p. 149; Cope on *Permian Batrachia*, American Naturalist, xviii. 1884.

## CLASS PISCES.

*Ichthyopsida* in which the epidermis may develope glandular cells, but not glands in the ordinary sense of the term, and the cutis is devoid of muscular elements. The exoskeleton is greatly developed, and consists always of a dermal portion (bone or dentine), to which enamel derived from the epidermis may be added. It takes the form of teeth, scales, or large scutes.

*Epidermic sensory organs are largely developed. The azygos fins are supported by fin-rays, as also are the borders of the paired limbs which have the form of fins. There is no Eustachian tube in the proper sense, no tympanic membrane or cavity, nor stapes in relation with the ear. The alimentary canal terminates very generally in a cloaca, or else the anus lies in front of the genito-urinary apertures. There is no vena cava inferior. An allantoid outgrowth of the digestive tract is invariably absent.*

The epidermis consists of polygonal cells in *Elasmobranchii*. It never develops a stratum corneum, but in some *Teleostei* and the *Dipnoi* the superficial layer of cells has a striated cuticular border. Flask-shaped mucous cells with the narrow end internal are very generally present, and in large numbers in some *Teleostei* and the *Dipnoi*. They occur in *Acipenser (Ganoidei)*, but not in *Elasmobranchii*. They appear to rise to the surface and there burst. Branched cells, both pigmented and non-pigmented, are found both in the epidermis and the cutis. They are connected with nerve-filaments. Some Fish, e. g. Turbot and Trout, have the power of altering their colour in relation with the nature of the bottom on which they are living. The epidermis at the breeding season often assumes a silvery appearance, and in some instances a brilliant coloration, e. g. Stickleback (*Gasterosteus*). The epidermic sensory structures are nerve-eminences and end-buds. The former are rarely absent altogether (*Balistes*); they may be generally distributed over the body, e. g. *Mugil*, or more or less limited to certain lines. These are typically, on the head a supra- and infra-orbital, and a mandibular line on each side, with a connecting supra-occipital line; on the body a lateral line, which follows the plane of division between the dorso- and ventro-lateral muscles, and more rarely a second line placed more on the dorsal aspect, and a third nearer the ventral surface. Scattered eminences may occur at the same time, e. g. Pike (*Esox*). They either project freely above the surface, or are sunk in grooves of the scales or in integumentary pits when scales are absent, e. g. *Silurus glanis*; or finally are lodged in canals which open externally from spot to spot. *Echinorhinus spinosus* and a few others among Sharks and the *Holocephali* have exceptionally an open groove in the region of the trunk. Canals are generally developed on the head, where they may be much branched as in *Elasmobranchii*; on the body also, but either only anteriorly, or posteriorly (some *Teleostei*), or throughout its whole length. The canals of the body are much branched in the Rays. The whole canal system and integumentary pits are filled with mucus secreted by certain of the lining cells. This mucus is gelatinous and firm in *Elasmobranchii*, softer in other Fish. *Elasmobranchii* have peculiar structures known as ampullae on the head, and *Ganoidei* nerve-sacs in the same region. The latter are minute depressions with sense-cells at the bottom, beneath which lies a space filled by jelly. The former are tubular, and the base of the



tubule is dilated and either simple or sacculated, and contains sense-cells in the lining epithelium. The ampullae are filled with gelatinous mucus. End-buds are as a rule plentifully scattered over the head and body in *Teleostei*, but they may be wanting entirely, e. g. in *Mugil* and *Esox*, where scattered nerve-eminences occur. They have only been detected in *Torpedo* among *Elasmobranchii*. But in all Fish with few exceptions, where they are replaced by nerve-eminences, they occur in the mouth and on the branchial arches. The sense-cells of the buds differ from those of nerve-eminences in extending from the surface to the base of the epidermis. End-buds are also generally prominent.

Curious 'eye-like' organs are imbedded in the skin of certain pelagic and deep-sea *Teleostei* (*Scopelus*, *Chauliodus*, &c.). According to peculiarities of structure these organs are divisible into 'eye-like organs proper,' 'pearl-like,' and 'phosphorescent' organs. They all agree in possessing an iridescent layer resembling a tapetum, and like it reflecting light. The mucus coating the surface of the body is often phosphorescent, and some Fish possess phosphorescent organs, e. g. an appendage beneath the head in *Eustomias*.

The exoskeleton is rarely absent, e. g. in many Eels and all electric Fish; it is sometimes rudimentary. The primitive form occurs in *Elasmobranchii* in the shape of dermal teeth (= placoid scales), similar in structure and development to oral teeth and borne upon a plate of bone formed in the cutis<sup>1</sup>. The *Siluroidei* among *Teleostei* have dermal teeth also, moveably articulated, however, to their bony supports, and these supports often fuse into large plates. In other Fish teeth tend to disappear, and the supporting bone constitutes the scales, scutes, spines, or shields of the exoskeleton. Teeth, however, are found on the skin between the mandibles of *Lepidosteus*, and as minute spines on the edges of its scales. The enamel, however, is homogeneous, the dentine tubular and a pulp-cavity absent. Minute denticles of non-tubular dentine are also found on the outer surface of the scales of *Protopterus* (*Dipnoi*). The spines projecting through the epidermis from the scales and scutes of *Acipenser* are homogeneous structures. The scales of *Lepidosteus* and *Polypterus* among living (as of many extinct) *Ganoidei* are covered with a layer of homogeneous enamel. They are lodged, as are the scales of *Teleostei* and *Dipnoi*, in sacs of the cutis. The scales thin out at their edges and vary much in size. They are cycloid or ctenoid according as their projecting margin is entire or denticulated. Among *Plectognathi* (*Teleostei*) the *Ostraciontidae* are covered with a mail of large polygonal plates; and the

<sup>1</sup> *Pristis*, the Saw-fish, one of the Rays, has a long flat prae-nasal cartilage. A linear series of teeth, similar in structure to the oral teeth of *Myliobatis*, another Ray, are implanted in sockets along the edge of this rostrum. They grow from persistent pulps. The Saw-fish is said to glide rapidly by a whale and to rip it with these weapons.

genus *Diodon* with its immediate allies has projecting spines with bare skin between. Bony shields of great size are found in many living *Siluroidei*, but especially in the extinct Ganoid *Placodermi* (*Pterichthys*, *Cephalaspis*) from Devonian and Carboniferous strata, but they are restricted to the fore-part of the body

The dermal exoskeleton appears to have given origin to the investing bones of the skull and shoulder-girdle, which adapt themselves more and more to the underlying cartilage, and eventually replace it in part in the former. The fin-rays supporting the azygos fins and the edges of the paired fins have a similar origin. Each ray primitively consists of a series of pieces, which are paired right and left in the azygos fins, dorsal and ventral in the paired.

The continuous azygos fin of the embryo persists in the adult of some Fish, e.g. the Teleostean Eel, Sole, Cod (*Anguilla*, *Pleuronectes*, *Gadus*) probably by reversion (Balfour). It is usually broken up into one or more dorsals, a caudal, and one or more anals. The fin-rays are horny in *Elasmobranchii*; cartilaginous throughout in chondrostean *Ganoidei* and the *Dipnoi*, but with a thin shell of bone formed in the perichondrium in the latter; whilst in *Teleostei* and bony *Ganoidei* they are ossified. In the latter case they may be *soft* and consist either of a series of joints or be branched dichotomously; or *entire*, i.e. spinose, and of one piece throughout. In some *Elasmobranchii* and in *Polypterus* the sections of the dorsal fin are carried each by a strong spine (ichthyodorulite); in a few *Teleostei* its posterior lobe contains only horny fin-rays, is soft and fatty, forming a small *adipose* fin (*Salmonidae*, some *Siluroidei*, &c.). The fin-rays of the ventral portion of the caudal fin are carried by haemal arches; but those of its dorsal portion, of the dorsal and anal fins by skeletal elements lying in the median fibrous septum dividing the right and left halves of the body (see p. 101). The caudal fin, which is an all-important organ of locomotion, is either heterocercal, homocercal, or diphyrcercal. It is heterocercal when the vertebral axis is bent dorsally and terminates in a lobe or point, and the caudal ventral lobe is placed at a greater or less distance from its extremity; homocercal when it is outwardly symmetrical, but in reality consists almost entirely of a caudal ventral lobe, the extension of the vertebral axis beyond the lobe being atrophied; and diphyrcercal when it is divided into equal dorsal and ventral lobes by a straight vertebral axis. A heterocercal caudal fin is found in *Elasmobranchii*, *Holocephali*, chondrostean and many extinct *Ganoidei*; a homocercal in living bony *Ganoidei*, and the majority of *Teleostei*; and a diphyrcercal in a few *Teleostei* and the *Dipnoi* (see p. 97). In some *Ganoidei*, living, e.g. *Acipenser*, *Lepidosteus*, and extinct, a single or double row of small spines known as fulcra extend along the anterior margins of the dorsal or caudal fin, and on the ventral edge of the latter as well in *Lepidosteus*.

The chondrocranium is always well-developed. It is massive in the Sturgeon and some *Teleostei*, e.g. Salmon, and its prae-nasal region is occasionally of great size, e.g. in some Rays, as *Pristis*, the Sturgeons, and a few *Teleostei*. It is interrupted by superior fontanelles in *Amia*; by lateral and basal fontanelles as well in *Polypterus* and *Lepidosteus* (*Ganoidei*). There are neither investing bones nor intrinsic centres of ossification in *Elasmobranchii* and *Holocephali*. In the latter the palato-ptyerygo-quadrata cartilage is continuous with the cranium; among the former it articulates with it in *Hexanchus* and *Heptanchus* (*Notidanidae*), whilst in others it is attached by ligament and by the hyomandibular<sup>1</sup>. A spiracular cartilage is sometimes found in the edge of the ligament anterior to the spiracle (*infra*). The lower jaw is a simple rod of cartilage articulating with the palato-ptyerygo-quadrata and connected to the cranium by the hyomandibular. In other Fish both intrinsic centres of ossification and investing bones are found, and, taking a Teleostean (p. 91) as a standard, the following points may be noted. The jaw-apparatus of *Acipenser* is only connected to the cranium by a hyomandibular and a symplectic cartilage, both partly ossified: the metapterygoid region of *Lepidosteus* has an articulation with the base of the skull; and the palato-ptyerygo-quadrata is continuous with the cranium in *Dipnoi*, forming also the sole support of the mandible. *Acipenser* possesses only a pro-otic, ali- and orbito-sphenoid and an ecto-ethmoid ossification in the cranium, and the mandibular cartilage is unossified as it is also in *Dipnoi*. Among the bony *Ganoidei* there is no supra-occipital, no pterotic: in *Polypterus* no epiotic distinct from the opisthotic. The prae-pituitary region contains in *Amia* two ali-, two orbito-sphenoids and ecto-ethmoids: in *Lepidosteus* two ali-sphenoids and a single bone, perhaps formed by coalesced ecto-ethmoids: in *Polypterus* two sphenoidal bones and ecto-ethmoids. The palatine and pterygoid bones of *Lepidosteus* are simply investing bones, as in many Amphibia. *Polypterus* has no symplectic. The lower jaw has more than one articular ossification, and in *Amia* a mento-meckelian. The *Dipnoi* have exoccipitals and palato-ptyerygoid ossifications. As to the investing bones of the skull there are very many variations. *Acipenser* has a large number, among which may be recognised a supra-occipital, paired parietals and frontals, and a huge parasphenoid. There are additional bones, not seen in *Teleostei*, to be found in bony *Ganoidei*, such as a squamosal over the pterotic region, a supra-temporal bone in *Amia*, &c. *Protopterus* among *Dipnoi* has a fronto-parietal, a median supra-ethmoid (as in the Salmon), two nasals, and a large supra-orbital on each side; *Ceratodus* an unpaired parietal and frontal and a pair of lateral bones, the outer perhaps a prae-opercular. The vomer is double in bony *Ganoidei*, absent in *Dipnoi*; in both the parasphenoid is large and extends backwards beneath the backbone as

<sup>1</sup> This palatal cartilage has an upper portion of the hyoid fused with it in the embryo of *Selachoides*.

it does in *Acipenser*. The praemaxillae are absent in the Sturgeons: the maxillae are represented by a chain of bones in *Lepidosteus*, and both praemaxillae and maxillae are absent in *Dipnoi*. The mandible is invested by a dentary bone alone in Sturgeons: by dentary, splenial, and angular in *Dipnoi*, and *Polypterus*, to which *Lepidosteus* and *Amia*, add a supra-angular and the former a coronoid. As to opercular bones, *Acipenser* has a large operculum: the *Dipnoi* have opercular and interopercular bones; the inter-operculum is absent in *Polypterus* and the prae-opercular fused with the squamosal: the prae-operculum is very small in *Lepidosteus*, the interoperculum of great size. *Amia* resembles a Teleostean. *Amia* has a single, *Polypterus* a double jugal bone between the mandibular rami. These bones are also found in some extinct *Ganoidei*, and must not be confounded with the branchiostegal rays of *Amia* and *Teleostei*, which carry on the series of opercular bones ventrally.

The hyoidean and branchial arches are unossified in *Elasmobranchii*, *Holocephali*, *Ceratodus*, and *Protopterus*. The hyoid is an unsegmented rod in the Dog-fish (*Scyllium*) and some other Sharks. It and the branchial arches are as a rule segmented and ossified typically (p. 93). The last arch present is usually rudimentary. There are seven branchial arches in *Heptanchus*, six in *Hexanchus* and *Protopterus*, five in other Fish. The fifth pair fuse into a median bone in *Pharyngognathi* (*Teleostei*). Gill-rakers or pointed cartilaginous processes crossing the branchial slits are borne upon the branchial arches in many *Elasmobranchii*, some *Teleostei* and the *Dipnoi*. Branchial rays radiate outwards from the branchial arches into the septa between the gill-pouches in *Elasmobranchii*: and in Sharks curved extra-branchial cartilages are attached to the bases of more or fewer of the branchial arches and lie close beneath the outer edges of the septa just mentioned.

The backbone is formed by the notochord with its sheath in a few *Elasmobranchii* (e.g. *Echinorhinus*), in *Holocephali*, chondrosteian *Ganoidei*, *Dipnoi*. Bony rings, more numerous than the arches, are formed in the sheath in *Holocephali*. In other Fish there are ossified amphicoelous vertebrae, between which the notochord persists. *Lepidosteus* alone has opisthocoelous vertebrae, and in development an inter-vertebral thickening of the cartilage which divides, forming, as in Sauropsida and Amphibia, the opposing faces of adjoining vertebrae. The vertebral centra originate in *Elasmobranchii* by the growth of the bases of both neural and haemal arches round the notochordal sheath, and the fusion of the growths with the vertebral thickenings of the sheath. Ossification in the centra thus formed takes place concentrically (*Cyclospondyli*) or radially (*Asterospondyli*). The centra in bony *Ganoidei* and *Teleostei* are formed chiefly by parosteal ossification, imbedding the bases of the arches neural and haemal (p. 100). The centra are united at their edges by ligament. The neural ridges form

a complete investment to the spinal cord in *Elasmobranchii* and *Holocephali*. They are differentiated into neural arches (=crural cartilages) which may or may not bear neural spines, and into intervening intercrural cartilages which are placed intervertebrally. These parts may be incompletely ossified. The haemal ridges in the caudal region are differentiated similarly. Small intercrural cartilages are present in *Acipenser*, and are perhaps represented in *Lepidosteus* and some *Teleostei* (p. 101). The ossified neural and haemal arches of *Amia* are connected to the vertebral centra by cartilage discs: in *Polypterus*, *Lepidosteus*, and *Teleostei* they are continuous with the centra and are formed by parosteal ossification round cartilage, which may or may not persist. The right and left arches are connected *inter se* above the spinal cord by either bone, cartilage, or ligament. The summits of the neural spines and of the haemal spines perhaps form the supports for the dorsal and anal fins respectively (p. 101). In all Fish a superior longitudinal ligament connects all the neural arches above the neural canal. Bony zygapophyses are formed near the bases of the neural arches in some *Teleostei*. A cartilaginous rod terminates the backbone in *Ganoidei*, some *Teleostei*, and the *Dipnoi*. It is surrounded by a bony sheath (urostyle) in some *Teleostei*, and gives support to more than one neural and haemal arch.

There are only two regions in the backbone, a dorsal and a caudal—the latter distinguished by the ventral fusion of the haemal arches or ribs (p. 100). The largest number of vertebrae is found in *Elasmobranchii*. In some of the latter, e.g. *Scyllium* and *Raja*, there are twice as many centra in the tail as there are myomeres and spinal nerves. The most anterior vertebrae coalesce with the skull in *Ganoidei*, some *Teleostei* and *Dipnoi*. In some *Elasmobranchii* at least, the two structures are articulated by distinct exoccipital condyles.

The ribs are cartilaginous in *Elasmobranchii*, *Holocephali*, chondrostean *Ganoidei*, and *Dipnoi*. They are always simple in form, and lie in *Elasmobranchii* in the fibrous septum between the dorso- and ventro-lateral muscles. In other Fish they lie close to the peritoneum, but their ends turn outwards in *Lepidosteus* into the septum named. They correspond to the myocommata, in which slender bones (epi-centrals, epi-neurals, epi-pleurals) may be formed in some *Teleostei*.

As to the limbs, the ventral fins are absent in a few *Teleostei*, e.g. *Muraenidae*, *Gymnotidae*, among *Physostomi*; *Syngnathidae* among *Lophobranchii*; *Ostraciontidae* and Gymnodonts among *Plectognathi*, or else represented by moveable spines, as in *Balistidae* and *Triacanthidae* in the order last named. Their occasional absence has been noted in *Protopterus*.

The shoulder-girdle is cartilaginous in *Elasmobranchii*, *Holocephali*, chondrostean *Ganoidei* and *Dipnoi*, ossified as a separate scapula and coracoid (claviculo-coracoid) in bony *Ganoidei* and *Teleostei*. It is of large

size in the two first-named orders, and the right and left parts are either continuous ventrally or united by ligament. A distinct supra-scapula is present in many *Elasmobranchii*, especially in Rays, where it is attached to the vertebral column, and in the Sturgeon, which has also a large clavicular process. The form of the parts varies much, e.g. in Rays the articular region is of great extent and much fenestrated. The bones are small in *Teleostei*, and there are many variations in their mode of ossification. The *Ganoidei* and *Teleostei* have investing bones known as supra-clavicle, clavicle, inter-clavicle, and post-clavicle, all derived apparently from the skin and lining membrane of the branchial cavity, and present in none of the higher Vertebrata (p. 97); and a supra-temporal scale-bone (the first of the lateral line) connects the clavicular series to the epi- and opisth-otic regions of the cranium. There are two investing bones also in *Dipnoi*, which ensheath the cartilage in *Protopterus* and *Lepidosiren*. The girdle is deeply imbedded in the muscles in the two last-named Fish, and the limb is articulated to its proximal, i.e. dorsal, extremity.

The pelvic cartilage is a continuous curved bar in *Elasmobranchii*, representing an ischio-pubic region, the part dorsal to the attachment of the limb, i. e. the iliac region, being absent or inconspicuous; but it is large in *Holocephali*, where the two halves of the girdle are united ventrally by ligament. Two minute cartilages are found in *Polypterus*: otherwise the pelvis is not represented in any Ganoid or Teleostean. A median cartilage bears the limbs in *Dipnoi*, and extends forwards as a pointed rod.

The fore-limb consists typically in *Elasmobranchii* of three basal cartilages,—pro-, meso-, and meta-ptyerygium, articulating each with a facet on the shoulder-girdle; of one or two outer rows of cartilaginous rods known as *radialia*, followed by horny fin-rays. The pro- is sometimes not differentiated from the meso-ptyerygium. Certain radialia intrude in Rays between the meso- and meta-ptyerygium, touching the shoulder-girdle. *Polypterus* among *Ganoidei* has rod-like ossified pro- and meta-ptyerygia and a broad meso-ptyerygium. All other *Ganoidei* and *Teleostei* have a meso-ptyerygium generally imbedded in the base of the first fin-ray, some intrusive radialia and a meta-ptyerygium. But this region of the limb may be entirely absent in some *Teleostei*. The radialia are well-developed in chondrosteian *Ganoidei* and *Polypterus*; they are usually small and nodular in *Teleostei*, a group in which movement of the limb takes place along the line of union between them and the more proximal parts. The fin-rays are ossified in *Ganoidei* and *Teleostei*, usually soft, sometimes entire, especially in the first. The hind-limb in *Elasmobranchii* and the *Holocephali* contains often only one basal cartilage, a metapterygium, but a second is sometimes present in the former, and is usually termed pro-ptyerygium. It probably represents an undivided pro- + meso-ptyerygium. There are radialia and fin-rays, as in the fore-limb. The most posterior fin-ray is usually large, and con-

nected with the cartilaginous bars of the claspers (pterygo-podia) in the male and their rudimentary representatives in the female. In all other Fish a metapterygium only is present, very broad and even secondarily segmented in chondrostean *Ganoidei*. The two metapterygia are also independent in them, except in *Scaphirhynchus*, where, as in bony *Ganoidei* and *Teleostei*, the two are united medianly with more or less completeness. The number of radialis is great in chondrostean *Ganoidei*. They have two rows; so too *Polypterus*; but other *Ganoidei* are reduced to a single row, usually inconspicuous and few. The fin-rays resemble those of the fore-limb. The *Dipnoi* differ from the preceding in having a limb composed of an axial series of cartilaginous pieces ranged end to end. These in *Ceratodus* from the second onwards bear a bilateral series of jointed cartilaginous rods diminishing in length to the apex of the limb, and continued outwards into horny fin-rays. *Protopterus amphibius* has a unilateral series of such rods, always very small, absent in *P. annectens* and *Lepidosiren*. Their limb is long and linear.

It may be noted that in some *Elasmobranchii* there are radialis, always few in number, on the posterior or inner edge of the metapterygium. They are probably secondary in origin. The ventral fins in all Fish have an abdominal position, except in some *Teleostei*, where they may shift forwards and become thoracic or even jugular in position (p. 83).

The muscles of the trunk and tail retain their segmentation. A fibrous septum in the median dorsal and ventral lines divides the musculature of one side of the body from that of the other. Another separates the dorso- from the ventro-lateral muscle-masses. The muscle fibres run longitudinally from one myocomma (septum between two muscle segments or myomeres) to the next. They are oblique in the ventro-lateral trunk muscles of *Elasmobranchii* and *Ganoidei*, and the corresponding region in *Protopterus* is divided into two oblique layers, as in Amphibia *Urodela*. The electric and pseudo-electric organs are apparently modified muscular tissue, except perhaps in *Malapterurus* (*Siluroidei*), a fish in which the organ lies beneath the skin and external to the muscles, and forms a nearly complete envelope round the trunk. The two organs in *Torpedo* (*Batoidei*) lie on either side the head, and are supplied by a nerve from the electric lobe of the medulla oblongata. In the Eel, *Gymnotus*, they replace the greater part of the ventro-lateral muscles of the tail, as do the pseudo-electric organs of Rays, *Mormyrus*, *Gymnarchus* among *Teleostei Physostomi*, and they are supplied by spinal nerves. Each organ consists of a number of long hexagonal capsules, placed dorso-ventrally in *Torpedo*, antero-posteriorly in the remaining Fish, and containing each an electric plate, to one surface of which the nerves are distributed, whilst the other is in relation with a gelatinous substance. The nerves break up into fine

branching primitive fibrils, and are remarkable for the extreme thickness of their sheaths. The neural aspect of the plate is negative electrically.

The brain fills the brain-case in embryonic Fish, but it finally occupies a very small part of that cavity, owing to the disproportionate growth of the cranial walls. The space left is filled by a fibrous and fatty arachnoid tissue. The cerebro-spinal membranes develop pigment cells, as in Amphibia. The nerve-centres are smaller in relation to the bulk of the body in this than in any other Vertebrate class, the ratio of brain to body being as low as 1 to 3000, and the spinal cord of a Sturgeon weighing 120 lbs. being no thicker than that of a Frog. The brain consists of the usual parts. The olfactory lobes are connected to the hemispheres by tracts of greater or less length in *Elasmobranchii* (with rare exceptions) and a few *Teleostei*, e.g. *Cyprinoidei*. They are hollow in *Ganoidei*. The cerebral hemispheres are the largest part of the brain in *Dipnoi*, and as a rule in *Elasmobranchii*; the corpora bigemina (optic lobes, mesencephalon) the largest in *Teleostei*. The hemispheres are solid in the last-named order, nearly or quite solid in *Elasmobranchii*, but contain large ventricles in *Ganoidei* and *Dipnoi*. In *Ceratodus* they have the greatest relative breadth, in *Protopterus* the greatest depth, in the class; and in the last-named the two lobes are separated nearly to their base. On the contrary, the division into two lobes is scarcely indicated in *Elasmobranchii*. The region of the thalami optici is always small, and is hidden dorsally by the hemispheres and optic lobes in *Teleostei*. The infundibulum is large, and bears lobi inferiores (hypoaria) except in Sturgeons, *Polypterus* and *Dipnoi*; they are solid in Rays, hollow in other *Elasmobranchii* and *Teleostei*. It bears also a saccus vasculosus in these two orders. The pineal gland is long, filamentous, and tubular in *Elasmobranchii*, *Acipenser*, and *Ceratodus*, and is attached anteriorly to the cranial roof. Its size varies much in other Fish. The pituitary body is excessively large in *Polypterus* and *Protopterus*, and is sometimes pedunculate, e.g. in *Lophius* (the Angler), among *Teleostei*. The mesencephalon is undivided in *Protopterus*; in other Fish it is bilobed, and the lobes contain large ventricles into which the cerebellum projects in *Teleostei*. The cerebellum is small, and like that of the Frog in the Sturgeon, *Polypterus* and *Dipnoi*. It is of fair size in *Teleostei*; often large, lobed, and even convoluted in *Elasmobranchii*. It is foliate in the Tunny (*Teleostei*). The medulla is very long and the fourth ventricle of great extent in *Elasmobranchii*, *Acipenser*, *Polypterus* and *Dipnoi*. The restiform tracts are often convoluted anteriorly, forming trigeminal lobes in *Elasmobranchii* and some *Teleostei*, or enlarged into vagal lobes, e.g. in *Cyprinoidei*.

The two optic nerves cross one another in *Teleostei*, the right nerve supplying the left eye, the left the right eye. In other Fish there is a chiasma. The fourth (trochlear) and sixth (abducens) nerves appear to be



absent in *Dipnoi*. The facial and auditory have a common root, as in many Amphibia and Reptilia. The glossopharyngeus is a separate nerve, with a separate foramen in the skull. The vagus has several roots (five at least) in *Elasmobranchii* and *Dipnoi*; in the latter and some of the former independent *ventral* roots as well. There is no spinal accessory, and the hypoglossus is represented by spinal nerves. The fifth, the facial in *Teleostei*, the glossopharyngeus and vagus have intracranial dorsal branches; that of the fifth in *Teleostei* extends down the body near the median dorsal line; it is connected both to the spinal nerves and the lateral line branch of the vagus, and supplies the muscles and integument of the dorsal fins. The lateral line branch of the vagus lies beneath the integument, except in *Elasmobranchii*, where it is deeply placed in the septum, between the dorso- and ventro-lateral muscles. The anterior roots of each spinal nerve pass in *Elasmobranchii* through or behind the neural arches, the posterior roots through or behind the intercalary pieces; they therefore alternate in position. In *Acipenser* the roots of the spinal nerves of one side of the body alternate in position with the roots of the other side. The spinal ganglia in *Teleostei* sometimes lie within the spinal canal, a most unusual position. The anterior end of the sympathetic system is connected to the vagus in *Elasmobranchii* and chondrostean *Ganoidei*, but in *Teleostei* to the third nerve, as in higher Vertebrata.

Tactile barbules are found on the head of the Sturgeon, the Cods, many *Siluroidei*. The nasal sacs are placed ventrally in front of or near the angles of the mouth in *Elasmobranchii* and *Holocephali*, on the dorsal aspect of the face in front of the eyes in *Ganoidei* and *Teleostei*. They have usually an anterior and posterior opening, the former being occasionally, as in *Polypterus* and some *Teleostei*, prolonged into a tube. A channel runs down to the angle of the mouth from the nasal chamber in Rays and some Sharks. In *Dipnoi* the anterior aperture lies just in front of the mouth and outside it, the posterior within it externally to the vomerine teeth. The mucous membrane is disposed in folds. Certain *Plectognathi* (*Tetrodon*) are said to have solid olfactory tentacles. *Protopterus* alone has an incomplete fenestrated nasal capsule. The eyes have no glands, and lids are represented by slight folds, most marked in *Elasmobranchii*, some of which, e. g. *Mustelus*, *Carcharias*, have a third eyelid or nictitating membrane. The bulb is imbedded in a fatty gelatinous tissue traversed by connective tissue fibres. It is small in *Dipnoi*, rudimentary in some deep-sea, cave- or mud-inhabiting *Teleostei*, but is usually large. In *Pleuronectidae* (Soles) both eyes come to be placed on the same side of the head. The cornea is flat, the sclerotic generally strengthened by calcifications. An argentea—a silvery or golden cellular layer, the colour due to minute crystals—lies externally to the choroid in most *Teleostei*, and extends into the iris. The latter is absent in *Dipnoi*; its musculature is feebly

developed. The ciliary muscle is perhaps wanting. The lens is spheroidal, and almost touches the cornea. A falciform process is present in most *Teleostei*; it ends in a bulbous expansion, the Campanula Halleri, which is attached at the equator of the lens. It is pigmented, vascular, and supplied with nerves; the Campanula contains muscular tissue, and is probably concerned in accommodation. A choroid gland or bipolar vascular rete is found in most *Teleostei* close to the optic nerve, and lying between the argentea and the choroid coat. It receives the blood of the ophthalmic artery coming from the pseudobranchia, and is supposed to represent the spiracular gill. The auditory structures are completely inclosed in cartilage in *Elasmobranchii* and *Dipnoi*, but in *Holocephali*, *Ganoidei*, and *Teleostei* the inner, i. e. cranial, wall is membranous. The aquaeductus vestibuli opens externally on the head in most *Elasmobranchii*. The connection between the vestibule and saccule is closed in *Batoidei*, bony *Ganoidei*, and some *Teleostei*; and in the latter the cochlear outgrowth (= lagena) is large. It contains a small otolith, the asteriscus, whilst the saccule has one of great size, the sagitta. Among *Teleostei* in some *Acanthopteri* (Percoids and Sparoids) a process of the air-bladder is applied to a membranous fenestra in the auditory capsule; in the *Clupeidae* a similar process enters the capsule and comes into relation with the vestibule, whilst in *Siluroidei* and *Cyprinoidei* a chain of bones derived from the vertebral centra and ribs connects the air-bladder to the vestibule.

Fish are very rarely edentulous, e. g. *Acipenser*, some *Lophobranchii*, but the former has larval teeth afterwards lost. *Protopterus* among *Dipnoi*, has two conical, *Ceratodus* two elongate vomerine teeth, whilst the palatopterygoid bone and the splenial bear peculiar ridged plates. The palatopterygoid cartilage and the mandible are dentigerous in *Elasmobranchii* and *Holocephali*. In bony *Ganoidei* and *Teleostei* the praemaxillae, vomers, parasphenoid, dentary, and branchial arches must be added to the list. The maxilla carries teeth in bony *Ganoidei*, but only in a few *Teleostei*, e. g. *Salmonidae*. The teeth are composed of dentine, which may obliterate the pulp cavity, and is coated or tipped with structureless enamel. The dentine in *Lepidosteus* is folded, as in many *Stegocephali* (Amphibia); and the plates of *Myliobatis* (*Batoidei*) are composed of hexagonal denticles set side by side, as in *Orycteropus* among Edentate Mammalia. The form of the teeth varies much: serrated or pointed plates in many Sharks: flat plates in *Cestracion* and some Rays (*Myliobatis*); very various but usually conical in *Ganoidei* and *Teleostei*. They are attached or implanted in a fibrous membrane, which moves forwards over the edge of the jaw in *Elasmobranchii*; by an elastic ligament which allows the tooth to bend backwards in some *Gadidae*, *Lophius*, the vomerine and palatal teeth of *Esox*, among *Teleostei*; in sockets, e. g. in *Sphyræna* (Barracuda Pike), and a few other *Teleostei*, to which they may be ankylosed, as in *Lepidosteus*;

or by special 'bone of attachment,' the most common mode. The formation of new teeth is in most instances perpetual, and in *Teleostei* the new enamel germs are derived from the rete mucosum, and not, as usual, from pre-existing germs. Vertical replacement is found in the pharyngeal teeth of *Pharyngognathi*.

Fish have no oral salivary glands. The tongue is a thickening of the mucous membrane covering the basihyal, with free edges and apex in *Elasmobranchii* and *Polypterus*. In the latter it contains muscular tissue, and special lingual muscles are said to be present in *Dipnoi*. The mouth is a curved or straight transverse aperture, ventral in *Elasmobranchii*, terminal in other Fish. The pharynx is perforated laterally by the gill-slits. The digestive tract takes a nearly straight course in *Holocephali*, a few *Teleostei*, and *Dipnoi*. The oesophagus is scarcely marked off from the stomach. It has sometimes pointed processes directed towards the stomach (some *Elasmobranchii* and *Teleostei*); large and branched in the basking Shark (*Selache*). Ciliated epithelium occurs in it in *Elasmobranchii* and *Ganoidei*. The stomach is a dilatation followed by a pyloric constriction in some *Teleostei*, e.g. *Gobius*, *Protopterus*; a siphonal bend, or a caecal pouch with a lateral pylorus in *Amia*, *Polypterus*, and very many *Teleostei*. In some of the latter the gastric glands have an epithelium unlike that of the stomach. The intestine is usually dilated at the pylorus, and in *Elasmobranchii* the dilatation is known as Bursa Entiana. It gives off in this region, in *Ganoidei* and most *Teleostei* (except e.g. *Siluroidei*, *Esox*, *Plectognathi*) caecal processes or appendices pyloricae, variable in number; arranged in a whorl or a linear series (*Salmonidae*); opening each by a separate aperture or united into bundles with a common duct; free or bound together by connective tissue into a solid mass in *Acipenser* and a few *Teleostei*, e.g. Tunny (*Thynnus*). Their epithelium may be ciliated (cf. p. 87). The remainder of the intestine is often straight, but in *Teleostei* may be somewhat convoluted. It contains in *Elasmobranchii*, *Holocephali*, *Ganoidei*, and *Dipnoi* a spiral ridge or valve, very well-developed in the two orders first named; but reduced in chondrosteian *Ganoidei*, *Lepidosteus*, and *Amia*. In some *Elasmobranchii*, e.g. *Zygaena*, *Carcharias*, it has the form of a lamella rolled upon itself. A rudiment of it is said to exist in the Clupeid *Chirocentrus* (*Teleostei*). The rectum is clearly marked off from the intestine by being dilated in *Ganoidei*. There are no intestinal glands, but goblet mucous cells occur in the epithelium. The rectum is lined by the same epithelium as the intestine, except in *Elasmobranchii*, where it is squamous. Ciliated epithelium is found on the edge of the spiral valve in *Elasmobranchii* or here and there in some *Teleostei*, e.g. John Dory (*Zeus faber*). Peculiarities are the presence of a rectal gland in *Elasmobranchii*; striation of the muscular coats of the digestive tract in the Tench (*Tinca*); the presence of capillaries between the epithelium cells

of the intestine in the air-swallowing Loach (*Cobitis fossilis*). The dorsal mesentery often becomes largely fenestrated, sometimes almost absorbed. A nearly complete ventral mesentery (p. 357) is found in the *Dipnoi*, a few other Fish (Muraenoids), and a posterior rudiment in *Lepidosteus*. The rectum ends in a cloaca in *Elasmobranchii* and *Dipnoi* common to it and the urogenital ducts. The anus in other Fish lies in front of the urogenital apertures.

The liver is unilobar in *Lepidosteus* and a few *Teleostei*, bi- or tri-lobed in other Fish. The two lobes are connected by peritoneum only in some Rays, e.g. *Torpedo*. They are of huge size, reaching to the cloaca in some Sharks. A gall-bladder is rarely absent, and is either imbedded in the liver or lies between its lobes; it varies much in form and size, e.g. it may reach to the anus, as in *Scomberidae* (Mackerels). There are several bile-ducts, but they usually unite into a single duct which opens near the pylorus. A uni- or bi-lobed pancreas is present in *Elasmobranchii*: it is large and lobed in *Acipenser*, small in *Lepidosteus* (? rudimentary), and a few *Teleostei*, e.g. *Esox*, but in the last named order it is generally either a diffused gland or absent altogether.

The external gill-clefts are exposed in all *Elasmobranchii*, and the first (post-mandibular) or spiracle is always so when present. They are protected in other orders by an opercular fold from the hyoid arch, in which opercular bones and sometimes branchiostegal rays (p. 93) are formed except in *Holocephali*. The spiracle is found in *Elasmobranchii*, in *Acipenser* and *Spatularia* among chondrosteans, and *Polypterus* among bony *Ganoidei*. Its gill, if retained, derives arterial blood from the hyoidean or opercular gill. The post-hyoidean gill pouches of the embryo retain the character of pouches in *Elasmobranchii*, where they are five in number, except in *Hexanchus* and *Heptanchus*, with six and seven respectively; and in *Holocephali*, where they are four. The septa, which are continued outwards from the branchial arches, atrophy more or less completely in all other Fish, and thus leave the gill-filaments projecting freely, at least at their apices. The respiratory tissue has the form of radiating folds when the septa are complete; of filaments supported by an axial cartilage when they are atrophied; longest about the centre of the arch or septum. The first set is borne upon the hyoid arch, or the operculum, when present: hence hyoidean or opercular gill. It is found in *Elasmobranchii*, *Holocephali*, *Acipenser*, *Scaphirhynchus*, and *Lepidosteus*, among *Ganoidei*, where it receives the venous blood of the first branchial artery or a branch of that vein in *Protopterus* and *Lepidosiren* among *Dipnoi*<sup>1</sup>: in many *Teleostei*, where it is known as pseudobranchia (a term also applied to the spiracular gill of *Ganoidei*), and is supplied with blood from the hyoidean artery. This pseudobranchia has the form of either a set of

<sup>1</sup> It is present in *Ceratodus*, but the source of its blood-supply is apparently unknown.

short free filaments, e. g. *Pleuronectidae*, many *Acanthopteri*, or a vasoganglion beneath the mucous membrane, e. g. *Esox*, *Cyprinus*, *Gadus*. The remaining sets of gill-folds or filaments are borne upon the anterior and posterior aspects of the septa or branchial arches, the branchial vein and artery running at the base of each septum, or the outer aspect of the arch. The gills are typically biserial. The fourth branchial arch, however, bears only a single, the anterior, row of filaments in many *Teleostei*, e. g. *Cyclopterus*, many *Plectognathi*, or no gill at all, e. g. *Lophius*; and in *Malthaea* among *Pediculati* (*Acanthopteri*) the third arch is uniserial, whilst the second only is gill-bearing in *Amphipnous cuchia* (*Physostomi Apodes*). The fifth arch has no gills except in *Hexanchus* and *Heptanchus*. *Ceratodus* among *Dipnoi*, has four biserial gills, and the septa are well developed; *Protopterus* has biserial gills on the third and fourth branchial arches, and only a single series on the fifth 'immigrants from the hind row of the fourth arch,' seeing that the blood-supply is derived from the fourth branchial artery (Boas). The gill-filaments of *Protopterus* are leaf-like. The *Lophobranchii* among *Teleostei* are peculiar in having tufted processes in the place of gill-filaments.

The gill-filaments are prolonged externally in embryo *Elasmobranchii*, in *Acipenser*, and many *Teleostei*, but are afterwards reduced. The young *Polypterus* has two pairs of external gills supplied from the hyoidean artery. *Protopterus*, among *Dipnoi*, has three pairs of external gills, supplied by the second, third, and fourth aortic arches, and attached close to the summit of the shoulder-girdle. Accessory respiratory organs are found in certain *Teleostei*. These take the form of (1) enlarged honey-combed superior pharyngeal bones in *Anabas scandens* (Climbing Perch) and its allies among *Acanthopteri*: (2) arborescent processes of the dorsal part of the branchial arches in *Clarias*, *Heterobranchus*, *Heterotis*, among *Siluroidei*: (3) a sac with vascular walls opening into the first gill-cleft in *Amphipnous cuchia* and *Saccobranchus singio* (*Siluroidei*). The above-named can exist out of water, but this is not the case with *Lutodeira chanos*, a Clupeid, which 'has an accessory gill developed in a curved caecal prolongation of the branchial cavity' (Huxley).

The outgrowth of the oesophagus, which forms the lungs of other Vertebrata, is absent in *Elasmobranchii*<sup>1</sup>, *Holocephali*, some *Teleostei*, e. g. *Pleuronectidae*, and various families and genera. Its aperture is ventral in *Polypterus* and *Dipnoi*, dorsal elsewhere; and in some *Teleostei* shifts backwards, even opening into the fundus of the stomach in *Clupeidae*. In this family the Herring has a duct leading from the hind end of the air-bladder, and opening on the left side of the sexual aperture. *Protopterus* has a divaricator muscle to the aperture, which leads into a vestibule in it, in *Lepidosteus*, *Polypterus*, and *Lepidosiren*. There is scarcely any duct in

<sup>1</sup> Unless represented by a dorsal caecum in some Sharks.

*Amia* and chondrostean *Ganoidei*, but a long one, the ductus pneumaticus, is found in the Teleostean sub-order *Physostomi*, while it is absent in the remaining sub-orders, hence often grouped together as *Physoklisti*. The lumen of the duct is, however, sometimes closed. The sac itself is double in *Polypterus*, *Protopterus*, and *Lepidosiren*, single in other Fish: it lies between the alimentary tract below, the aorta and kidneys above: it is covered by peritoneum only on its ventral surface, and is sometimes protected in *Cyprinoidei* and *Siluroidei* by a partial or complete bony capsule. Its inner surface is produced into ridges, regular in *Lepidosteus* and *Ceratodus*, irregular in *Amia*, *Protopterus*, *Lepidosiren*, and some *Teleostei*, or else it is smooth. It derives its supply of blood either from the aorta or caeliac artery in chondrostean *Ganoidei*, *Lepidosteus*, and *Teleostei*, or by two pulmonary arteries arising, as in Amphibia, from the fourth branchial veins (fourth aortic arches) in *Polypterus*, *Amia*, and *Ceratodus*, or by a single artery from the common aortic root of the left side, produced by the union of all the branchial veins, in *Protopterus* and *Lepidosiren*. Its blood is returned by a pulmonary vein into the left division of the sinus venosus in *Dipnoi*, into the systemic veins, either portal, hepatic, or cardinal in all other Fish. Its capillaries form radiating tufts in the *Cyprinoidei*: vaso-ganglia, i. e. bipolar retia, in many Teleosteans, e.g. *Anguilla*, *Gadus*, *Perca*. The function of the sac in most instances is almost entirely hydrostatic; hence the name air- or swimming-bladder: but when the air within can be renewed, as in *Dipnoi* especially, it must also act as a lung. But in all Fish, when the branchiae are in full activity, it receives a supply of pure arterial blood.

In some *Plectognathi*, e.g. *Diodon*, an air sac opens into the ventral side of the pharynx. It is distensible, and when inflated, these Fish float on the surface, and are driven about by the currents.

The heart lies in a pericardial cavity, shut off from the rest of the coelome by an oblique or vertical fibrous septum. The two cavities communicate by a single canal, in *Chimaera* (*Holocephali*), *Acipenser*, and *Spatularia*, by a bifurcating canal in *Elasmobranchii*. The heart itself consists of a sinus venosus, auricle, ventricle, and a tubular prolongation of the latter containing several series of valves, the conus arteriosus, a structure which is aborted in all *Teleostei* except in the Clupeid *Butirinus* (p. 88). The sinus venosus is divided into a right systemic and a left pulmonary section in *Dipnoi*. It opens into the auricle by an elongated aperture guarded by two valve-like folds, or in bony *Ganoidei* and *Dipnoi*, by several eminences. The auricle is thin-walled, its muscles disposed in interlacing ridges, and its ventral wall coalesces with the conus in bony *Ganoidei*, less completely in *Dipnoi*. In *Lepidosiren* its cavity is divided by a fenestrated muscular septum; by a dorsal fibrous ridge in other *Dipnoi*. There are no auriculo-ventricular valves in this order: two valves with chordae tendineae

in most other Fish : four in *Amia*, six in *Polypterus* and *Lepidosteus*. The walls of the ventricle are thick, and contain a lymphatic space in *Teleostei* and *Ganoidei*. Muscular ridges project into its cavity, especially in *Dipnoi*, and there is an incomplete septum in *Lepidosiren*. The conus is spirally twisted in *Dipnoi*, and at the same time slightly folded upon itself. It contains several rows of valves, variable in number, but most numerous in bony *Ganoidei*. One row is especially prominent in *Dipnoi*, and in *Protopterus* and *Lepidopterus* the valves in this row coalesce into a ridge. It is opposed by another ridge of coalesced valves, and with these two ridges there coalesces also in both *Protopterus* and *Lepidosiren* a septum which cuts off the origins of the two anterior from the origins of the two posterior pairs of aortic arches. The septum is incomplete in *Ceratodus*. The effect of this arrangement, coupled with the peculiar structure of the heart, is to send into the two first pairs of arches in *Ceratodus* a current of mixed arterial and venous blood ; of pure arterial in the other two Dipnoans (Boas).

A sub-branchial artery or ventral aorta springs from the conus, or from the ventricle in *Teleostei*, where its entrance is guarded by a pair of valves, remnants of the anterior row of the conus. The commencement of this vessel is dilated, and is termed *bulbus aortae*. It gives origin to the aortic arches, or branchial arteries, which are placed at some distance apart one from the other except in *Dipnoi*, where their roots are close together, as in Amphibia. There are five branchial arteries in *Elasmobranchii*, *Holocephali*, chondrostean *Ganoidei* and *Lepidosteus* ; the first supplies the hyoidean, or opercular gill, the remainder the gills of the branchial arches. *Hexanchus* and *Heptanchus* have respectively one and two additional arches. The hyoidean vessel springs from the first branchial artery, not from the ventral aorta, in *Polypterus* and *Protopterus*, and carries venous blood ; but it supplies no gill in the first-named Fish. The hyoidean vessel is an artery carrying arterial blood and supplying the pseudobranchia in *Teleostei*, and takes origin from the ventral end of the first branchial vein. In this order there are typically four branchial arteries. The branchial veins fall dorsally either into a median vessel or into a right and left epibranchial artery, which fuse into a median vessel. This vessel in either case is the subvertebral aorta, which is continued to the tip of the tail as the caudal artery. The common carotids arise from the dorsal extremity of the hyoidean vein or, in *Teleostei*, artery (*supra*), which is connected dorsally to the subvertebral aorta or epibranchial artery. The two carotids are connected across the base of the skull (except in *Dipnoi*) by a vessel, thus making a *circulus cephalicus*. The internal carotids arise from this connecting vessel. The venous blood returns to the sinus venosus by a right and left ductus Cuvieri, formed by the fusion of the jugular and subclavian veins with the posterior cardinal veins (p. 352). The right ductus in *Lepi-*

*dosteus*, the two ductus in *Polypterus*, enter the auricle, not the sinus. There is a hepatic-portal and a renal-portal system, the latter supplied by the branches of the caudal vein. The hepatic veins enter the sinus venosus independently, and there is no vena cava inferior. The lymphatic system consists of vessels lodged in the myocommata and other fibrous septa, and of spaces surrounding the chief vessels, and a right and left or a single sub-vertebral canal. Masses of adenoid or lymphatic tissue imbed the kidneys and the testes in *Dipnoi*, and are connected across the median line by several bands. And in some Ganoids (*Acipenser*, *Lepidosteus*) and many *Teleostei* the anterior part of the kidney is converted into a vascular adenoid tissue. Lymphatic hearts, single in the Eel (*Anguilla*) or double in *Silurus*, open into the caudal vein. The coelome opens externally by abdominal pores in most *Elasmobranchii* (except four genera of *Scyllidae*, *Cestracion*, *Notidanidae*, and *Rhinidae*), in *Holocephali*, *Ganoidei*, some physostomous *Teleostei* (female *Salmonidae*, *Mormyrus*, *Muraenoidei*), and the *Dipnoi*. The two pores lie close to the anus in *Holocephali*, *Ganoidei*, *Salmonidae*, and *Mormyrus*, close behind the cloaca in *Ceratodus*, at its margin, or just within it, in *Elasmobranchii*. When double in *Protopterus*, they open into the cloaca behind the rectum; when single, externally and in front of it, and either within or without the limits of the sphincter muscle. There is a single pore in *Muraenoidei*, which opens into the ureter close to its external aperture.

The thyroid gland is a large mass in *Elasmobranchii*, lying at the anterior end of the ventral aorta: in *Teleostei* it is represented by masses of reddish follicles lying ventrally to the same vessel, and scattered for a greater or less distance along the branchial arteries. The thymus is paired: each gland lies at the dorsal extremities of the branchial sacs in *Elasmobranchii*: at the dorsal ends of the last pair of branchial arches close beneath the mucous membrane of the branchial cavity in *Ganoidei* and *Teleostei*. In the latter it is largest in half-grown individuals, and atrophies in the adult. A spleen is always present.

The pronephros seen in the embryo *Acipenser*, *Lepidosteus*, and Teleostean appears to atrophy completely. The mesonephros forms the permanent kidney in *Ganoidei*, *Teleostei*, and *Dipnoi*, but in *Elasmobranchii* its hinder portion becomes specially enlarged, quite or nearly independent of the fore-part, and acquiring ducts of its own, represents the metanephros of higher Vertebrata. The anterior portion of the mesonephros is in this case converted into epididymis in the male, parovarium in the female. The size and form of the mesonephros are very variable. It is especially large in chondrostean *Ganoidei*, and it extends in many *Teleostei* far into the caudal canal. The two glands fuse anteriorly and posteriorly in chondrostean *Ganoidei*; and in some *Teleostei* even for their whole length. In bony *Ganoidei* and *Dipnoi* they are short, and restricted to the posterior part of



the coelome. In all cases they lie subvertebrally. The metanephros of *Elasmobranchii* is more or less lobulated. The duct lies sometimes in the substance of the gland in *Teleostei*, at its outer margin in *Ganoidei*, on the ventral surface in *Dipnoi*, and the several ducts (rarely a single duct) in *Elasmobranchii* proceed from its inner border. The duct in *Teleostei* is probably an archinephric duct: in *Elasmobranchii* that of the mesonephric region is a true mesonephric (or Wolffian) duct, from which a Müllerian duct has been split off in development, as is probably the case also in *Dipnoi*. The *Ganoidei* present a difficulty. The renal duct has a second duct opening into it near its centre, as well as into the coelome, which is usually regarded as a Müllerian duct, but the homology is uncertain. If correct, then the anterior part of the duct is a Wolffian duct, from which a Müllerian duct has been split off, and the posterior part is an undivided archinephric duct. The ducts, archinephric or mesonephric, fuse terminally, and the fused portion is dilated in *Elasmobranchii*; provided with a lateral outgrowth on each side in *Amia*; or a median outgrowth (urinary bladder), sometimes of great size, in *Teleostei*. The fused portion is functionally a urogenital sinus in both sexes among *Ganoidei* and in the male *Elasmobranchii*; and in the latter it receives the metanephric ducts or ureters which in the female open into the lower ends of the mesonephric ducts before they fuse. The ducts finally open into the cloaca in *Elasmobranchii* and *Dipnoi*, externally behind the anus in *Ganoidei* and in *Teleostei*, in the latter either into a sinus, common also to the genital ducts, or else separately behind the genital opening, as is the case also in *Holocephali*. Some *Teleostei*, e. g. Gobies, Blennies, have a long urogenital papilla. *Protopterus* has a so-called urinary bladder opening into the cloaca between the rectum and the sexual ducts. Peculiarities are the conversion of the anterior part of the mesonephros in *Acipenser*, *Lepidosteus*, many *Teleostei*, into adenoid tissue, into which the kidney duct does not extend, and the retention of nephrostomata, variable in size and number in many *Elasmobranchii*, e. g. *Acanthias*, *Scyllium*, &c. For the supra-renal capsules see p. 354, *ante*.

Occasional hermaphroditism has been observed in Cyprinoids, the Mackerel (*Scomber*), Herring (*Clupea harengus*), &c. Among *Teleostei* *Acanthopteri* a testis is constantly found imbedded in the wall of the ovary in *Chrysophrys* and *Serranus*, and the last-named Fish is said to be self-impregnating. The glands are small when immature, and are typically paired. A single ovary is found, however, in *Scyllidae*, *Galeidae*, *Carcharidae* among *Elasmobranchii*, and a few *Teleostei*; a single testis in a very few of the latter. The ova are carried away in *Lepidosteus* and *Teleostei* with one exception, by ducts continuous with the ovarian capsule (p. 89). They are shed into the coelome in *Elasmobranchii*, *Holocephali*, *Dipnoi*, *Ganoidei*, in the *Salmonidae* and *Muraenidae* among *Teleostei*

*Physostomi*. In the latter they are conveyed outwards by the abdominal pore or pores; in *Ganoidei* by the supposed Müllerian ducts; in the other three orders by Müllerian ducts or oviducts proper. These have in *Elasmobranchii* a common internal median aperture, a narrow ciliated duct, a nidamental gland which secretes a shell and the albumen of the egg, and is largest in the oviparous genera, and a dilated posterior part or uterus, in which the ova develop in viviparous species. The oviducts are convoluted in *Dipnoi*, and their walls glandular. In *Ceratodus* the ova are laid in strings imbedded in albumen. The ovaries of the *Muraenidae* are plate-like bands; of *Salmonidae* lamellate; in other *Teleostei* saccular, the ova being produced by a small lateral streak on one wall, e. g. *Ophrydium barbatum*, by processes of the wall, e. g. *Lophobranchii* or by lamellae transverse, e. g. *Clupea harengus*, or longitudinal, e. g. *Zeus faber*. The sticky coat of the ova appears to be formed from the follicle cells.

The testis is saccular only in the Teleostean *Syngnathus acus*; it is composed in all other Fish of tubuli seminiferi. The sperm is conveyed by vasa efferentia to the mesonephros in *Elasmobranchii*, *Holocephali*, chondrostean *Ganoidei* and *Lepidosteus*. It appears to be shed into the coelome in *Dipnoi*, and is thence conveyed away either by the abdominal pores or by Müllerian ducts, which are present; the latter *may be* the case with *Polypterus* and *Amia*, as it was once supposed to be with other Ganoids. The ducts in *Teleostei* are continuous with the gland, as in the female, except in *Muraenidae*, where, though they are present, the sperm is shed into the coelome, whence it is conveyed away by the single abdominal pore. The ducts are often dilated terminally, or furnished with vesiculae seminales. The Müllerian ducts open in *Elasmobranchii* and *Dipnoi* into the cloaca dorsally to the rectum; in *Holocephali* externally between the anus and urinary apertures. For *Ganoidei* and *Teleostei*, see p. 427.

Copulatory organs (= pterygopodia) are developed in connection with the metapterygium of the hind-limb in *Elasmobranchii* and *Holocephali*. A cartilaginous skeleton supports a deep groove, into which opens a saccular gland in Sharks and *Holocephali*, a compound tubular gland in Rays. Sperm has been found in the sac in some Sharks and the *Holocephali*. Dilator and flexor muscles are connected with the apparatus. Impregnation is internal, as it must be in viviparous *Teleostei* (*infra*). The sperm 'milt' in other Fish is shed over the ova after they are laid.

The majority of Sharks (except e. g. *Scyllidae*, *Scylliolamnidae*, *Cestracion*) and the Torpedo among the Rays, certain *Teleostei* (many *Bleniidae* and *Cyprinodontidae*) are viviparous. The Teleosteans in question retain the ova in the ovary, the *Elasmobranchii* in the uterine portion of the oviduct; and in some instances (*Mustelus laevis*, *Carcharias glaucus*) the yolk-sac is thrown into folds, which fit into corresponding depressions of the vascular uterine walls, forming a kind of placenta. Among *Teleostei*

the female *Aspredo* (*Siluroidei*) carries the ova attached to the soft ventral skin; *Solenostoma* (*Lophobranchii*) in a pouch between the ventral fins, and formed partly by them; the male *Syngnathidae* (*Lophobranchii*) carry them in a sub-caudal pouch; and in some *Siluroidei*, e. g. *Arius*, within the pharynx<sup>1</sup>. The egg-shell in oviparous *Elasmobranchii* is chitinous, with an aperture at one end; usually oblong, with the corners produced into processes, which are often tendril-like<sup>2</sup>. The zona radiata in *Teleostei*, and the ovular membranes in other Fish, are perforated by one or more micropyles. The ovum of *Elasmobranchii* is very large; of *Teleostei*, with one large or several smaller yolk-spherules; of *Acipenser*, deeply pigmented. Segmentation is total but unequal in *Acipenser* and *Lepidosteus*, partial in the ova of all other Fish which are telolecithal. The embryo has a more or less prominent yolk-sac. Larval peculiarities are noticeable, e. g. the external gill-filaments of *Elasmobranchii* and some *Teleostei*; the external gills of *Polypterus*; the praeoral disc with suctorial papillae of *Lepidosteus*; peculiar spines, bony plates, growths on the fin in many *Teleostei*. Young *Pleuronectidae* have the eyes normal in position until they assume a horizontal posture in swimming, when one of the two rotates to the opposite side of the head. The Teleostean family *Leptocephalidae* appear to be arrested forms.

Fish, like Amphibians, are often sexually mature before they are mature in other respects. Their power of reproducing lost parts is confined to the fins. Many grow as long as life lasts, e. g. for over a hundred years (Carp, Pike); others attain a certain standard of size and are short-lived, e. g. Stickleback, Cyprinodonts, many Clupeids. Sexual dimorphism occurs, e. g. the male Teleostean is smaller than the female, and is often brilliantly coloured, temporarily or permanently. The flesh of some forms is poisonous always or at certain times, and is due in many cases to the food. The mucus of the body is often poisonous, and special poison glands are sometimes found, e. g. in connection with the dorsal spines of *Synanceia* (*Scorpaenidae*), or a perforated opercular spine, as in *Thalassophryne* (*Batrachidae*) among *Teleostei Acanthopteri*. The majority of fish are carnivorous; some omnivorous; a few, like the Mulletts and Carps, vegetable-feeders.

Many fish are entirely marine, others exclusively fresh-water, while others again pass indifferently from fresh to sea-water, and *vice versa*, e. g. *Pleuronectes*. Some few ascend rivers to spawn, e. g. *Acipenser*, *Salmo*;

<sup>1</sup> The male 15-spined Stickleback (*Gasterosteus spinachia*) spins a nest for the ova with a continuous thread. The material for the thread is secreted at the breeding season by the epithelium of the tubuli uriniferi and accumulates in the urinary bladder. Möbius, A. M. A. xxv. 1885; Prince, A. N. H. (5) xvi. 1885.

<sup>2</sup> In two Australian Rays (*Trygonorhina fasciata*, *Rhinobatis vincentianus*) the shell contains more than one ovum—a unique peculiarity; Haacke, Z. A. viii. 1885. The same thing occurs occasionally in the common Hen.

others descend to the sea, e.g. *Anguilla*, the Eel. Instances are known of truly marine fish living in fresh water, e.g. a Shark in Lake Nicaragua; a Goby, Blenny, *Atherina* in the lakes of N. Italy. Marine fish are either littoral, pelagic, or abyssal. The latter are chiefly represented by *Anacanthini*, a few *Acanthopteri*, and certain families of *Physostomi*. Eels descend to the greatest depths. Many *Cyprinoidei* and *Muraenoidei* of the temperate zones become quiescent in cold weather; and some, e.g. Carp, may be frozen without loss of life. Many tropical fish, e.g. some *Siluroidei*, *Protopterus*, burrow in mud during the hot season, when the rivers and pools dry up, and pass into a state of quiescence, which may last apparently for several years.

The first remains of fish occur in Upper Silurian rocks, as spines, scales, cephalic shields, part of a jaw-bone, and coprolites, probably belonging for the most part to *Elasmobranchii*, some perhaps to *Ganoidei*. These two orders appear in numbers in Devonian strata, and some of the *Ganoidei* closely approach the *Dipnoi*, if they are not really Dipnoans. *Ceratodus* occurs in Permian strata, existing genera of Sharks in Cretaceous. *Teleostei* are found in the last-named rocks, and exceed the *Ganoidei* in numbers, but it is possible that the order is represented in the Lias. *Teleostei* replace *Ganoidei* almost completely in Tertiary times.

The Class Pisces may be subdivided into the following orders:—

I. *Elasmobranchii* (= *Plagiostomi*). Skeleton, for the most part cartilaginous; no investing bones; caudal fin heterocercal; paired fins large; ventral fins abdominal; copulatory organs present in male; mouth transverse and ventral; nostrils ventral; five to seven external gill-clefts, and usually a spiracle; upper jaw a moveable palato-quadrangle cartilage; optic nerves forming a chiasma; a spiral valve in the intestine; a terminal cloaca and a contractile conus arteriosus with several rows of valves; ova large and few; impregnation internal; viviparous or oviparous; embryo with external gills. Contains two sub-orders: (1) *Squalidae* or *Selachoidei*, the Sharks, which are cylindrical in shape; have the gill-clefts placed laterally; free eyelids; and the pectoral limb not connected to skull; (2) *Rajades* or *Batoidei*, the Rays, which are flattened; have the gill-clefts ventrally placed; and the pectoral limb connected to the skull.

*A Shark*—*Chlamydoselachus*—*from Japanese waters, has lately been described, which has pronged teeth like the Cladodonts of the Middle Devonian period. Its mouth is anterior as in other Vertebrata; its two nostrils are on the dorsal aspect of the face as in Teleostei; it has a large free opercular fold to the hyoid; six gill-clefts and an heterocercal tail scarcely bent up. It is the oldest living type of Vertebrata. See Garman, Bull. Mus. Comp. Zool. Harvard College, xii. No. 1, 1885.*

II. *Holocephali* differ from I. in having an opercular fold covering the gill-clefts, which are only four, and a naked skin; the palato-quadrangle and hyomandibular coalesced with the skull; no cloaca but the anus, Müllerian and urinary ducts opening separately. *Chimaera* from the northern, and *Callorhynchus* from the southern hemisphere.

I. and II. are often grouped together as *Chondropterygii*.

III. *Ganoidei*. Skeleton, cartilaginous or ossified; investing bones always present in relation with cranium and shoulder-girdle; dermal skeleton forming large scutes or scales; ventral fins abdominal; an operculum with opercular bones; gill filaments free; a spiracle sometimes present as in I; optic nerves forming a chiasma; a spiral valve in the intestine; anus in front of a urogenital aperture; abdominal pores present; an air-bladder with pneumatic duct; a conus as in I; ova small, impregnated after exclusion.

The living *Ganoidei* are (1) *Chondrostei*, with a heterocercal caudal fin; naked skin, partially covered with large and small bony scutes and a notochord not divided into vertebrae. *Acipenser*, *Scaphirhynchus*, *Spatularia* (= *Polyodon*). (2) Holostean, or bony *Ganoidei*, represented by three freshwater families. (i) *Polypteridae* with two genera, *Polypterus* and *Calamoichthys*, the former from West Africa and the Upper Nile, the latter from Old Calabar. The pectoral fins are lobate; the body covered with rhombic scales, the caudal fin homocercal. (ii) *Lepidosteidae* represented by *Lepidosteus* from North and Central America and Cuba, with fossil remains in Europe. The fins have fulcra; the caudal fin is slightly heterocercal; the scales rhomboid; the vertebrae opisthocoelous. (iii) *Amiadae* represented by *Amia calva* from North America. The scales are cycloid and large; the caudal fin homocercal.

There are many fossil forms. Accounts of them will be found in Günther, Study of Fishes, 1880, and in the decades of the English Geological Survey.

IV. *Teleostei* (Osseous Fish). Skeleton well ossified; a bony operculum with branchiostegal rays; investing bones of skull and shoulder-girdle well developed; caudal fin homocercal, rarely diphyrcercal; optic nerves decussate; spiral valve and conus absent; anus in front of genital and urinary apertures which may be separate or form a urogenital cloaca.

This order may be subdivided into—

1. *Physostomi*. Duct present to air-bladder; ventral fins either absent (*Apodes*, e.g. *Muraena*, *Anguilla Gymnotus*) or abdominal in position, e.g. *Clupeidae*, *Salmonidae*, *Cyprinidae*, *Siluroidei*. Many are freshwater forms only.

2. *Anacanthini*. Azygos and ventral fins with jointed fin-rays only; the ventral either jugular or thoracic; air-bladder, when present, without a duct except in *Lota vulgaris*, the Burbot or freshwater Cod. *Gadoidei*, *Pleuronectoidei*. Marine.

3. *Acanthopteri*. Some of the rays of the dorsal, anal, and ventral fins are spinous; scales usually ctenoid; no duct to air-bladder, e.g. *Percidae*, *Gasterosteidae*, *Scomberidae*, &c. Mostly marine.

4. *Pharyngognathi*. Resemble 3, with which the group is often classified; but the two fifth branchial arches are fused into a single bone, e.g. *Labridae* or Wrasses. Marine. •

5. *Plectognathi*. Globular or much compressed laterally; skin naked or furnished with large scutes or spines; ventral fins absent or represented by spines; praemaxillae and maxillae firmly united; no duct to air-bladder, e.g. *Ostracion*, *Diodon*, *Tetrodon*. Marine.

6. *Lophobranchii*. Long tubular snout with terminal edentulous mouth; dermal skeleton composed of large plates; sub-opercular aperture very small; gills composed of processes arranged in tufts. *Pegasidae*; *Syngnathidae*.

2-6 are often grouped as *Physoklisti*.

V. *Dipnoi*. Body covered with scales; caudal fin diphyccercal; paired limbs with a central axis; with branchiae and lungs; persistent notochord without vertebral centra; a spiral valve in intestine and a cloaca; abdominal pores; a conus of large size spirally twisted. The order contains two sub-orders.

(1) *Monopneumona*. With single lung; large cycloid scales; paired limbs with bilateral rays. *Ceratodus* from rivers of Queensland.

(2) *Dipneumona*. Lung double; paired fins linear. *Protopterus annectens* and *P. amphibius* from tropical Africa, with five gill-clefts and a lateral membrane to the paired fins, and *Lepidosiren paradoxa* from Brazil, with four gill-clefts and no lateral membrane to the paired fins.

*Elasmobranchii*. See p. 279.

*Holocephali*. Leydig, *Chimaera*, Archiv für Anat. und Physiol. 1851.

*Ganoidei*. *Skull of Acipenser: structure and development*, W. K. Parker, Ph. Tr. 173, 1882; *Skull of Lepidosteus*, Id. ibid. *Structure and development of Lepidosteus*, Balfour and W. N. Parker, ibid. with lit. cited. *External gills of Polypterus*, Steindacher, Hyrtl. SB. Akad. Wien, lx. Abth. i. 1869.

*Teleostei*, p. 89-90, 98, 102. *Augenähnliche Organe der Fische*, Leydig, Bonn. 1881; *Macchie splendenti of Scopelus*, Emery, Mitth. Zool. Stat. Naples, v. 1884. *Leptocephalidae*, Kölliker, Z. W. Z. iv. 1852; Carus, Ueber die *Leptocephalidae*, Leipzig, 1861. *Eyes of Pleuronectidae*, Agassiz, 'Young Stages,' &c., Proc. Amer. Acad. xiv. 1879.

*Sexual organs of Muraenoids*, Brock, Mitth. Zool. Stat. Naples, ii. 1881. *Viviparous Teleostei*, Ryder, Proc. U. S. Nat. Museum, viii. 1885. *Relations of Yolk to Gastrula*, Cunningham, Q. J. M. xxvi. *Pelagic stages of Young Fish*, Agassiz and Whitman, Mem. Harvard Mus. xiv. (1), 1885.

*Dipnoi*, Ayers, J. Z. xviii. 1885, with lit. cited. *Fins of Dipnoi and species of Protopterus*, Schneider, Z. A. ix. 1886. *Ceratodus*, Günther, Ph. Tr. 161, 1871; Huxley, P. Z. S. 1876. *Nostrils in Lepidosiren*, Huxley, ibid. *Skeleton and nervous system of Protopterus*, Wiedersheim, J. Z. xiv. 1880; *Brain*, Fulliquet, Recueil Zool. Suisse, iii. 1886. *Heart, branchial arteries* (also in bony *Ganoidei*), Boas, M. J. vi. 1880. *Ovarian ovum of Protopterus*, Beddard, Z. A. ix. 1886.

## CLASS CYCLOSTOMI (*Marsipobranchii*).

*Elongated Eel-like Ichthyopsida, with the mouth not supported by jaws, as in other Vertebrata; with small azygos fins, but devoid of paired fins<sup>1</sup>; no exo-skeleton; with a single nostril, and six or seven pairs of branchial pouches.*

The azygos fin is small and confined to the tail in the *Myxinoidei*, but extends forwards continuously along the back in the larval Lamprey or *Ammocoetes*, whereas in the adult or *Petromyzon* the antero-dorsal portion is separated off as a dorsal fin.

The superficial cells of the epidermis in the Lampreys (*Petromyzon-*

<sup>1</sup> Dohrn believes that the two ridges, one on either side the anus in *Petromyzon*, represent remnants of pelvic fins. See Mitth. Zool. Stat. Naples, vi. 1885.

*tidae*) develop a cuticular border pierced by fine pores. The deep cells are prismatic and stalked. There are also (1) superficial goblet cells; (2) large oblong club cells, with a distinct membrane and lamellated contents, which gradually reach the surface as they increase in size, and there burst; as well as (3) granular cells of unknown function, spherical or ovoid in shape, with a membrane and nucleated granular contents, and fine processes extending towards the corium. In *Myxine*, the Hag-fish, the superficial cells of the epidermis are all goblet cells, two to three layers deep, which give origin for the most part to the abundant mucus these fishes throw off. There are besides large oblong cells with granular contents, which reach the surface and burst; and spherical 'spider' cells with clear contents, central stellate granular mass, and a distinct membrane. These two kinds of cells appear to correspond respectively with the club and granular cells of the Lamprey. *Myxine* possesses also on each side of the body a series of pores leading into pit-like glands imbedded in the subcutaneous tissue. They originate as solid ingrowths of epidermis. Their cells are of two kinds—'spider' cells and thread cells—the latter oblong or ovoid, with remains of a nucleus at one pole, a central granular core, and contents differentiated into a thread, wound transversely at the surface, longitudinally in the deeper layers. As soon as the cell is mature, the thread begins to unwind. The epidermis of *Petromyzon Planeri* contains scattered rod cells, terminating in sensory hairs. *P. fluviatilis* possesses end buds, each containing but a few cells, and on the head elevated upon papillae. Nerve eminences, somewhat sunk in pits, are found in *Petromyzon*, arranged in an upper and lower lateral line, and the three typical lines can be traced upon the head. *Myxine* has none of these structures. There is a remarkable fatty subcutaneous tissue. The myomeres of the body retain their primitive arrangement in Lampreys, but in *Myxine* the ventro-lateral portion is broken up into an outer oblique layer, and into ventral longitudinal but interrupted bundles. The myomeres overlap one another in the Lampreys, and there are numerous longitudinal fibrous septa stretching from one myocomma to the next succeeding. The compartments thus formed are filled by the muscle plates.

The cranium is entirely cartilaginous. It has no roof in the *Myxinoidei*, and is only partially roofed in the adult Lamprey. It always retains a large basicranial fontanelle. There appear to be well-developed palatine, pterygoid, quadrate, and hyomandibular regions, a hyoid arch, and in *Myxinoidei* traces of two branchial arches. The Lamprey is said to have distal rudiments of Meckel's arch. A large basi-hyo-branchial bar supports the tongue. It is carried by the hyoid arch, with which it is continuous in *Myxinoidei*, and by which it is 'clamped' in *Petromyzon*. In the latter there are five upper labial cartilages, one median and two paired, and an annular cartilage supports the margin of the mouth. It represents

the two anterior lower labials seen in the Anuran Tadpole. There are also three minute lower labial cartilages paired right and left. The upper and lower barbules of the *Myxinoidei* are supported by cartilaginous rods, but there are no labial cartilages. The Lampreys have a complicated cartilaginous framework supporting the branchiae and the heart. It lies superficially, and must be compared with the extra-branchial cartilages of Anuran Tadpoles and Sharks. The notochord is large, with a tough fibrous sheath. There are small cartilaginous neural arches in the Lamprey, but not in *Myxinoidei*, and in the former two cartilaginous rods are applied to the ventro-lateral aspect of the notochord in its whole extent. Cartilaginous rays support the azygos fins.

The brain has the usual parts, but in the larval Lamprey the thalami optici and mid-brain are scarcely separated and are elongated, as is also the medulla oblongata. There are two olfactory lobes, and the cerebellum is a simple transverse commissure. The cerebral hemispheres are solid in the *Myxinoidei*. The spinal cord is flattened dorso-ventrally. The anterior and posterior roots of the spinal nerves alternate with one another, and do not unite in the Lampreys, but they both divide into dorsal and ventral branches. In *Bdellostoma* and *Myxine* there are two anterior roots to every posterior root throughout a portion of the cord at least. Their ventral branches unite, and not their dorsal; but the dorsal branches derived from each pair of anterior roots fuse together. There is no sympathetic system, but the intestinal branches of the vagus extend nearly the whole length of the digestive tract. The nostril is single, even in development, though the olfactory lobes are double. It is tubular, and the tube is supported by cartilage, which in the *Myxinoidei* forms a series of rings. A passage leads from it to the pharynx, which is blind in the Lamprey, but opens in the *Myxinoidei* in front of the velum. The eye in the latter wants the eye-muscles, the sclerotic, the iris and lens. In the larval Lamprey (*Ammocoetes*) it remains beneath the epidermis, derm and subdermic tissues, which represent the cornea; there is no iris, and the lens retains the embryonic structure. At the metamorphosis the eye travels to the surface, and becomes fully developed. The ear in the Hagfish consists of a vestibule and single semicircular canal. In the Lamprey there are two vertical semicircular canals, with ampullae as usual, and indications of cochlear and saccular outgrowths. There are motile cilia in the vestibule, as in the otolithic vesicles of Mollusca, &c.

The mouth of the adult Lamprey is concave, suctorial, fringed by a soft lip bearing numerous short filamentous processes, and armed with numerous epidermic teeth. In the *Myxinoidei* it has barbules above and below, and the teeth are reduced to a single upper tooth and to two rows borne by the supra-lingual cartilage. The *Ammocoetes* has a hood-shaped mouth with a fringe of tentacles. The tongue (so called) is of immense size, especially in



the *Myxinoidei*. The mouth (=stomodaeum) is separated from the pharynx by a depending fringed velum in the *Myxinoidei*. The *Ammocoetes* has a right and left velar fold; but in the adult a valve with seven projecting filaments overhangs the entrance to the bronchus below the oesophagus (*infra*) and connects the remnants of the two velar folds which project backwards into it. The alimentary canal is straight. The fore-gut (=oesophagus and stomach) is narrow, the mid-gut (=small intestine) begins with a sudden dilatation, into which opens the bile duct; and the hind-gut (=large intestine and proctodaeum) is very short. The mid-gut is separated from both fore- and hind-gut by a valve, and in the Lampreys contains a projecting fold or typhlosole, which, beginning on the dorsal side of the intestine, makes a slight spiral twist and ends on the ventral side, and is richly supplied with blood-vessels. The epithelium of the mid-gut is ciliated throughout in *Ammocoetes*, but in the Lamprey only here and there. The liver consists in the Hags of two separate lobes, each with its own duct and a gall-bladder appended to the point where the ducts fuse and form a common duct. It is united to the ventral abdominal wall in Lampreys, and in the *Ammocoetes* has a tubular structure with ciliated bile-ducts. At the metamorphosis the tubular structure is lost; fat appears in the cells; the gall-bladder and bile-duct are absorbed. The mid-gut atrophies more or less at the same time. The pancreas is perhaps represented in the Lampreys by an acinous gland opening into the widened commencement of the mid-gut on the left side. The anus lies in front of the urogenital sinus in the adult<sup>1</sup>.

The respiratory system consists of gill-pouches or sacs, seven on each side in the Lampreys; six, or very rarely seven, in *Myxine*; six or seven in *Bdellostoma*. An eighth, or anterior pouch, is indicated in the embryo Lamprey, but disappears. It corresponds probably with the spiracular cleft of *Elasmobranchii*. In the *Myxinoidei* and the *Ammocoetes* these pouches open internally into the oesophagus; in the *Petromyzon* into a tube or bronchus underlying the fore-part of the oesophagus, and ending blindly behind. This bronchus is said to be the oesophagus of the *Ammocoetes*, the oesophagus of the adult being a new structure which grows forwards from behind at the metamorphosis, and opens into the pharynx above the bronchus. Each branchial pouch has a separate external opening in the Lampreys and *Bdellostoma*, and the separate openings in the *Ammocoetes* are united by a deep furrow. In *Myxine* there are only two ventrally-placed external openings, with which the pouches communicate by separate tubes. A ductus oesophageo-cutaneus, or tube, arising from the oesophagus behind the last pouch on the left side, opens externally with the left common aperture in *Myxine*, with the last pouch of the left side in *Bdellostoma*. It is not found in Lampreys. The inner

<sup>1</sup> The anus represents the blastopore in *P. Planeri* (Shipley, P. R. S. xxxix. 1885).

surfaces of the pouches carry a series of longitudinal vascular folds, and in the Lampreys tracts of the branchial epithelium are ciliated.

The heart has the usual piscine structure, a sinus venosus, auricle and ventricle. The bulbus aortae is small, the ventral aorta long, and gives off as many branchial arteries as there are branchial sacs. Its anterior part is deeply cleft, so that the three or four anterior branchial arteries of either side come off from a right and left common vessel. The sub-intestinal vein of the embryo persists in the adult, and is distributed to the liver forming the portal vein. Its anterior part is said to be pulsatile in *Myxine*. The blood corpuscles of the Lamprey are circular and nucleated.

The segmental duct persists, and is not divided into Müllerian and Wolffian ducts. It has a coelomic opening in the embryo *Ammocoetes*, afterwards closed or lost. The kidney in *Ammocoetes* consists at first solely of a pronephros with funnels opening into the pericardial region of the coelome. This pronephros is afterwards aborted, whilst the anterior part of the mesonephros becomes functional. It is said to be aborted in its turn at the metamorphosis, a posterior series of segmental tubes being developed at the same time. The pronephros of *Myxine* persists, and lies in the pericardial cavity into which its tubes open. It is cut off, together with the anterior part of the segmental duct, from the mesonephros. This latter consists of the remainder of the segmental duct and a series of short simple segmental tubes, one to each segment. The segmental ducts of the adult open into a urogenital sinus, into which the coelome also opens by a pair of abdominal pores. The sinus in the Lamprey communicates with the exterior by an aperture placed on the apex of a papilla. The papilla lies behind the rectal opening, and is inclosed together with it by a right and left fold of the skin. The arrangement is essentially the same in *Myxine* (Ewart). In the *Ammocoetes* the segmental ducts open into the rectum, but the separation of the urogenital sinus from the rectum, and formation of abdominal pores take place just before metamorphosis. The male and female genital glands are unpaired. In *Myxine* the suspensory duplicature of peritoneum is broad. The glands in *Petromyzon* are lobed. Both ova and spermatozoa are shed into the coelome, and pass outwards through the abdominal pores and urogenital sinus. The ova are impregnated externally to the body. The ovum of *Petromyzon Planeri* is invested by an adhesive mucous coat and a membrane composed of an inner perforated, and an outer structureless layer, and there is a micropyle. Segmentation is total but unequal; and the archenteron is formed by invagination. The epiblast cells grow over the larger yolk cells. The ovum of *Myxine* is inclosed in an elliptical horny case with processes at each pole. Each process ends in a three-armed anchor, by which the ova adhere one to another in strings, and are probably attached to sea-weed.

The *Myxinoidei* afford the only instance of parasitism among Verte-

brata. They eat their way into the coelome of other Fish, e.g. Cod, Sturgeon, &c. The Lampreys attach themselves to Fish by the suckorial mouth, and scrape their flesh away with the teeth of their tongue.

The Cyclostomi are divided into two Orders as follows:—

1. *Hyperoartia*. Dorsal fin well developed; nasal passage closed. One family, *Petromyzontidae*, the Lampreys, both marine and fluviatile, with several genera found in various parts of the world; *Petromyzon*, in Europe, America, Japan, and West Africa; *Mordacia*, in Tasmania and Chili; *Geotria*, in South Australia and Chili; *Ichthyomyzon*, west coast of North America.

2. *Hyperotreti*. Dorsal fin feebly developed; nasal passage opening into the pharynx. One family, *Myxinoidei*, containing two genera, *Myxine*, the Hag-fish, from the northern seas and Pacific coasts of temperate South America; and *Bdellostoma*, from the southern seas (Cape of Good Hope, New Zealand, coasts of Chili). Exclusively marine.

*Anatomy of Petromyzon Planeri*, Langerhans, Untersuchungen über *P. Planeri*, Freiburg, 1873. *Metamorphosis, &c.*, Schneider Beiträge zur Vergleich. Anat. &c., der Wirbelthiere, Berlin, 1879. *Development*, Balfour, Comparative Embryology, ii. 1881; *of visceral arches*, Dohrn, Mitth. Zool. Stat. Naples, v. 1884. *Myxinoidei*. Vergleich. Anat. des Myxinoiden, J. Müller, Berlin, 1835-40-41; cf. Abhandl. Akad. Berlin, Classis Phycica. 1834,-36,-38,-39. *Epidermis of Petromyzon*, Foettinger, Bull. Acad. Roy. Belg. (2) 41. 1876; *summary of do., and on Myxine*, Blomfield, Q. J. M. xxii. 1882.

*Cranium*, W. K. Parker, Ph. Tr. 174. 1883; cf. Huxley, Journal of Anat. and Physiol. x. 1876. *Skeletal tissue*, Gegenbaur, J. Z. v. 1870. *Head Muscles*, Fürbringer, J. Z. ix. 1875.

*Brain in Ammocoetes and Petromyzon Planeri*, Wiedersheim, J. Z. xiv. 1880; *in Petromyzon*, Ahlborn, Z. W. Z. xxxix. 1883.

*Cranial nerves of Petromyzon*, Ahlborn, Z. W. Z. xl. 1884. *Spinal and visceral nerves of Cyclostomi*, Ransom and D'Arcy Thomson, Z. A. ix. 1886.

*Pronephros of Myxine*, Weldon, Q. J. M. xxiv. 1884; *sexual products*, Cunningham, Q. J. M. xxvii. (1), 1886. *Urogenital system of Cyclostomi*, W. Müller, J. Z. ix. 1875.

*Abdominal pores and urogenital sinus*, Ewart, Journal of Anat. and Physiol. x. 1876.

## SUB-PHYLUM AND CLASS CEPHALOCHORDA.

### (*Acrania*; *Pharyngobranchii*).

*Marine Chordata, with a body pointed at each end, and provided with a continuous dorsal, anal, and caudal cuticular fin. There are no paired limbs: no skull, vertebral arches and centra: no jaw-arches: no differentiated brain, sympathetic nervous system, or auditory organ: no heart, spleen, kidneys, or sexual ducts. There is but one genus contained in the group—Amphioxus—with species found near the coasts in various parts of the world. The animal, when adult, lives buried in sand with the oral aperture just exposed.*

The epidermis consists of a single layer of columnar cells, ciliated in the larva, with interspersed sense-cells furnished each with a stiff projecting hair, and continuous basally with a nerve-fibre. The cutis is transparent and non-nucleated. The sub-cutaneous tissue contains a remarkable system of anastomosing (lymph?) tubes, lined by an endothelium, and connected with two ventrally-placed tubes running longitudinally one in each metapleure. The notochord extends nearly from one end of the body to the other, is pointed at each extremity, and consists of a series of transverse discs with a dorsal furrow containing a retiform tissue, the whole enveloped in two sheaths. The outer sheath sends out dorsal laminae, which inclose the spinal cord; and ventral laminae, which extend into the walls of the body and the epipleures (*infra*). These laminae are continuous with the sheaths (myocommata) of the myomeres both of the epipleures and of the body behind the branchial region. The myomeres, 62 in number in *A. lanceolatus*, are arranged on each side in a continuous series. The dorsal and ventral sections of each myocomma which are not separated organically from one another, meet at an angle pointing forwards. There is also a small and remarkable set of transverse ventral muscles. The muscles are striated rhombic plates devoid of sarcolemma. The nervous system consists of a spinal cord with a central canal, both of which swell out anteriorly. The anterior enlargement probably corresponds to the hind- and mid-brain with that part of the fore-brain which extends dorsally as pineal gland (?), a structure represented by the so-called olfactory nerve, which is really a tube opening externally in a ciliated depression. The tube represents an aperture left when the neural plate folds over in development to form the neural tube or canalis centralis. The ciliated depression is at first median and dorsal, and afterwards shifts to the left side. Three pairs of nerves arise from the anterior enlargement. The spinal nerves possess dorsal and ventral roots which are not connected outside the cord (Rohon). The ventral roots are purely motor, and arise as short columns. The dorsal are the principal and, according to most authorities, the only, spinal nerves. Their roots possess no ganglia, and the right and left series alternate more or less one with another. The grey matter consists only of ganglion cells. A sac, containing sense-cells with refractile hairs, opens on the dorsal wall of the oral cavity in the centre of a disc of ciliated cells. It is probably an organ of smell or taste, and is derived from the left anterior entero-coelic pouch of the larva (*infra*). It is doubtful whether the pigment speck at the anterior end of the brain can be considered as an eye.

The mouth is a somewhat oblique ventral slit surrounded by twelve cirrhi, which are supported by rods borne upon a ring of twelve pieces, and covered by papillae rich in sense-cells. The oral cavity, produced by a forward growth of the epipleures, is separated from the pharynx by a free fold or velum with fringed edges and many sense-cells. The velum can be

constricted by a muscle. Its aperture represents the original larval mouth. The pharynx extends for nearly half the length of the body, and is traversed from end to end by a ventral hypopharyngeal groove, the homologue of the endostyle in *Urochorda*, and, like it, furnished with ciliated cells. Its walls are pierced by oblique branchial slits, more than 100 in number, in fully grown individuals. The slits open externally into an atrial or peribranchial cavity. The bars that separate them are alternately complete and incomplete, and in the latter case free at their ventral ends. The slits are consequently U-shaped. The bars are supported by elastic rods, all connected at their dorsal ends, and their inner or pharyngeal surface is covered by a ciliated epithelium. The peribranchial cavity originates at an early period by the growth of a right and left fold, or epipleure, from the dorsal region, which meet and fuse ventrally, leaving a ventrally-placed abdominal pore some little distance in front of the anus. The epipleures form two prominent longitudinal folds—the metapleures—one on either side the median ventral line. These folds, therefore, border a ventral furrow; but at the time, when the genital products are ripe, the consequent distension of the epipleures smooths them away. The peribranchial cavity on each side extends behind the abdominal pore for a short distance, and the two cavities are continuous beneath the pharynx from side to side. The epipleures contain the genital glands on their inner surface in the slight extension of the coelome which they inclose. Their outer walls are muscular, and, as before stated, the muscles are divided into myomeres. The water used in respiration and the genital products escape by the abdominal pore, but the latter not invariably. The pharynx is constricted posteriorly into an 'oesophagus,' followed by a widening, the stomach. The intestine runs straight to the anus, which lies asymmetrically on the left side. The anal aperture has a sphincter muscle. A liver caecum opens into the stomach, generally on the right, more rarely on the left, side, and projects into the peribranchial cavity. Its lining cells, as well as those of the stomach, contain a green pigment. The vascular system consists of a dorsal aorta, double in the region of the pharynx, single behind it. The sub-intestinal veins unite to form a vena porta, which supplies the walls of the liver-caecum. The vein bringing away the blood from the caecum runs ventrally beneath the pharynx, and sends up to the dorsal aortae, but only along the complete branchial bars, branchial vessels, which are provided with small pulsatile dilatations at their ventral ends. Anteriorly to the pharynx the ventral vessel is dilated and sinuous. It gives off a right and left branch to the velum and a wide vessel on the right side, which enters the right aortic trunk. The corresponding vessel on the left side is seemingly rudimentary. The whole system is tubular, and the portal vein and ventral pharyngeal vessel are said to be contractile. The blood corpuscles are for the most part amoeboid leucocytes. Rohon states that

*Urochordata*  
system

there are a few oval red haematids. A tubular ciliated saccule, extending on the left side from the margin of the mouth to close behind the velum, where it opens into the pharynx, is supposed by Hatschek to represent a kidney, and to be homologous with the infra-neural gland of *Urochorda*. It is said to be mesodermic in origin. Ray Lankester has pointed out the existence of two tubes, one on each side, opening into the posterior region of the peribranchial cavity at one end, and at the other into the coelome (?). They are possibly renal. The coelome in the region of the body behind the peribranchial cavity is capacious, and contains a coagulable lymph. Its extensions forward above the pharynx and into the epipleures are small.

The ovaries and testes are segmentally arranged, and lie about the level of the union between the lateral trunk and ventral transverse muscles. They consist at first of masses of cells lying beneath the inner wall of the epipleures, from which they are probably derived. A central cavity appears in each mass, and the cells, which are now placed peripherally, develop into ova and spermatozoa respectively. The ripe products appear to be set free by rupture of the inner epipleural wall into the peribranchial cavity, whence they may escape by the abdominal pore; sometimes, however, through the branchial slits into the pharynx, and thence by the mouth. The ovum undergoes total, and at first fairly regular segmentation. There is an invaginate gastrula, and the coelome is an entero-coele, which is divided from before backwards into a series of paired sacs, the primitive somites; see p. 334. It may be added to what is stated there that the two anterior paired sacs grow forward into the head on either side of the notochord, and that an anterior sac, at first single, then dividing into a right and left half, originates from the fore-end of the archenteron. The left sac remains small, acquires an opening to the exterior, and becomes the organ of taste or smell mentioned above p. 438. The right sac increases in size, and takes up a position anterior to the mouth and below the notochord. Hatschek does not state its ultimate fate, but it gives origin presumably to mesoblastic structures. A somewhat similar anterior entero-coelic pouch is seen in the larva of *Balanoglossus*: see *Enteropneusta* among Vermes.

Ray Lankester, Q. J. M. xv. 1875; Langerhans, A. M. A. xii, 1876; Rolph, M. J. ii. 1876; Schneider, Beiträge zur Vergleich. Anat. Berlin, 1879; Balfour, Q. J. M. xx. 1880; Rice, American Naturalist, xiv. 1880; Rohon, Dk. Akad. Wien, 45. 1882; Hatschek, Arb. Zool. Inst. Wien, iv. 1882; Id. Z. A. vii. 1884.

*Oviposition*, Milnes Marshall, Journal of Anat. and Physiol. x. 1876.

SUB-PHYLUM AND CLASS UROCHORDA (= *Tunicata*).

*Degenerate Chordata, which are either simple or compound (colonial), fixed or free, with a test usually containing cellulose, and secreted by the ectoderm. The nervous system is reduced to a single ganglion, except in one group (Larvacea); the notochord confined to the tail, which, with the exception of the same group, is a provisional or larval structure. There is a single or double exhalant aperture by which the water escapes that has traversed the pharynx Hermaphrodite. There is usually a metamorphosis.*

The class contains three distinct orders. The *Larvacea* are small in size, and have a flattened swimming tail moveably attached near the posterior extremity of the body on its ventral surface, towards which it bends. The *Thaliacea* are free-swimming, and more or less barrel-shaped. Among the *Ascidieae*, the *Ascidieae Salpaeformes* (*Pyrosoma*) are colonial, and the colony has the form of a cylinder closed at one end, open at the other, with the Ascidiozooids placed vertically to the surface, in a common test or Ascidiarium; the *A. Compositae* form fixed colonies with the Ascidiozooids contained within an Ascidiarium, sometimes grouped into systems or coenobii; and the *A. Simplicies* are fixed, and either solitary and of a compressed shape, or united by creeping stolons (*Clavelinidae*).

The ectoderm consists of a single layer of polygonal cells. The cells of the anterior region of the body in *Larvacea* are large, and secrete a hyaline gelatinous and sticky substance, which forms the so-called 'house.' This house is sometimes of great size, and extends over the swimming tail. It is separated by one cavity from the greater part of the body, and by another from the tail, which moves freely within. It is detached and renewed at short intervals. When the house is small, the ectoderm cells left uncovered by it are modified, and in *Fritillaria urticans* some of them develop thread cells. The test is very thin and delicate, and is shed from time to time in *Doliolum*. It is thicker in other Urochorda, and either transparent or when very thick more or less opaque, gelatinous or tough, and in the *Ascidieae Compositae* and *Salpaeformes* it constitutes a continuous investing mass in which the zooids are lodged. The substance of the test is chiefly cellulose except in *Doliolum*; it is often fibrillated, and in some *A. Compositae* calcareous deposits occur in it, especially in autumn. The cells of the ectoderm generally proliferate and wander into it, and the cells thus imbedded may become pigmented or vacuolate. It is also often penetrated by blood-vessels. The body walls are composed of muscular and connective tissues. The muscle fibres are fusiform or filiform, and not striated. The fibres form sphincters round the oral and the atrial apertures. Elsewhere they may be arranged either irregularly, or in longitudinal and circular layers, or in circular hoops round the barrel-shaped body (*Thaliacea*) which are either independent (*Cyclomyaria*) or united (*Desmomyaria*). In

*Larvacea* the muscles are striated (Fol), and are restricted to the tail, where they form two bands, which are segmented into myomeres. The connective tissue cells are often pigmented. The caudal notochord of the *Larvacea* and of the larva is rod-like, and composed of a clear substance, like cartilage in consistency, inclosed within a delicate sheath, beneath which are remains of the cells of which the tail was originally composed. In the larva the clear substance appears first of all as a series of discs one behind the other, which ultimately fuse.

The nervous system in the larva consists of two anterior dilatations, the foremost vesicular, the second with a fine canal, and of a posterior nerve, which runs along the tail. At the root of the tail there is a ganglionic enlargement, from which a pair of nerves passes off to the corresponding myomere. Similar pairs of nerves are given off to succeeding myomeres. Their points of origin are dilated, but apparently not ganglionic in all instances. The anterior dilatation of the brain opens externally by a pore, left when the neural groove closes to form the neural tube. In *Larvacea* the nervous system is somewhat similar. There is an anterior pyriform ganglion, connected by a nerve containing an internal fine canal to a ganglion at the root of the tail. The caudal nerve gives off successive sets of nerves, and lies on the left side of the tail, owing to a twist in that organ. In other Urochorda the nervous system is either from the first a simple ganglion, or becomes reduced to it during the metamorphosis. This ganglion gives off branching nerves, both anteriorly and posteriorly<sup>1</sup>. A process of the ganglion in *Larvacea* and *Thaliacea* extends towards a ciliated tubular depression opening dorsally and anteriorly into the pharynx, in front of the peripharyngeal bands. The cavity of the ganglion has been said to open into this tube in the larva and the young *Salpa*. The ciliated depression (= ciliated sac, dorsal or olfactory tubercle) alluded to is found universally in Urochorda; and in many *Ascidiae Simplices* and *A. Compositae* a system of glandular tubes, surrounded by blood sinuses, underlies the nerve ganglion, and opens into the depression. This neural gland has been considered to be renal in function, and to be the homologue of the pituitary body of Vertebrata. As to organs of special sense, the oral tentacles of *Ascidiidae*, &c., are probably tactile in function. So too certain modified ectoderm cells bearing cilia, surrounding the oral aperture of *Larvacea*, and fringing even the margins and tip of the tail in *Kowalewskaia*. They occur also on the lobes of the oral and atrial apertures in *Doliolum* and *Salpa*, as well as on the body surface. Orange-red

<sup>1</sup> In certain simple Ascidians the ganglion is connected posteriorly to a nerve, 'the visceral ganglionic cord,' which contains ganglion cells, and passes along the dorsal edge of the pharynx, then between the rectum and so-called oesophagus, inclines to the right, and ends between the two lobes of the liver. It is derived from the main cord of the larva, which extends from the brain to the root of the tail and along that organ. See E. van Beneden and Julin, Archives de Biol. v. 1884, pp. 317-321, and cap. II. p. 337 et seqq.



spots, probably visual in function, are found, one between each of the lobes surrounding the oral aperture in many *Ascididae*. *Pyrosoma* and *Salpa* have a pigmented outgrowth of the ganglion, with a refracting body imbedded. And the larva has an eye with a concave pigmented retina and complex lens within the anterior dilatation of the nervous system. An otolith borne on a stalk is found in the same position in the larva. The *Larvacea* have a large vesicular otocyst containing an otolith on the left side of the anterior ganglion, and the 'nurse' in *Doliolum* has a similar structure on the left side of the body, connected by a nerve to the ganglion.

The oral or 'inhalent' aperture leads into a pharynx. A groove—the endostyle—extends along the ventral aspect of this cavity, except in *Kowalewskaia*, which has in its place a right and left row of ciliated tooth-like processes. This endostyle is lined by mucus-producing cells and ciliated cells. Anteriorly its lips are connected with the posterior of two ciliated peripharyngeal bands surrounding the oral aperture, which is continuous on the dorsal aspect of the pharynx with a ciliated ridge or fold, the dorsal lamina. This lamina extends backwards to the opening of the 'oesophagus.' Its edge is sometimes denticulated, forming a single or double row of languettes. Posteriorly the endostyle is connected to the oesophagus by a ciliated line, which comes also into connection with the posterior end of the dorsal lamina. The mucus secreted is chiefly carried forwards, and as it passes upwards to the dorsal lamina, it is drawn out into long strings by the current of water entering the oral aperture, and catches up all floating food-particles with which it is laden. It is then conveyed along the dorsal lamina into the oesophagus. In *Larvacea* the pharynx has two latero-ventral outlets or stigmata, one on the right, the other on the left, surrounded by a ring of ciliated cells, and developed each from a pharyngeal outgrowth meeting an ectodermal ingrowth. Other Urochorda have a single atrial, exhalent or cloacal aperture. This aperture is placed dorsally, either near the oral aperture (*Ascidiae Simplicies* and some *Compositae*) or at some distance from it (other *Compositae*), or else at the opposite pole of the body (*A. Salpaeformes*, *Thaliacea*). It leads into a 'peripharyngeal' or atrial cavity, which surrounds the pharynx, except along the line of the endostyle, and is limited anteriorly by the line of the peripharyngeal bands. The cavity is lined by an epithelium derived from the ectoderm, from which it is formed by one or two invaginations. In the latter case the two apertures fuse. In certain buds, however, it appears to be formed by pharyngeal outgrowths. The lateral walls of the pharynx are often folded longitudinally and are perforated by ciliated slits (stigmata), between which run blood-channels. The slits lead into the atrial cavity. Among *Thaliacea*, the pharynx in *Doliolum* is represented by a vertical membrane perforated by only two rows of slits,

and in *Salpa* it is reduced to the dorsal lamina with a great gap on either side of it.

The digestive portion of the alimentary canal is formed as an outgrowth of the archenteron. It is ciliated in part or wholly, especially the intestinal section. It lies either behind the pharynx, or to the left side of it (some *A. Simplices* and *Compositae*), or is reduced in size and placed quite to the ventral side, as in *Pyrosoma*, *Doliolum*, and *Salpa*, and in the last it forms, with the other viscera, a small mass termed 'nucleus.' The first portion of it ('oesophagus') is narrow, and variable in length. The stomachal region is more or less dilated, and the intestinal tubular. The anus opens on the ventral surface between the stigmata, or on the right side in *Larvacea*. In other Urochorda the intestine has an adoral and dorsal twist, and the anus opens just within the atrial aperture, i.e. is dorsal in position. When this aperture is terminal and posterior, the course of the intestine is still towards the dorsal aspect. In *Larvacea* there are no specialised gland cells at all in the digestive tract. Glandular caeca coat the stomach in many *A. Simplices* and *Compositae*, and in the *Molgulidae* form a lobed mass. In most Urochorda a system of clear tubes ramifies over the intestine and sometimes the stomach as well, occasionally anastomosing freely (some *Salpae*) and ending in ampullae (*Ascidia*, *Perophora*, *Salpa*, *Pyrosoma*). They open by one or two large tubes into the posterior part of the stomach. Their function is not clear, but cilia have been detected in them in *Perophora* and *Doliolum*.

A heart is absent only in *Kowalewskaia*. In other *Larvacea* it lies more or less ventrally close to the stomach, is elongated transversely, and at either end of the longer axis is a large cell. Between the two cells stretch muscle fibres. In other Urochorda the heart is tubular, with circular muscle cells, and is contained in a pericardial sheath. It lies ventrally on the right or left side, close to the stomach, in front of it, along it, or, in *Clavellinidae* and many *A. Compositae*, behind it. In all Urochorda the direction of its beats undergoes periodic reversal. In *Larvacea* there are no vessels and no blood corpuscles—nothing but irregular and small spaces representing a coelome. The direction of the currents can only be detected when the blood is infested with parasitic organisms. Other Urochorda possess vessels in connection with both ends of the heart. A main blood-channel lies below the endostyle, another above the dorsal lamina. The two are connected by transverse vessels encircling the pharynx, which in their turn are connected by minute longitudinal interstigmatic vessels. The latter are absent in *Pyrosoma*. There are sometimes large longitudinal vessels running on the inner surface of the pharynx, connected to the transverse vessels where they cross them, e.g. in *Pyrosoma*, many *Ascidiae*, &c. Branches from the pharynx pass into the body walls and test. The visceral vessels are connected to the dorsal vessel of the heart and pharynx.

Both dorsal and ventral cardiac vessels give off branches to the test. The blood has a clear plasma with nucleated and usually rounded corpuscles, many of which are sometimes pigmented (opaque white, yellow, red, brown, purple, blue). Specialised renal glands are not present (? the neural gland). Many *Ascididae*, however, have clear vesicles in masses round the intestine and in the body walls, containing concretions. And in the *Molgulidae* there is a sac-like organ close to the pericardium, containing rounded concretions, in which uric acid has been detected. A yellowish-green mass usually coats the first part of the intestine in *A. Compositae*, and perhaps corresponds to the clear vesicles of the *Ascididae*.

All Urochorda are hermaphrodite, but the male and female organs appear to become mature at different times. Sexual organs are absent, or at least atrophied, in the nurse forms of *Salpa* and *Doliolum*, in the Cyathozoid of *Pyrosoma*, and in certain generations of *Botryllus*. Both testes and ovary in *Larvacea* are simple saccular organs, devoid of ducts. They lie behind the stomach, and their contents are set free by dehiscence of the body walls, and the organism then dies. In other Urochorda the organs are either more or less saccular, as in *Ascidia*, or else branching tubes, and their ducts either open close together or by a common aperture, as in *Doliolum*, into the atrial cavity, and close to the anus. There is but a single ovum in *Pyrosoma* and *Salpa*. In most Urochorda except the *Larvacea*, follicular cells surround the ovum, and are inclosed with it in a membrane. The follicle cells sometimes give origin to a chorion enveloping the ovum, and in some instances grow out into long external villiform processes. Within the chorion appear in many instances a number of so-called test-cells. The origin and fate of both the follicular and the test-cells are involved in much difficulty (see lit. cited below). Impregnation and sometimes development take place in the atrial cavity, in a special incubatory pouch opening near the anus (some *A. Compositae*), or within the ovary, as in *Pyrosoma* and *Salpa*. Segmentation is regular, except in *Pyrosoma*, where it is meroblastic, a germinal disc being formed. There is an invaginate gastrula, or in *Molgula* (? all species) a gastrula by overgrowth. In *Salpa* the developing embryo is nourished by a placenta formed, in part at least, by follicle cells; and certain cells—gonoblasts—derived from the follicle cells have been stated to take the chief part in the formation of the embryo itself (Salensky), but details vary in different species. Except in *Salpa*, *Pyrosoma*, and *Molgula tubulosa*, there is a larva which resembles in many respects one of the *Larvacea*. It possesses a straight swimming tail, supported by a notochordal rod, moved by lateral muscles, and containing an extension of the nervous system. After a certain period of free existence, the larva attaches itself by means of the glutinous secretion of glands borne by three papillae developed at the anterior end of the body. The papillae subsequently atrophy, and the

organism remains attached by processes of the test. The tail atrophies, and some of its cells appear to become blood-corpuscles, whilst the shape of the body undergoes profound changes. Except in the *Larvacea*, in the sexual forms of *Thaliacea*, and the majority of *A. Simplicis*, asexual generation takes place by budding or fission. In the *Clavellinidae* there is a creeping stolon which produces buds, and the new organisms remain in vascular connection with the parent. In the *A. Compositae* and *A. Salpae-formes* colonies are formed in which the individuals are enveloped in a common test. As to the *Compositae* the larva buds in *Distaplia* and continues to develop, whereas in *Pseudodidemnum gelatinosum* it dies away, and in *Amareucium proliferum* the post-abdomen (i.e. hind section of the body) divides transversely into several pieces, each of which becomes a new zooid, whilst the parent grows a new post-abdomen. In *Botryllus* the first individual is asexual, buds, dies away, and this process is continued for several generations. The zooids thus formed are arranged in star-like groups (systems or coenobii) round a common cavity, into which their atrial pores open. The germinal disc in *Pyrosoma* develops in the posterior region into a transitory Cyathozoid, in the anterior into the four first Ascidiozooids of the colony, which are connected to or continuous with the Cyathozoid. Alternation of generations occurs in the *Thaliacea*. The asexual generation or *nurse* has a ventral posterior stolon. This stolon grows to a great length in *Salpa*, and is constricted into a series of buds, which remain connected for a lengthened period, and are set free collectively from the parent as sexual or chain *Salpae*. The chain is eventually broken up. In *Doliolum* the stolon is small. It develops a number of primitive buds, which are set free, and creep over the parent by means of pseudopodial processes of the ectoderm cells. They become attached to a dorsal and posterior process of the body, where they multiply by transverse division, and are arranged in linear series, two lateral and one median. The dorsal process lengthens as the number of buds increases. The lateral series of buds grow into *nutritive zooids*. The epithelium of the stolon, and of the bases of these zooids, is peculiarly modified, and the products of digestion appear to pass from the zooids to the parent, which loses its pharynx and digestive tract whilst its muscle-bands enlarge. The zooids of the middle series grow, and are eventually set free as *foster-mothers*. The foster-mother is asexual, and carries away attached to its peduncle a few primitive buds, which divide, forming fourteen to twenty secondary buds. These develop into the sexual *Doliolum*. The ovum in both *Salpa* and *Doliolum* produces the nurse. *Anchinia* probably resembles *Doliolum* more or less closely. The cylindrical body with attached buds, which become sexual animals or produce creeping buds, is probably a detached part of a dorsal (?) process. The nurse is not known unless it is the form from Naples described by Wagner.

The Urochorda are divisible into the three following Orders:—

I. *Larvacea* (= *Copelatae*). Free-swimming; body small, more or less oval, provided with a long swimming tail, containing a notochordal rod; a temporary gelatinous case, secreted by the ectoderm, which is renewed from time to time; two stigmata: *Appendicularidae* (*Oikopleura*, *Fritillaria*, *Kowalewskaia*).

II. *Asciidiacea*. Either sessile, and then simple, social, or compound, or free-swimming and colonial. Test well developed, and often massive; stigmata numerous, and pharynx large and specialised.

(1) Sub-order *Asciidae Simplicis*, fixed or free, solitary or social: sometimes producing by gemmation colonies, in which the Ascidiozooids are connected by a common vascular system, but each retains its own test. The oral and inhalent apertures are near to one another, at the same end of the body. *Molgulidae* (free as a rule), *Cynthiidae*, *Asciadiadae*, and *Clavellinidae* (colonial).

(2) Sub-order *Asciidae Compositae*. Fixed; colonial; Ascidiozooids imbedded in a common test; often connected by a common vascular system; and generally grouped more or less regularly in systems round a central cavity, into which the exhalent apertures of the zooids open. Body simple (*Botryllidae*); divisible into a 'thorax' and 'abdomen' (*Didemnidae*); or into a 'thorax,' 'abdomen,' and 'post-abdomen' (*Polyclinidae*). Gemmation universal.

(3) Sub-order *Asciidae Salpaeformes*. Free-swimming pelagic colony, in the form of a hollow cylinder, closed at one end and open at the other, at which its extension takes place. Zooids placed perpendicularly to the surface, with the oral aperture external, the cloacal internal, and leading into the central hollow of the cylinder. *Pyrosomidae* with one genus *Pyrosoma*, which is phosphorescent.

III. *Thaliacea*. Free-swimming; more or less barrel-shaped, with oral and cloacal apertures at opposite ends of the body; test very thin; muscles circularly arranged; and viscera contracted into a small compass, and laterally placed. An alternation of generations. *Doliolidae* (= *Cyclomyaria*) the muscles in complete hoops; two transverse rows of stigmata; *Doliolum*; *Anchinia*. *Salpidae* (= *Desmomyaria*) muscular hoops incomplete and sometimes uniting; pharynx reduced to the dorsal lamina, on either side of which is a large space; *Salpa*.

*Larvacea*, Fol, Études sur les Appendiculaires, Geneva, 1872. *Vertebration of tail*, Ray Lankester, Q. J. M. xxii. 1882. *Ovogenesis, &c., in Appendicularia*, A. B. Lee, Recueil Zool. Suisse i, 1884.

*Asciidiacea*, see pp. 106-7. *Ascidians of Provence*, Roule, An. Mus. Hist. Nat. Marseille, ii. 1884; Id. Recueil Zool. Suisse, iii. 1886; Id. A. Sc. N. (6) xx. 1886. *On place of Clavellinidae*, Herdman, Proc. Roy. Soc. Edin. x. p. 716. *Development of Clavellina*, Seeliger, J. Z. xviii. 1885. *Asciidae Compositae*, Herdman, Challenger Reports, xiv. 1886, and Nature, xxix. 1883-84. *Synasciidae*, Giard, A. Z. Expt. i. 1872; ii. 1873. *Botryllus*, Krohn, A. N. 35, 1869.

*Pyrosoma*, Keferstejn und Ehlers, Zool. Beiträge, Leipzig, 1861; Huxley, Tr. L. S. xxiii. 1862; Kowalewsky, A. M. A. xi. 1875.

*Thaliacea*. *Doliolum*, Uljanin, Fauna und Flora des Golfes von Neapel, x. 1884. *Salpa*; *testis and alternations of generation*, Salensky, Z. W. Z. xxx. Suppl. 1878; *gemmation*, Id. M. J. iii. 1877; Seeliger, J. Z. xix. 1886; *development of ovum*, Salensky, Mittheil. Zool. Stat. Naples, iv. 1883. *Anchinia*. Wagner, A. Z. Expt. (2) iii. 1885; Korotneff, Z. W. Z. xl. 1884; Kowalewsky and Barrois, A. N. H. (5) xii. 1883.

*Egg and envelopes in Urochorda*, Fol; Sabatier, Recueil Zool. Suisse, i. 1884;

and Roule, *ibid.* ii. 1885. Salensky on *Salpa* (*supra*); Seeliger on *Clavellina lepadiformis*, SB. Akad. Wien, lxxxv. Abth. i. 1882. *Segmentation and postembryonal development*, E. van Beneden et Julin, Archives de Biol. v. 1884; vi. 1886.

For literature, see Herdman, Tunicata, Challenger Reports, vi. 1882; xiv. 1886<sup>1</sup>.

## PHYLUM MOLLUSCA.

*Coelomate Metazoa, which are primitively bilaterally symmetrical: with a soft integument, generally ciliated and richly supplied with glands: with an integumental fold forming a mantle or pallium, and a ventral muscular thickening of the body walls known as the foot. There is usually an external shell borne upon and secreted by the mantle. Vascular processes of the body wall form gills or ctenidia adapted to aquatic respiration. The nervous system consists typically of a pair of cerebral ganglia united by connectives to a pair of pedal and a pair of pleural ganglia, the latter continuous with a ganglionated visceral loop, of greater or less extent. There is a pair of otolithic vesicles or otocysts; a heart, and a partly lacunar blood-system; one or two renal sacs or nephridia. A large gland or liver generally opens into the alimentary canal. There is a characteristic larval form or Veliger.*

Bilateral symmetry is retained in *Cephalopoda*, *Scaphopoda*, *Lamelibranchiata*, and some few *Gastropoda*. But in the majority of the last-named class there is a marked external and internal asymmetry, the latter shown by the position of certain of the organs (heart, termination of the intestine) and the loss of others (a nephridium a gill); the former by the disposition of the dorsal part of the body or visceral dome and the mantle fold, as well as by the shape of the shell. In some cases, however, a secondary external symmetry has become established as in some *Opisthobranchia* and *Pulmonata*. The *Pteropoda*, though as a rule externally symmetrical, are internally asymmetrical. The mantle fold is disposed in a characteristic manner in the different classes. It is never absent in the embryo, though sometimes lost in the adult of some *Pteropoda* and *Gastropoda*. It is a continuous fold except in *Lamelibranchiata*, where it is formed by independent right and left folds. The same is the case in the *Scaphopoda*—but here the mantle folds unite or conalesce ventrally as they do in some *Lamelibranchiata*. The space inclosed between the mantle fold and the body is the mantle- or sub-pallial cavity. The foot assumes various shapes equally characteristic of the various classes: it is rarely completely aborted as in certain *Gastropoda* (*Opisthobranchia Haplomorpha*) and a few *Lamelibranchiata* (*Ostreidae*). It extends

<sup>1</sup> An account by Herdman of *Larvacea*, *Pyrosoma*, and *Thaliacea* will appear in a forthcoming volume of the Challenger Reports.

normally along the ventral surface below and behind the head to the posterior limit of the body. It varies in size and shape, and may be simple (*Lamellibranchiata*, many *Gastropoda*), or divided transversely into segments, the pro-, meso-, and meta-podium (some *Gastropoda*). In the *Pteropoda* the median part of the foot is rudimentary: but there are two large lateral swimming lobes, homologous probably with the epipodial lobes of the *Gastropoda*, and, like them, supplied by nerves from the pedal ganglion. The foot is still more modified in *Cephalopoda*. One portion of it, the fore-foot, as proved by the nerve-supply from the pedal ganglia, has grown round the head, and is produced into lobes or arms characteristic of the class. It may correspond with the lateral lobes of the foot in *Pteropoda* which grow round the mouth in the order *Thecosomata*. Another portion of the foot—the mid-foot—forms two lobes which usually fuse together, and constitute the siphon: and a third portion—the hind-foot—is represented by the valve of the siphon. The homologies of these three divisions of the foot are by no means certain, as the development of this region of the body is apparently greatly altered by the presence in it of a plentiful food-yolk.

The shell is essentially a cuticular structure, calcified by Lime carbonate with the exception of a thin superficial layer, the periostracum or epicuticula; but occasionally calcification fails to take place. In Di-branchiate *Cephalopoda* the shell is developed when present in a sac formed by the closure of two dorsal integumentary folds. In *Spirula* alone do these folds fail to unite. The way in which the shell is first formed in Tetrabranchiate *Cephalopoda* is unknown. In all other Mollusca the larva possesses a shell-gland developed as a pit of the epiblast on the dorsal aspect of the visceral dome. This gland rarely persists in the form of a sac, as in a few Pulmonate *Gastropoda*, but it is usually everted, and on this everted surface the shell commences its development. Its subsequent growth is dependent on the mantle. It extends with the extension of the mantle-edge, and an increase of thickness takes place from the surface of the mantle already covered. In some instances, e.g. Tetrabranchiate *Cephalopoda* and a few *Gastropoda*, the animal as it grows in size, quits a portion of the shell which is then closed off by a calcareous septum, The processes and ridges of the shell are formed by folds and processes of the mantle-edge, its colours by pigment-secreting glands in the same region. The actual shape of the shell is very variable. It is composed of a single piece, except in the *Gastropoda Isopleura* where it consists of a longitudinal series of plates one behind the other, and the *Lamellibranchiata* where it consists of a right and left valve, connected, however, by a median dorsal ligament to be regarded as an uncalcified portion of the shell.

The dorsal or antipodial region of the body has a thin integument, and constitutes the visceral dome or hump. It is scarcely marked in

*Lamellibranchiata*, is co-extensive with the foot in some *Gastropoda*, in others developed along a dorso-pedal axis, but with rare exceptions it is in this Class, whether large or small, spirally twisted from behind forwards along the right side of the animal. There is a consequent displacement of the ctenidia, viscera, and the nephridial and anal apertures. In *Cephalopoda* and *Pteropoda* it is also much enlarged but along an oblique axis, which is directed backwards between the dorso-pedal and antero-posterior axes. A spiral torsion of this dome is observed only in one family of *Pteropoda*, the *Limacinidae*; but whilst the *Cephalopoda* have retained bilateral symmetry it is almost certain that the *Pteropoda* have acquired it. A head is well-developed and distinct in *Gastropoda Anisopleura* and Gymnosomatous *Pteropoda*. It is obscured in *Cephalopoda* by the growth round it of the foot. In other Mollusca it is more or less rudimentary.

The respiratory organs are ctenidia, or gills, external processes of the body. In some instances, *Pteropoda*, a few *Gastropoda*, respiration is carried on entirely by the surface of the skin. There can be little doubt, however, that such forms have lost the gills. A ctenidium consists essentially of an axis containing an afferent and efferent blood-vessel and giving support on either side to a series of vascular lamellae or processes, the surface of which is ciliated except in *Cephalopoda*. The ctenidial axis remains either free, e.g. *Nautilus*; or partly free, partly attached to the side of the sub-pallial space; or attached throughout its whole length, e.g. Dibranchiate *Cephalopoda*. The respiratory processes it bears generally assume a most complicated structure in *Lamellibranchiata*. The ctenidia are always lodged in the sub-pallial space, which may be much enlarged in the region where they lie forming a branchial cavity. In the *Polyplacophora* there are a number of them, but in all other Mollusca they are typically two, one on each side of the body. In the majority of *Gastropoda* the primitive left ctenidium is aborted. Occasionally both are aborted, and then respiration is carried on either by secondarily developed vascular ridges lodged in the sub-pallial space, as in the Limpet, or by the part of the mantle which forms the roof of the branchial cavity, as in Pulmonate *Gastropoda*, or by the surface of the body.

The nervous system consists typically of a pair of cerebral ganglia, placed above the oesophagus, and two pair, pedal and pleural, placed below it. The two members of each pair of ganglia—cerebral, pedal and pleural—are united to one another by nerve-commissures: the cerebral to the pedal and pleural, as well as the pedal to the pleural, by nerve-connectives. Commissures and connectives vary in length, and consequently there is not only a greater or less degree, but also a varying mode of concentration of the ganglia among themselves. The cerebral ganglia supply the head, the organs of touch, the otocysts (except in *Lamelli-*



*branchiata*?), and the cephalic eyes as well as the pharynx. The pedal ganglia supply the foot. The pedal nerves are sometimes connected by a series of transverse commissures. Each pleural ganglion is continued backwards into a nerve which unites posteriorly below, rarely above the intestine, with its fellow, forming a visceral loop. This loop typically carries a pair of visceral ganglia, and a posterior abdominal ganglion. The pleuro-visceral system thus constituted supplies the viscera and the walls of the body exclusive of the foot, and special ganglia are not infrequently developed on its nerves. In *Fissurella* and *Haliotis* (*Gastropoda Anisopleura*), the pedal ganglia are replaced by long cords with an outer coat of ganglion cells, extending down the foot and connected by transverse fibrous commissures. The pleural ganglia are only incompletely differentiated from the anterior ends of these cords. In *Chiton* and its allies there are pleural as well as pedal cords both connected with a cerebral ring, all alike invested with ganglion cells. The cords are derived in *Chiton*, as are the ganglia in nearly all Mollusca, from the epiblast. It is possible that these forms of nervous system represent a primitive state, and that the concentration of ganglion cells into ganglia is a later state. A pair of buccal ganglia are developed in the *Glossophora* in connection with the buccal mass upon which they lie. They supply the salivary glands, oesophagus and radula, and are connected to the cerebral ganglia; but it appears that in *Fissurella*, *Haliotis* and *Turbo* they are really connected to the pleuro-pedal centres, their connective only *traversing* the cerebral ganglia (Haller).

Special sense-cells provided with immobile sense-hairs have been found in the epidermis of *Gastropoda* and *Lamellibranchiata*. A special patch of ciliated epithelium lies close to the base of the gills. A ganglion in connection with a nerve derived from one of the visceral ganglia or from the visceral loop underlies this patch. The whole constitutes the osphradium, an organ which probably detects changes in the water passing over the gills. The osphradium occurs in all groups of Mollusca except *Scaphopoda*. An olfactory (?) pit is found near the eye in *Cephalopoda*. Cephalic eyes are absent in *Scaphopoda* and *Lamellibranchiata*, and are rudimentary in *Pteropoda* if present. Eyes of a simple or complex structure are scattered along the mantle-margin in many *Lamellibranchiata*. In two instances (*Pecten*, *Spondylus*) these mantle-eyes bear a singular resemblance to the Vertebrate eye: the visual rods are turned away from the light, and there is a cellular lens derived however from the mesoblast. A cellular lens and visual rods, turned as in *Pecten* and *Spondylus*, are again met with in the dorsal eyes of certain species of the Gastropod genus *Onchidium*. These three instances are, so far as is known, the sole exceptions to the rule that the visual rods of Non-Vertebrates are directed towards the light. A cellular lens also only recurs among Non-Vertebrates

in the Medusa *Charybdaea*<sup>1</sup>. The otocysts nearly always lie close to the pedal ganglia. They generally arise from the epiblast as pits which close forming a vesicle, sometimes as solid ingrowths. They contain one or more calcareous otoliths, and are lined by an epithelium which is generally ciliated and occasionally provided with sense-hairs.

The digestive tract is composed of a stomodaeum, a mesenteron, and in some instances at least a proctodaeum. The stomodaeum in the *Glossophora* is muscular, has appended salivary glands, and contains an organ known as radula, composed of a chitinous membrane bearing chitinoid teeth, developed within a sac (radular or odontophore sac), and growing throughout life. It is borne in turn upon a subradular membrane and cartilages, the latter always, the former sometimes, moved by muscles, the whole constituting the odontophore. The shape and arrangement of the teeth vary much; for development, &c., see p. 115. The mesenteron is of some length. It is rarely straight, and its disposition is affected by the mode of growth of the visceral dome. It makes a single simple bend upon itself in *Cephalopoda* and *Pteropoda*, the concavity of the bend being turned to the pedal ganglia. In other Mollusca it is more or less coiled. A stomachal widening can generally be distinguished. A liver is always present in the shape of either simple caeca appended to the stomach or of a large gland, paired except in *Cephalopoda*. The cells of the liver follicles are of three kinds—granule cells, ferment and lime-producing cells. The first-named are always present. Ferment-cells are said to be absent in *Pteropoda*, whilst the last-named are absent in *Lamelli-*

<sup>1</sup> Patten has very recently published a most important paper on the eyes of Molluscs and Arthropods (Mitth. Zool. Stat. Naples, vi. 1886). He points out on pp. 544-5 the following general features. The Molluscan hypodermis, especially where exposed to light, has a cuticula divisible into an outer structureless layer, the *corneal* cuticula, and an inner *retinidial* cuticula in which ramify the terminations or *retinidia* of the hypodermis nerves. Every eye consists as a rule of a number of eye-elements or *ommatidia*, which may and do occur isolated as well as aggregated. Every ommatidium is composed of 2-4 central cells or *retinophorae* fused together, and inclosing an axial nerve, and of one or more surrounding circles of pigmented cells or *retinulae*. In the more primitive instances both retinophorae and retinulae terminate, each cell in its own cuticular rod, with a retinidium or nervous rete; in more specialised instances the retinulae do not possess rods. A collection of ommatidia in which the rods of the retinophorae and retinulae, or of the former alone, constitute a continuous layer, and the retinulae retain their pigment and position surrounding the retinophorae, is to be termed a *retineum*. When the retinophorae alone retain their rods, and each group of retinophoral cells is completely isolated, the resulting structure is an *ommateum* as in the compound eyes of certain *Lamellibranchiata* and *Arthropoda*. If the retinulae belonging to each ommatidium lose not only their rods but also their pigment, and are transformed into ganglion cells, then the collection of eye-elements constitutes a *retina* as in Vertebrata, *Pecten*, *Spondylus*, and *Onchidium* (?). It may be added that the retinophorae terminate in a fibre continuous with a nerve; the retinulae in root-like fibres which enter the basement membrane of the hypodermis; that the former contain nuclei, one of which is large, the latter a nucleus which is non-nucleolate. The nerve-fibres of the retinulae lie between the cells, as is the case in the hypodermis at large; whilst the retinophorae not only contain an axial nerve-fibre, but have others surrounding them externally. The axial nerve-fibres form a rete in the rods. The greatest number of types of eye are found in the Lamellibranch *Arca*.

*branchiata* and *Pteropoda*, and some *Gastropoda* (see pp. 116-7). The anus opens into the sub-pallial space. Its typical position is posterior and always above the foot. In one division of *Gastropoda*, the *Anisopleura*, where torsion of the visceral dome has taken place, it is either on the right side or anterior. It has the same anterior position, either on the right or left side, in *Pteropoda*.

All Mollusca are furnished with a heart except the *Scaphopoda*. This heart consists of a thick-walled ventricle giving off an aorta single or double, and receiving blood from a single (most *Gastropoda*, *Pteropoda*) or double (i. e. right and left) auricle, in both cases obviously derived from a special dilatation and thickening of the branchial veins bringing back the blood from the ctenidia. But in *Nautilus* (*Cephalopoda Tetrabranchiata*), the only Molluscan with four gills, and therefore four efferent branchial veins, the four auricular dilatations are not well marked, and scarcely if at all thickened. The arterial system of vessels is very well developed, and capillaries are present in many *Cephalopoda* and some Pulmonate *Gastropoda*, but as a rule the blood-system is to a great extent lacunar. Sinuses or veins with defined walls usually convey the blood to the ctenidia. Amoeboid corpuscles are always present. Haemoglobin is very rarely found. Haemocyanin—a copper-containing pigment, blue when oxydised, colourless when deoxydised, and acting as an oxygen-carrier, has been detected in various Mollusca. The heart is lodged in a pericardium or secondary coelome. It is apparently a closed off portion of the coelome which is not filled with blood and communicates with the exterior through the nephridia, in *Nautilus* alone by independent openings. The rest of the coelome has the form of irregular spaces filled with blood and lodging the viscera. The entrance of water into the blood-system, either through special pores, inter-epidermic channels, or through the nephridia and the pericardium, appears to be very questionable. A 'pericardial gland' which appears to have an excretory function is present in *Cephalopoda*, some *Gastropoda* and various *Lamellibranchiata*.

There are four nephridia or renal sacs in *Nautilus*, two in other Mollusca, with the exception of the *Pteropoda* and the majority of the *Gastropoda Anisopleura*, in which one sac is aborted. They communicate internally with the pericardium and open externally near the anus, except in *Lamellibranchiata* where the apertures are anterior. The nephridial sac is often differentiated into a non-secreting duct, and a glandular portion which is frequently dark-coloured from the presence of excretory products in the epithelium. It is ciliated internally except in *Cephalopoda*, and the ciliary currents appear to set outwards<sup>1</sup>.

<sup>1</sup> Cells of a whitish colour and containing uric acid are found in lines between the coils of the intestine in *Cyclostoma elegans*, forming the 'Concrement-drüse'; Barfurth, Z. A. vii. 1884. Cells either pigmented or not pigmented, and containing uric acid are found scattered as a 'diffuse

The sexes are united in *Pteropoda*, euthyneurous *Gastropoda Anisopleura*, and a few *Lamellibranchiata*. Among the last-named different parts of the same sexual gland may be male or female; or, as in *Ostrea edulis* and the other groups referred to, there is an hermaphrodite gland in which sperm and ova develop near to one another, or side by side. The glands themselves are simple in structure. In *Cephalopoda* they are developed in the walls of the pericardium, as they appear to be in the Gastropodan *Neomeniae* and *Chaetoderma*. In these latter the genital products are set free through the nephridia, in *Cephalopoda* by special ducts. The glands in other Mollusca are continuous with their own ducts, but in some *Lamellibranchiata* the latter may open into a common sinus with the nephridial ducts, or as in *Scaphopoda* into the nephridium. There is no accessory genital apparatus of any kind in *Lamellibranchiata* and *Scaphopoda*. But other Mollusca possess at least an intromittent organ, in *Cephalopoda* a modified arm, in others a process of the body-walls, either remote from or connected to the genital aperture; a gland which secretes albumen for the ova; and in some cases organs such as a uterine dilatation, receptaculum seminis, vesicula seminalis, together with special glands. These accessory organs are most complicated in *Pteropoda* and hermaphrodite *Gastropoda*. Impregnation of the ovum may take place externally to the organism, as in *Cephalopoda* (? all), *Scaphopoda*, *Chiton* and *Zygobranchia* among *Gastropoda*, and most *Lamellibranchiata*; within the genital duct in *Pteropoda* and most *Gastropoda*. The spermatozoa are contained in spermatophores in *Cephalopoda* and pulmonate *Gastropoda*. The ova vary much in the amount of food-yolk they contain, and therefore in their mode of segmentation. They are largest in *Cephalopoda* where the only part of the ovum that segments is, as in the Sauropsida, a disc of protoplasm. The ovum is devoid of primary egg-membranes in *Gastropoda* and *Cephalopoda*.

The Mollusca with the exception of *Cephalopoda* pass through a typical larval development, in two stages—a Trochosphere and a Veliger stage. The Molluscan Trochosphere has a ventral mouth, bent intestine, and ventral or terminal anus. It has a praeoral lobe, variable in size, but encircled by a band of cilia—the velum—at its base, with in some cases a postoral band of fine cilia (Mc'Murrich, A. N. H. (5), xvi. 1885). It is especially characterised by a ventral projection between the mouth and anus, the rudimentary foot, and by a dorsally placed depression lined by epiblast—the shell-gland. It passes into the Veliger stage in which the velum enlarges, and in the larvae of *Pteropoda* and *Gastropoda* is drawn out into at least two lobes, one right, the other left: the shell gland may secrete a chitinous plug, but it flattens out (except in a few

kidney' in certain regions of the integument and walls of the pericardium of some *Gastropoda Opisthobranchia*; Trinchese, Arch. Biol. Ital. iv. 1884.

instances) and forms an area upon which the shell begins to develop, while its edges thicken and extend, and eventually form the edges of the mantle: the foot also enlarges in a manner characteristic of the group to which the Veliger belongs. It generally bears an operculum upon the dorsal aspect of its hinder extremity in *Pteropoda* and *Gastropoda*, whilst in *Lamellibranchiata* a byssus gland appears as an epiblastic involution at its edge. Both operculum and byssus gland may persist or disappear. Individual peculiarities occur in different groups—e.g. *Chiton*, *Dentalium*, and many *Lamellibranchiata* possess a flagellum or tuft of cilia projecting from the centre of the velar area; a posterior tuft of cilia may also occur. The normal course of development may be abbreviated or modified in freshwater, terrestrial or viviparous forms. The *Cephalopoda* have a modified development owing to the presence of food-yolk. The yolk-sac appears to occupy the position of the foot, and the velum is either not represented at all, or only in a very rudimentary manner. The edge of the blastoderm is ciliated in some instances. The shell-sac is formed by two dorsal folds, and does not appear to be homologous with the shell-gland which is therefore not represented.

The great majority of Mollusca are water-breathers, and marine in habitat: some *Gastropoda* and *Lamellibranchiata* are fluviatile and lacustrine: and a few *Gastropoda* are terrestrial and air-breathers. The remains of *Cephalopoda*, *Pteropoda*, *Gastropoda* and *Lamellibranchiata* occur in the lower Silurian strata.

The Mollusca may be grouped in two main divisions, the *Glossophora* and *Lipocephala* of Ray Lankester, sometimes also termed *Cephalophora* and *Acephala*. The division *Lipocephala* comprises the single class *Lamellibranchiata*; the division *Glossophora* the four classes *Cephalopoda*, *Scaphopoda*, *Pteropoda* and *Gastropoda*.

The *Pteropoda* and *Cephalopoda* are associated together by Professor Lankester as *Cephalopoda*—the class here called *Cephalopoda* receiving the name *Siphonopoda*. This arrangement has not been followed because the *Pteropoda* seem to be a group which are really asymmetrical and have acquired an external symmetry. External asymmetry is preserved in the *Limacinidae* with their spirally twisted visceral dome and shell; and in the spiral shell of the larval *Cymbulia* and *Tiedemannia*. The occasional presence of an operculum in the adult and larva; the asymmetry observable in the osphradium, and nephridium, and in the position of the anus; the structure of the genital organs are points in which the members of the class strongly resemble the *Gastropoda*, as they do also in development. The cephalic appendages of the *Pteropoda* have probably nothing to do with the arms of a Cephalopod. The latter are supplied by the pedal nerve, whilst the buccal cones of *Clio*, the only Pteropod very accurately monographed, are supplied by the cerebral ganglia. It is possible that the arms of the Cephalopod represent the epipodium. In this case they may be compared with the epipodia of Thecosomatous *Pteropoda* which have grown round the mouth. And in the three lobes of the

median foot, as seen in *Clio*, structures are present which might well represent the lobes and valve of the funnel in a Cephalopod. But the last mentioned are points on which there is great difference of opinion. See Grobben, 'Morphologische Studien über den Harn und Geschlechtsapparat, &c., der Cephalopoden' Arb. Zool. Inst. Wien, v. 1884, pp. 44-70, for a recent discussion of them and of the affinities of *Cephalopoda*.

#### BRANCH I. GLOSSOPHORA.

Mollusca in which the head region is more or less developed, and is always provided with an odontophoral apparatus and radula.

#### CLASS CEPHALOPODA.

*Bilaterally symmetrical Glossophora, with the head surrounded by a portion of the foot which is produced into tentacle-bearing lobes or sucker-(sometimes hook-) bearing arms; with a part of the foot modified to form a siphon; and a muscular contractile mantle-fold subserving both respiration and locomotion. The shell is variable in structure, sometimes internal or absent; when external usually chambered. The visceral dome is elongated. The ctenidia, which are usually two in number, the anus and nephridial apertures, are posterior. The vascular system is highly developed, and consists of a ventricle and usually two auricles, with a pair of branchial hearts. The pericardium is large, the nephridia saccular. The sexes are separate, and the sperm is enveloped in a spermatophore. Chromatophores are remarkably well developed in the integument.*

The fore-foot has grown round the head, and its margins are produced into lobes or arms; of the arms there are eight in *Octopoda*, ten in *Decapoda*, arranged in pairs. The four pairs of arms in *Octopoda* are similar, and are sometimes connected laterally to one another by a thin membrane which may extend almost to their tips. The fourth pair (reckoning the median dorsal pair as the first) is modified in the *Decapoda* into a pair of long extensile arms which can be partially or completely (e.g. *Sepia*) retracted into sacs at their bases. The arms are provided on their adoral aspect, or at their expanded extremities in the case of the long arms of *Decapoda*, with suckers or acetabula arranged in 1-4 rows, or with hooks. The suckers of the *Decapoda* are stalked, and the cup has a marginal horny ring armed in some instances with pointed teeth. They are sessile and devoid of a ring in *Octopoda*. In *Nautilus* (*Tetrabranchiata*), the fore-foot is divisible into an outer and inner portion. The outer portion surrounds the whole head, and is thickened dorsally where it abuts against the coil of the shell and forms the hood<sup>1</sup>. It carries nineteen tentacles on

<sup>1</sup> The fossils known as *Aptychus*, *Anaptychus*, *Synaptychus*, and *Trigonellites*, which are sometimes found within the aperture of the shell in certain *Ammonoidea*, or just outside it, or entirely dissociated from it, have at various times received different explanations. Of these the two which are probable are the following: (1) that they were secreted by the surface of a hood corresponding

each side, of which two are median and dorsal. The inner portion forms three distinct lobes in the female, i. e. a right and left lateral lobe, present also in the male, and an inferior or ventral lobe, represented in the male by three groups of lamellae. The lateral lobes each carry twelve tentacles, and are divided in the male into two portions, a more dorsal with eight tentacles, and a ventral which carries four tentacles on the right side, and is known as anti-spadix, but on the left is represented by the spadix, a conical body terminated by imbricated lamellae, and supposed to have a sexual function like the hectocotyliised arm in *Dibranchiata* (p. 464). The tentacles are long solid cylindrical bodies, retractile into muscular sheaths. The sheath with its tentacle probably corresponds to a single sucker of the *Dibranchiate* arm. The median portion of the foot forms the siphon, the base of which is covered by the mantle fold. It consists in *Nautilus* of a right and left lobe with the free edges simply apposed, but in all *Dibranchiata* grown together so as to form a tube. The hind part of the foot is perhaps represented by the valve of the siphon, absent in *Octopoda*, which projects from the body-wall within the siphon.

The body or visceral dome is elongated in an oblique direction between the dorso-pedal and antero-posterior axis. It is never twisted spirally. Its sides are expanded into a pair of variously shaped fins in *Decapoda* which are only exceptionally present in *Octopoda* (*Pinnoctopus*, *Cirrhoteuthis*). The mantle forms a free fold round the edge of the visceral dome. The dorsal margin of the fold in *Nautilus* is enlarged and reflected over the shell: it is very shallow in *Dibranchiata*. The ventral or posterior part of the fold is of great extent in all *Cephalopoda* and incloses a branchial cavity.

There is no shell in the *Octopoda* except in the female *Argonauta*, but a rudimentary shell-sac appears on the anterior dorsal aspect of the visceral dome and then aborts. The external calcareous shell of *Argonauta* is formed by the expanded ends of the pair of dorsal arms. It lodges the animal which is not fixed to it, is single-chambered and coiled. The shell-sac of *Decapoda* gives origin to a shell which does not lodge the animal; it either remains open as in *Spirula*, or closes so that the shell is internal, in other living forms, as well as in the extinct *Belemnitidae* and perhaps in the extinct *Spirulirostra*. The shell of *Spirula* is coiled, chambered, and the chambers are connected by a siphuncle (*infra*). That of *Spirulirostra* is very similar; of the *Belemnitidae* straight. But in these extinct forms calcareous lamellae are superadded to the chambered shell. The latter is known in *Belemnitidae* as 'phragmacone:' the lamellae as 'guard' or 'rostrum,' and their prolongation forwards, whether

to the hood of *Nautilus*; (2) that they are the homologues of the nuchal cartilages of *Dibranchiata*, a view based on their microscopic structure. See Von Ihering, Neues Jahrbuch f. Mineral. Geol. und Palaeont. 1881, i.

horny or calcified, as 'pro-ostracum.' The chambered shell is not developed in any living *Decapoda* except *Spirula*. The part homologous with the guard is alone present. It constitutes the sepiostaire, or cuttle-bone of *Sepia*, composed of calcareous lamellae inclosing air spaces, and the horny pen, or gladius of *Loligo*, composed of conchiolin.

The shell of *Tetrabranchiata*, the living *Nautilus* and the extinct *Nautiloidea* and *Ammonoidea*, is external and is secreted by the mantle: but nothing is known as to the initial phase of its development. It is either straight, loosely or closely coiled, and then either in a spiral like a snail, or more generally in the same plane as in *Nautilus* and many extinct forms. It is chambered, and the last or largest chamber is the one occupied by the animal which is attached to it by a muscle. Successive chambers are separated from one another by septa, and the unoccupied chambers are filled with air. The external edges of the septa are simple in *Nautiloidea*, but in the older chambers of the *Ammonoidea* are thrown into folds. A forwardly projecting fold is known as a 'saddle:' one that projects backwards as a 'lobe.' The edges of the folds are generally not simple but wavy, sometimes in a highly complex manner. The chambers are traversed by a tube—the siphon or siphuncle, which has membranous walls, prolonged from the integument, protected however by an outer coating of nacre continuous with the substance of the septa. This nacreous coat or 'collar' may form a complete investment or only a partial one to the membranous siphuncle. In the latter case it projects backwards from the septa in nearly all *Nautiloidea*, forwards in *Ammonoidea*, except sometimes in the first chambers. The siphuncle is placed centrally in most *Nautiloidea*, but it may be either near the concave or the convex side of the shell. The latter is its position in *Ammonoidea*, except occasionally in the first chambers. In *Nautilus* the convex side of the shell corresponds to the ventral aspect of the animal, as it appears to do in *Ammonoidea*; but extinct *Nautiloidea* vary in this respect, even within the limits of the same genus.

The first chamber of the shell or protoconch has certain special features. In *Ammonoidea*, as also in the chambered shell of *Dibranchiata*, it is enlarged as compared with the next chamber; its anterior wall is bulged inwards by the siphon which does not extend through it; it is slightly dilated and covered with nacre forming the nucleus; and is often traversed by a 'pro-siphon' not connected with the siphuncle. In the *Nautiloidea* it is small as compared with the next chamber and only slightly curved, not coiled as in the coiled *Ammonoidea*, and the siphuncle traverses it and commences at its apex, which is marked externally by a 'cicatrix.' The presence of this cicatrix has been explained on the supposition that there is a deciduous protoconch (Hyatt). The differences observable have led some authorities to associate the *Ammonoidea* with



the *Dibranchiata*. The shell is often variously ornamented externally with striae, knobs, &c.; it is composed of an outer layer with round or oval calcareous bodies irregularly arranged, and coloured in *Nautilus* and many *Nautiloidea*, and an inner layer of nacre or mother of pearl which is laminated and forms the whole substance of the septa.

The ectoderm consists of a single layer of cells with striated cuticular borders. Cilia are found on the tentacles and eyes of *Nautilus*. The underlying connective tissue contains near its surface a layer of chromatophores, and of cells containing iridescent rods. The former are under the control of the nervous system, the centre appearing to lie in the optic ganglia. The chromatophore consists essentially of a cell charged with pigment granules either scarlet, yellow, blue, or brown, one colour in each cell. By the expansion of the cell the pigment is diffused, by its contraction concentrated. The cell has been described as lying in a space traversed by radial fibres which are attached to the cell-membrane, and supposed by various authorities to be muscular, nervous, or composed of connective tissue. See the original authorities, *infra*. The arms, siphon, and the mantle fold forming the walls of the branchial cavity are muscular. The mantle is contractile, the contractions expelling the water from the branchial cavity for purposes of respiration, and when forcible subserving locomotion as well. Masses of a peculiar cartilage are formed in the body-walls, supporting the nervous system, the siphon in *Nautilus*, the bases of the fins in *Sepia*; and in all *Decapoda* on the dorsal aspect of the neck as nuchal cartilages, and on the opposing points of the mantle surface as dorsal cartilages, the latter present also in *Octopoda*; and as 'siphon-hinge' cartilages or sockets at the sides of the siphon in *Decapoda* which receive fleshy processes developed on the mantle surface. Pores variable in number exist on the back of the head, or at the bases of the arms, leading into sub-integumental sacs of unknown function. A sac exists at the base of each long arm in *Decapoda*; and in *Loligo* the arm may be partially, in *Sepia*, *Sepiola*, and *Rossia* completely, coiled within it.

The nervous system consists of three pairs of ganglia concentrated round the oesophagus—a cerebral, a pedal, and a pleuro-visceral. They have a band-like form in *Nautilus*, and are not well differentiated from the connectives. The cerebral ganglia are connected with buccal ganglia in the *Dibranchiata*, a single pair in *Octopus*, a double in *Decapoda*. The pedal ganglia supply the arms and lobes of the fore-foot, as well as the siphon. The pleuro-visceral give off a large number of nerves in *Nautilus*, to the mantle, branchiae, and genitalia; in *Dibranchiata* right and left pleural and visceral nerves to the mantle, to the branchiae and viscera respectively. Each pleural nerve ends in a ganglion stellatum, from which nerves radiate into the mantle. The *Dibranchiata* also possess a well-developed enteric system of nerves connected with the buccal ganglia and

visceral nerves. *Nautilus* alone has a right and left osphradial papilla, supplied from the visceral ganglia, between the bases of the gills on each side. A ciliated olfactory pit lies behind the eye in *Dibranchiata*, a triangular olfactory (?) papilla below the eye in *Nautilus*. The nerve in both instances originates from the spot where the pedal and optic ganglia unite. The eye is a prominent stalked cone in *Nautilus*, with a flattened end, which is pierced by a small central hole. This hole leads into the cup-shaped interior of the eye, which is lined by the retina. The latter is therefore bathed with sea-water. The eye in *Dibranchiata* is sunk in the head, except in *Procalistes*, where it is stalked. The retinal chamber is closed; its anterior surface is occupied by a biconvex lens divisible into a smaller outer and a larger semi-globular internal part, the two separated by a membrane. The two parts are secreted by the outer and inner layers respectively of an epithelial body (= ciliary body), which surrounds their margins. In front of the closed retinal chamber is an iris, supported by a cartilage, and containing a sphincter muscle; in front of the iris a transparent cornea, which is perforated in the centre by an aperture in certain *Decapoda*, the *Oegopsidae*, e.g. *Ommastrephes*. The *Octopoda* have a sphincter-like eye-lid; *Sepia* and some other *Decapoda* a horizontal ventral eye-lid. The retina of *Nautilus* consists of a single layer of cells, each ending in a visual rod, and pigmented round the base of the rod, and an underlying layer of ganglion cells (?). It is regarded in *Dibranchiata* as composed either of a single layer of cells, each furnished with a visual rod, and an underlying layer of ganglion cells, a delicate limiting membrane separating the two (Carrière); or as composed of a single layer of retinal cells, forming an inner layer of rods with swollen bases, and an outer layer of nucleated cell-bodies, the two divided by a limiting membrane, which is derived from a layer of small cells, 'Limitans-zellen,' which form a prominent zone at the outer edge of the retina. The visual rods in this case consist of two rhabdomeres, and two to four rhabdomeres fuse into a rhabdome (Grenacher)<sup>1</sup>. The eye of the *Dibranchiata* is inclosed in cartilage, which is pierced by the nerves. These come from a large optic ganglion connected by a short nerve to the cerebral ganglion. A cellular 'white' body lies at the margin of the optic ganglion anteriorly. The otocysts are a pair of vesicles imbedded in *Dibranchiata* in a cavity of the cephalic cartilage, and attached to the pedal ganglion by a nerve, which is

<sup>1</sup> Patten regards the 'retinal cells' as retinophorae, as they possess double rods and an axial nerve-fibre. The 'Limitans-zellen' are ganglionic cells, and are modified retinulae homologous with the retinulae of Gastropod ommatidia, and with the inner layer especially of ganglionic cells in the eye of *Pecten*. The closer juxtaposition of the broad ends of four retinophoral rods, has misled Grenacher into supposing that these are rhabdomes. A unique feature in the Cephalopod eye is the presence of pigment in the retinophorae round the axial nerve-fibre. See Patten, Mitth. Zool. Stat. Naples, vi. pp. 623-25, and for explanation of terms, the note, p. 452 of this book.

derived, however, from the corresponding cerebral ganglion. There are a number of otoliths in *Nautilus*, a single otolith in *Dibranchiata*.

The mouth is provided with two jaws like a parrot's beak, calcified in *Nautilus*, chitinous in *Dibranchiata*, the larger ventral in position<sup>1</sup>. They are borne upon the extremity of a prominent buccal cone or mass, which is surrounded externally by an integumentary fold or buccal membrane<sup>2</sup>. The cone contains a radula. The oesophagus is wide and dilated near the apex of the visceral dome in *Nautilus*, narrow in *Dibranchiata*, and provided in *Octopoda* with a crop-like dilatation. The stomach is large, and its walls are muscular and like the gizzard of a bird in *Nautilus* and *Octopus*. The pyloric is near the cardiac aperture, and leads into an intestine, slightly coiled in *Nautilus* and *Octopoda*, which terminates in an anus situated in the branchial cavity, between the bases of the gills in *Nautilus*, more anteriorly on the posterior wall of the body in *Dibranchiata*. A caecum is appended to the intestine near the anus in *Nautilus*, close to the pylorus in *Dibranchiata*. In the latter it may be short and round, or longer and spirally coiled. Its internal surface is generally produced into folds or processes. A pair of glandular (? salivary) masses lie in the buccal cavity in *Nautilus*. A pair of glands with a single duct lies externally to the buccal mass behind the nervous centres in all *Dibranchiata*, and a second pair in front of them in some *Octopoda*. The duct opens in front of the radula. There is a liver surrounded by a firm membrane, composed of four lobes in *Nautilus*, two lobes in *Dibranchiata*. There are two bile ducts, which unite, and open into the intestine in *Nautilus*, into the intestinal end of the caecum in *Dibranchiata*. The so-called pancreas exists in three forms: as a yellowish coloured part of the liver opening into a dilatation of the bile duct in *Octopoda*; as glandular masses impacted in the thickened walls of the bile duct in *Loligo*; or as glandular caeca appended to the bile duct in other *Decapoda*. A gland known as the ink-bag opens in all *Dibranchiata*, either near (*Sepia*) or into the rectum, of which it is a diverticulum. It has been found in specimens of extinct *Belemnitidae*. Its inky secretion—a pigment known as Sepia—serves to hide the animal when attacked or alarmed.

The heart is placed posteriorly near the summit of the visceral dome. It is square in *Nautilus*, and receives four branchial veins, one at each corner. It is more or less pyriform in *Decapoda*, and transversely oval in *Octopoda*, and in both it receives two branchial veins, which at their cardiac ends are dilated, muscular, and contractile, thus forming two auricles. The ventricle gives off a cephalic and abdominal aorta, at its opposite extremities

<sup>1</sup> The fossil beaks of *Tetrabranchiata* are known as *Rhyncholites*.

<sup>2</sup> This buccal membrane is lobed; it sometimes bears suckers, and is supplied by nerves derived from the brachial nerves, and therefore from the pedal ganglia. Viauillon regards it as representing a series of arms nearly aborted with well-developed interbrachial membranes. See C. R. 100, 1885.

in *Nautilus* and *Decapoda*, close together in *Octopoda*. The arterial system is very complete and much branched in *Dibranchiata*. It is said to lead into true capillaries in some cases, or into coelomic sinuses in others. The venous blood is collected into a large median postero-ventral vein, the vena cava, which branches into four branchial arteries in *Nautilus*, into two in *Dibranchiata*. These traverse the walls of the nephridial and visceropericardial sacs on their way to the ctenidia, up which they run on their ad-pallial, i.e. in *Dibranchiata*, fixed aspect. Each vessel is dilated in the order just named, at the base of the ctenidium, into a muscular branchial heart; and before it enters the ctenidial axis, it receives veins from other parts of the body. Attached to the base of each branchial heart, and depending into the visceropericardial sac, is an appendage, the pericardial gland of Grobben, or so-called fleshy appendage. It corresponds in *Nautilus* to vascular appendages of the branchial arteries, which project into the visceropericardial sac, and resemble the vascular tufts which project from the same vessels into the nephridial sacs both of *Nautilus* and *Dibranchiata*. The blood contains amoeboid corpuscles and haemocyanin.

The visceropericardial sac (pericardium, secondary coelome) is of very large size in *Nautilus* and *Decapoda*. It includes the heart, the roots of the branchial <sup>veins</sup> arteries, the branchial hearts of *Decapoda*, stomach, and, except in the male *Sepia*, the genital organs as well. The testis in *Sepia* is contained in an almost closed diverticulum of it. It communicates in *Nautilus* with the branchial cavity by a right and left aperture close to the openings of the posterior pair of nephridial sacs; in *Decapoda* with the nephridial sacs themselves, by a wide slit-like opening in *Oegopsidae*, e.g. *Ommastrephes*, by a small pore in *Myopsidae*, e.g. *Sepia*. The corresponding sac is reduced in *Octopoda* to a small space which incloses the pericardial gland, and opens into the nephridial sac of its side by a pore; to a narrow canal connecting each space to the genital sac; and to the genital sac itself. This series of spaces is sometimes spoken of as the water-canal system. It is absent in *Argonauta Argo* and *Ocythoë tuberculata* (= *Tremoctopus Carenae*).

The respiratory organs consist in *Tetrabranchiata*, i.e. in *Nautilus*, of two, in *Dibranchiata* of a single pair, of ctenidia, free in the former, attached by one aspect in the latter. The branchial artery runs up the attached or in *Nautilus* the homologous side, the vein on the free surface. A mass of cells, with intervening blood-lacunae, is situated in the line of attachment in *Dibranchiata*. It is possibly a blood-making gland. The surfaces of the ctenidia are disposed in a series of respiratory folds transverse to the ctenidial axis. The folds differ in shape in *Octopoda* and *Decapoda*.

There are four nephridial sacs in *Nautilus*, two in *Dibranchiata*, each opening by its own aperture, which in *Dibranchiata* is often produced into a papilla. The four sacs of *Nautilus* and the two of *Octopoda* are independent. In *Decapoda* they are either connected to a median sac lying

between them (*Sepia*), or fused into one as in the majority, e. g. *Loligo*. The walls of these sacs are covered by a more or less flattened epithelium, except at the spot where they are in contact with the branchial arteries. The latter here give off a number of caecal and branched venous appendages. The nephridial epithelium coating these vascular tufts is columnar and longitudinally striated, its surface covered with a slimy secretion, in which reddish-coloured crystals, also occurring loose in the sac, are commonly found, as well as greenish-coloured spheres. Crystals and spheres alike appear to be excretory products<sup>1</sup>. Vascular tufts of a similar character are given off by the branchial arteries of *Nautilus* into the visceropericardial sac. The pericardial gland appended to the branchial hearts (*supra*) in *Dibranchiata* appears to be a structure of excretory character. It is a somewhat conical body, which contains a number of caeca communicating by one (*Sepia*) or several (*Eledone*) slits with the visceropericardial sac, and lined by an epithelium continuous with that of the sac. At the bases of the caeca the epithelium becomes glandular.

The sexes are separate. The single testis and ovary are formed from the walls of that part of the visceropericardial sac or secondary coelome in which they lie, and from which the ciliated ducts are prolonged to the exterior. The left duct is rudimentary in both sexes in *Nautilus*; there are two ducts in the male *Eledone moschata* (*Octopoda*), and the female of *Ommastrephes* (*Decapoda*), and of *Octopoda*, except *Cirrhoteuthis*, whereas in other instances there is but one duct, that of the left side. The vas deferens has a widened glandular section, and bears an accessory gland, and near its termination a large sac, Needham's sac, in which the spermatophores are contained. It ends in a papilla, which may be of great extent, in *Octopoda*. The spermatophores are cylindrical bodies of some length and complicated structure, containing not only sperm but an exploding substance as well. The oviduct in *Octopoda* has as a rule a dilated portion (present but unilateral in *Nautilus*) with walls produced into glandular leaflets, forming an albumen gland. In *Decapoda* a similar gland opens into the end of the oviduct. The oviduct, like the vas deferens, opens between the anus and nephridial aperture. *Nautilus* possesses a nidamental gland, situated on the mantle, the *Decapoda* a pair of such glands, in both cases composed of lamellae. A third gland, composed of coiled tubes, is present in most female *Decapoda*.

With the exception of a few *Dibranchiata* (e. g. *Ommastrephes*), a remarkable change affects one of the arms in the male. It is enlarged either at its apex or base, and the suckers of the enlarged portion obliterated.

<sup>1</sup> Solger found that sulph-indigotate of soda (= indigo carmine) when injected under the skin of an *Eledone moschata* made its appearance in this excretory epithelium as well as in solution in the cavities of the nephridia. Cf. Z. A. iv. 1881. Injection of the same substance into the blood of *Mammalia* is followed by its excretion in the kidney and the liver.

It is then said to be hectocotylised. In *Argonauta Argo*, *Ocythoë tuberculata* (= *Parasira catenulata*), *Tremoctopus violaceus*, and *T. quoyanus*, this arm or *Hectocotylus* is set free, and reproduced after each act of sexual congress. It develops within a sac, which then bursts, disclosing a large arm with peculiar suckers, and a terminal saccule. The latter bursts in its turn, setting free a 'Needham's' filament. The modified arm is in all cases charged with spermatophores, which appear to gain access to it by an aperture on its aboral surface. When it is detached it is carried away by the female in the branchial cavity<sup>1</sup>. The ova are either inclosed, each in a special capsule, which is attached to some foreign object; or carried in the shell (*Argonauta*); or a number are imbedded in a mass of gelatinous material, fixed (*Loligo*) or floating. Segmentation is partial, the protoplasm collecting in a terminal disc. The yolk is not inclosed in the alimentary canal, but is lodged in what appears to be a median part of the foot, in the head, neck, and mantle. Cilia have been observed on the blastoderm.

The *Cephalopoda* are marine, some littoral like *Octopus*, others pelagic like *Spirula*, *Sepia*, &c. All are carnivorous, and some, e.g. *Architeuthis*, attain a gigantic size. The oldest *Cephalopoda* belong to the *Nautiloidea*, and appear in Cambrian strata. Of existing genera, *Loligo* is found in the Lias, *Ommastrephes* and *Sepia* in the Oxford Clay.

The class *Cephalopoda* is divisible into two orders.

I. *Tetrabranchiata*. Shell external; straight or coiled; chambered; the last chamber inhabited by the animal, the remainder filled with gas. A membranous tube or siphuncle traverses the chambers. Mostly extinct: one genus only, *Nautilus*, living, with the following characters. The part of the foot surrounding the mouth forms lobes which bear sheathed tentacles; the siphon is formed by two free folds. The eyes are simple open sacs; there is a pair of osphradial papillae. The visceropericardial sac opens externally by two apertures. There are two pairs of gills and nephridial sacs; two genital ducts, the left rudimentary in both sexes. No auricles, no branchial hearts nor ink-bag.

(1) *Nautiloidea*. Shell straight or bent; coiled, and then snail-like, or disc-like; aperture simple, sometimes much contracted; ventral side indicated by a notch. Sutures mostly simple, or waved; rarely denticulated. Septa concave forwards. Siphon often contracted by internal deposits; siphuncular collars generally directed backwards. Protoconch conical, with a cicatrix.

(2) *Ammonoidea*. Shell usually coiled and disc-like; rarely snail-like or straight; aperture simple, or with lateral and ventral processes. Sutures waved, and often denticulated. Siphon always marginal; never contracted by internal deposits. Protoconch globular or ovate. *Aptychus* or *Anaptychus* generally present (p. 456, note).

*The form of the protoconch, mode of commencement of the siphon, absence of*

<sup>1</sup> The ventral lobe of the buccal membrane in the female *Sepia* contains two pouches; in *Loligo* one. After congress spermatophores are found on the buccal membrane, and after a time spermatozoa in the pouches in question, which they reach by their own movements. The female *Loligo* has been observed holding the newly laid ova in front of the mouth. Vialetteon, C. R. 101. 1885. See ante, note, p. 461.

*cicatrix, presence of a pro-siphon, and character of the Aptychus, make it possible that the Ammonoidea belong to the Dibranchiata.*

II. *Dibranchiata*. Shell chambered and partially external (*Spirula*); or chambered with a guard, and internal (*Belemnitidae*); plate-like and internal (*Decapoda*); or absent (*Octopoda*). An external calcareous but not chambered shell in the female *Argonauta Argo* (*Octopoda*) formed by a pair of arms. Foot surrounding mouth produced into sucker-bearing arms. Lobes of siphon fused. Eyes large; retinal chamber closed by a lens; no osphradia. A single pair of ctenidia; a pair of auricles and branchial hearts; and of nephridia into which the visceropericardial sac opens. Two vasa deferentia in *Eledone moschata*; two oviducts in *Ommastrephes*, and in *Octopoda*; otherwise genital duct unpaired. An ink-bag.

(1) *Decapoda*. Ten arms; one pair much elongated; suckers pedunculate, and strengthened by a horny ring; lateral body fins. Nidamental glands usually present. *Belemnitidae* extinct; Mesozoic (Trias to Chalk); ? Tertiary. *Oegopsidae*, cornea perforate, e. g. *Ommastrephes*; *Myopsidae*, cornea closed, e. g. *Sepia*, *Loligo*. *Spirulidae*, a chambered skull; *Spirula Peronii*, warmer seas.

(2) *Octopoda*. Eight arms, with a more or less developed inter-brachial membrane. Eyes with a sphincter-like lid. *Cirrhoteuthidae*. *Philonexidae*, e. g. *Ocythoë*, *Argonauta*; *Octopidae*, e. g. *Octopus*, *Eledone*.

*Cephalopoda*, Keferstein, Bronn's, Klass. und Ordn. des Thierreichs, iii. 2, 1862-66; Hoyle (*Systematic and distribution*), Challenger Reports, xvi. 1886.

*General account of Nautilus*, Ray Lankester, Encyclopaedia Brit. (ed. ix.), xvi. p. 670 et seqq. *Osphradium and genital ducts*, Id. and Bourne, Q. J. M. xxiii. 1883. *Male and female; differences*, Bourne, Nature, xxviii. 1883.

*Dibranchiata. Skin; chromatophores; suckers*, Girod, A. Z. Expt. (2), i. 1883; ii. 1884. *Chromatophores*, Blanchard, C. R. xcvi. 1883 (A. N. H. (5) xi.); *Physiology*, Krukenberg, Vergleich. Physiol. Studien, i. 1. 1880. *Suckers*, Niemiec, 'Les ventouses,' &c., Recueil Zool. Suisse, ii. 1885. *Ctenidia, development and structure*, Joubin, A. Z. Expt. (2), iii. 1885. *Nervous system of Ommastrephes*, Hancock, A. N. H. (2), x. 1852. *Eye*, Carrière, 'Seh-Organ der Thiere,' Leipzig, 1885; Grenacher, Abhandl. Nat. Gesellsch. Halle, xvi. 1884; cf. note, p. 452, ante; *of Procalistes*, Ray Lankester, Q. J. M. xxiv. 1884. *Digestive organs (histology)*, Livon, Journal de l'Anat. et Physiol. xvii. 1881. *Pancreas*, Vigelius, Z. A. iv. 1884; Biol. Centralbl. ii. 1882-83; *Physiology*, Bourquelot, A. Z. Expt. (2), iii. 1885. *Ink-bag*, Girod, A. Z. Expt. x. 1882. *Excretory organs and pericardial glands*, Grobben, Arb. Zool. Inst. Wien, v. 1884; Vigelius, Archiv. Nederl. f. Zoologie, v. 1879-82; Solger, Z. A. iv. 1881. *Sex organs*, Brock, Z. W. Z. xxxii. 1879; Id. *Males of Sepioloidea*, Z. W. Z. xl. 1884.

*Various points relating to anatomy, &c.*, Brock, 'Phylogeny,' &c., M. J. vi. 1880; Id. Z. W. Z. xxxvi. 1882. *Thysanoteuthis*, Vigelius, Mitth. Zool. Stat. Naples, ii. 1881.

*Cartilage of Cephalopoda*, Fürbringer, M. J. iii. 1877.

*Homology of siphon and arms*, Brooks, American Journal of Science and Art, xx. 1880.

*Spirula*, Owen, A. N. H. (5), iii. 1879; P. Z. S. 1880.

*Gigantic Cuttle-fish, &c.*, Verrill, U. S. Commission of Fish and Fisheries, Report for 1879, Part vii. Washington, 1882.

*Fossil Cephalopoda*, Zittel, Handbuch der Palaeontologie, Abth. I. ii. Th. 3. 1884; *Genera of Fossil Cephalopoda*, Hyatt, Proc. Boston Soc. Nat. Hist. xxii. 1882-83. *Development of shell in do.*, Branco, Palaeontographica (N.S.), 26 and 27, 1879-81. *Relation of Ammonites*, Munier-Chalmas, &c. C. R. 77, 1873. *Ammonites, composition of shell*, Suess, SB. Akad. Wien, lxi. Abth. i. 1870.

## CLASS SCAPHOPODA.

(*Soleniconcha*; *Prosopocephala*).

Glossophorous Mollusca, with a shell shaped like an Elephant's tusk, and open at both ends, the small as well as the large. Its concave side is dorsal, the convex ventral. The mantle, which lines the shell, arises in the larva as a right and left dorsal fold, which grow towards the ventral aspect, and fuse one with the other, except for a short distance, in front and behind. The tube thus formed extends both backwards and forwards over the animal. The shell develops in a corresponding manner, and is at first incomplete ventrally. The head is cylindrical, and bears the mouth at its extremity, surrounded by a circle of tentacles. Two pads, one right, the other left, at the base of the head and above the foot, give origin to a number of ciliated contractile processes, terminated by flat expansions. It is possible that they represent the ctenidia. The foot is long, and trifold at its extremity.

The nervous system consists of a pair of cerebral ganglia, united by long connectives to a pair of pedal ganglia, to which the pleural ganglia are closely apposed. The visceral loop is long, and placed below, i.e. in front of the anus. There are no eyes, but a pair of otocysts is attached to the pedal ganglia. The digestive tract possesses a buccal mass, inclosing a radula armed with five longitudinal rows of simple teeth. The alimentary canal consists of an oesophagus, a short stomach, into which open two large symmetrically placed liver lobes, an intestine, which forms several coils and finally opens on the ventral surface in the middle line. There is no heart. The coelome consists of a series of channels and sinuses, and is filled by a colourless blood. There are two nephridial openings, one on each side the anus. The nephridial chamber is perforated by the intestine, and is beset with a number of small caeca. The genital gland lies dorsally. It is alike in both sexes, and consists of a median tube bearing three rows of caeca—one dorsal, two lateral. The duct opens into the nephridial sac on the right side.

Segmentation is unequal, the gastrula invaginate. There are three ciliated rings surrounding the body in front of the mouth, and representing the velum. The body lengthens behind the ciliated rings. There is a



rudimentary shell-gland, and perhaps a foot-gland. The anus is formed as a proctodaeum.

There are three genera, *Dentalium*, *Siphonodentalium*, and *Entalium*. The animal lives with the anterior extremity plunged into the sand on the sea coast, at depths of ten to a hundred fathoms. *Dentalium* occurs fossil in Carboniferous strata.

*Dentalium*, de Lacaze Duthiers, A. Sc. N. (4), vi. 1856; vii. and viii. 1857. *Development*, Kowalewsky, Annales Mus. Nat. Hist. Marseilles, i. 1883. *Comparison with Cephalopoda*, Grobben, Arb. Zool. Inst. Wien, v. 1884 (p. 44 of his paper).

### CLASS PTEROPODA.

*Pelagic Glossophora with the median foot much reduced, but with two large lateral pedal lobes (epipodia?) developed into swimming organs. Visceral dome elongated and secondarily symmetrical, rarely coiled spirally; either naked or covered with a shell. No ctenidia; anus, generative and nephridial apertures placed anteriorly, and usually on the right side of the body. Hermaphrodite.*

The bilateral symmetry of the *Pteropoda* is without doubt a symmetry secondarily acquired (p. 455), and in many points, both of development and anatomy, they closely resemble the *Gastropoda*. The foot is very small in size. In *Clio* it consists of two pro-meso-podial lobes, and a small metapodium. The latter bears an operculum in *Spiralis* and *Heterofusus* (*Limacinidae*), and the Veliger of *Cymbulia* and *Tiedemannia*. The two swimming lobes are probably homologous with epipodia, and generally appear later than the other parts of the foot. In the *Pteropoda* with shells, or *Thecosomata*, they grow round the head, which is consequently not distinct in this order. In the *Gymnosomata*, where the adult has no shell, the head is furnished with two pairs of cephalic tentacles—an anterior pair, which is not represented in *Thecosomata*, and a posterior nuchal pair. The latter are eye-bearing in *Gymnosomata*, in the adult *Creseis*, and the young *Tiedemannia* and *Spiralis* among *Thecosomata*. The mantle aborts in *Gymnosomata*; it forms a deep fold on the ventral aspect in *Thecosomata*; but in the *Limacinidae*, with a spirally twisted visceral dome, the fold is dorsal in position. All *Pteropoda* are furnished with a larval shell, formed by the everted shell-gland. A secondary shell is added subsequently. Both are thrown off in *Gymnosomata* and the *Cymbulidae*; the larval shell only in *Hyaleidae*; while both persist in *Creseis* (= *Styliola*). The *Cymbulidae* form a third persistent hyaline shell of cartilaginous consistency. In other *Thecosomata* the shell is also hyaline, and apparently highly calcified,

It is spirally coiled in *Limacinidae*, in other *Thecosomata* symmetrical. The larval shell of *Cymbulidae*, however, is spiral.

The epidermis is ciliated in *Clio*. There are cutaneous glands, pigment cells, and calcareous concretions in the integument. *Tiedemannia* has a rich development of chromatophores.

The nervous system consists of the cerebral, pedal, pleural, and visceral ganglia. They are concentrated round the oesophagus, especially in *Thecosomata*. The otocysts are closely attached to the pedal ganglia. The structure of the eyes on the nuchal tentacles is unknown. A right osphradium appears to be present in *Thecosomata*, and in *Pneumodermon* among *Gymnosomata* is innervated in the typical way.

The oral aperture is armed with various tentacle-like processes, which are inserted in *Gymnosomata* within its margin. *Clio* has three pairs, the surface of which is covered with epithelial papillae, each furnished with a sense-cell, and giving exit to the ducts of unicellular glands, which nearly fill the central cavity of each process or 'cephaloconus.' They act as organs of adhesion in securing the prey. *Pneumodermon* has a pair of arms, which bear pedunculate muscular suckers on their oral faces. Tentacle-like processes are found near the mouth in some *Thecosomata*, but their structure does not appear to have been investigated. The oral cavity of *Clio* and *Pneumodermon* contains a pair of eversible sacs armed with chitinoid hooks. A pair of chitinoid jaws is generally present, in addition to the radula. Salivary glands are absent or rudimentary in *Thecosomata*. There is a long oesophagus, a stomach, and intestine. The anus is on the left (?) side in *Hyaleidae*, *Cymbulia*, and *Tiedemannia*, on the right in all other *Pteropoda*. A liver is well developed in *Thecosomata*, but in the *Gymnosomata* is represented only by caecal processes of the stomach walls. The auricle is not sharply marked off from the blood sinuses. Its aperture into the ventricle is guarded by valves. The ventricle is well-developed, and gives off an aorta, which divides into an intestinal and cephalic branch. Its ultimate ramifications open into a system of irregular coelomic sinuses. The general surface of the body is respiratory in *Gymnosomata*. *Pneumodermon*, however, possesses three contractile and richly ciliated processes at the apex of the visceral dome, in and out of which the blood passes. A semilunar series of folds within the branchial cavity on the body wall of *Hyalea*, and a transverse shield-shaped ciliated area on the wall of the mantle fold in the same *Pteropod* and some other *Thecosomata*, have had a respiratory function assigned to them. The nephridium opens near the anus. It is saccular, and in some, probably in all instances, opens into the pericardium. Unicellular glands open into it in *Clio*, and in the *Hyaleidae* its walls are said to be spongy and opaque. There is an hermaphrodite gland, an hermaphrodite duct, which may be dilated near its termination, a receptaculum seminis, and albuminiparous gland. The hermaphrodite

duct opens near to but in front of the anus. In *Pneumodermon* a copulatory organ lies within the aperture of the duct, but in other *Pteropoda* it lies at some distance in front of the aperture. It is always in- and e-vaginable<sup>1</sup>.

The ova are laid in a mass of albumen, and are usually found floating on the surface of the sea. *Clio* attaches the mass to sea-weeds when confined in aquaria. Segmentation is unequal. The velum is bilobed and large, except in *Hyaleidae*. The larva of *Gymnosomata* (*Clio*, *Pneumodermon*) loses the velum and shell, and then passes into a second larval form provided with three zones of cilia girding the body—one anteriorly, in front of the foot; the other near the middle; the third posteriorly. The first atrophies early; the middle one has been observed in a nearly adult *Clio*, and the hindmost in a *Pneumodermon*.

The *Pteropoda* are exclusively pelagic and carnivorous. They are found in all seas, sometimes, e.g. *Clio*, in immense numbers. Fossil forms, all extinct, appear in Cambrian strata.

There are two orders :—

(1) *Thecosomata*, with mantle fold and shell; with three living families, *Hyaleidae*, *Cymbuliidae*, and *Limacinidae* (*Spirialis*), and the fossil families *Conulariidae*, *Tentaculitidae*, and *Thecidae*.

(2) *Gymnosomata*. Mantle fold and shell absent in adult; a second larval form with three ciliated bands; with the living families *Clionidae*, e.g. *Clio* (or *Clione borealis*, *Pneumodermonidae*, and *Pterocymodoceidae*.

Keferstein, Bronn's Klass. und Ordn. des Thierreichs, iii. 2. *Clio borealis*. Wagner, 'Die Wirbellosen des Weissen Meeres,' Leipzig, 1885. *Cymbulia*, external shape and position in shell, Macdonald, P. R. S. xxxviii. 1884-5. On certain *Gymnosomata*, Boas, Z. A. viii. 1885.

Cephalic appendages of *Gymnosomata*, especially of *Clio*, Pelseneer, Q. J. M. xxv. 1885. Structure of suckers, Niemic, Recueil Zool. Suisse, ii. 1885.

Histology of *Pteropoda*, &c., Paneth, A. M. A. xxiv. 1885.

## CLASS GASTROPODA.

*Glossophora*, with a foot, which, except in certain swimming forms, is simple, median, and flattened into a broad, sole-like surface by the contractions of which the animal crawls. It is often divided into three successive regions, pro-, meso-, and meta-podium, by lateral constrictions.

<sup>1</sup> Wagner (op. cit.) states that *Clio* possesses, (1) a short copulatory organ containing a male receptaculum seminis; (2) a long excitatory organ; both of them in- and e-vaginable. When two individuals meet, they perforate reciprocally each other's body, with the excitatory organ, from which masses of granules are discharged into the coelome. They separate, after having mutually filled the male receptacula. Congress of each of these two individuals with an ovigerous individual is necessary for the fertilisation of the ova, the sperm received on the first occasion being now transferred.

SUB-CLASS I. GASTROPODA ISOPLEURA (= *Amphineura*).

Gastropoda, in which the primitive bilateral symmetry is retained not only in the head and foot, but also in the mantle and visceral dome. The anus is posterior. The antero-posterior axis, joining mouth and anus, is long: the dorso-ventral (dorso-pedal) axis short. The pedal and visceral nerve-cords are straight, parallel with one another, and extend the length of the body: ganglionic enlargements are developed feebly or not at all. The circulatory organs, ctenidia, nephridia, and genital ducts are paired and bi-laterally symmetrical.

The epidermis consists of a single layer of cells, with a cuticula in which microscopic calcareous spines (*Chaetoderma*), spicules, or plates (*Neomeniae*) are imbedded in connection apparently with the cells of the epidermis. In *Polyplacophora* (*Chiton*, &c.) similar calcareous spines and plates, and in some instances chitinous spines, occur on the margins of the mantle, whilst a series of eight calcareous shell-plates covers the median dorsal region. These plates articulate one with the other, and their outer margins are overlapped by a fold of the integument. The foot is narrow and long in *Polyplacophora*, very narrow and inclosed in a groove in *Neomeniae*, and only indicated in the posterior part of the body in *Chaetoderma*. It is ciliated in the two last-named groups, and it has a foot-gland opening below the mouth in *Neomeniae*. The mantle fold is well developed in *Polyplacophora*, and surrounds both head and foot. In the *Neomeniae* and *Chaetoderma* it is reduced to a collar surrounding the anus, unless the edges of the groove inclosing the foot may be regarded as its homologue as well. The head is not prominent: it is partially surrounded by a projecting fold in *Polyplacophora*, the homologue of the tentacles and cephalic lobes or lips of *Anisopleura*. The central nervous system consists in the *Polyplacophora* of a nervous ring situated at the base of the cephalic fold, and connected to two pairs of lateral cords, one pair, the visceral cords, extending down the sides of the body and united posteriorly above the anus; the other pair, the pedal cords, extending down the median line in the foot. The whole of this system is orange in colour, and consists of both nerve-fibres and ganglion-cells. There is a pair of buccal ganglia and a pair of sub-radular ganglia connected with the cephalic ring. The pedal cords are connected across the median line by numerous and irregular transverse fibrous commissures. The *Neomeniae* have distinct cerebral enlargements, and in *Proneomenia* the pedal as well as the visceral cords are connected posteriorly. Transverse pedal commissures are present; and in *Proneomenia* transverse commissures between the pedal and visceral cords<sup>1</sup> *Chaetoderma* has a bi-lobed cerebral enlargement, from which the pedal and visceral cords take origin. These cords unite together posteriorly;

<sup>1</sup> One or two similar connections have been found in *Chiton*.

and the common cord thus formed on each side unites with its fellow above the anus. There are no pedal commissures, and the single ring surrounding the oesophagus appears to correspond with the buccal ring. The nerve-cords contain ganglion-cells, as in *Polyplacophora*. Sensory organs lodged in cavities of the shell-plates have been described in the last-named order, and in some genera eyes as well. The latter may be exceedingly numerous, and are furnished with a transparent cornea, pigmented envelope, lens and retina.

The mouth is more or less ventral in position. There is a muscular pharynx. A radula is absent in *Neomenia*, present and furnished with very complex transverse rows of teeth in *Polyplacophora*, with many teeth in *Proneomenia*, and a single tooth in *Chaetoderma*. A remarkable sensory sub-radular organ is found in *Chiton*. Small lobed buccal (salivary?) glands are present in *Chiton*, and a pair of long salivary tubes in *Proneomenia*. Two saccular glands open into the oesophagus in *Chiton* (? all species). Their epithelium undergoes remarkable colour changes during secretion, and they are amylolytic, or salivary, in function. The intestine is straight in *Neomeniae* and *Chaetoderma*; ciliated in the former, and provided with lateral liver caeca, with a single liver caecum in *Chaetoderma*. It is convoluted and ciliated in *Polyplacophora*, and there is a right and left liver caecum, both lobulated and furnished with acini. The rectum opens on a papilla in *Polyplacophora*, between the two branchial plumes in *Chaetoderma*, and in union with the nephridial opening in *Neomeniae*. The heart is situated posteriorly in a pericardial cavity. It consists of a ventricle and right and left auricle in *Polyplacophora*: and, so far as is known, only of a simple ventricle in other *Isopleura*. There is a dorsal aortic trunk running forward. There are apparently no specialised branchiae in *Proneomenia*. They lie near the anus in the mantle cavity, and are tufted in *Neomenia*, paired in *Chaetoderma*. In the *Polyplacophora* they have the form of small ctenidia, arranged in the mantle furrow at the side of the foot, and numbering sixteen or more on each side. The nephridia open into the pericardial cavity. They have the form of short wide sacs with a common external aperture in *Neomeniae* into the anus, or separate openings, one on each side the anus, in *Chaetoderma*, and in these two orders they serve as genital ducts. They are long, extend forwards, and are folded upon themselves in *Chiton*, the folded portion bearing numerous secretory acini; and they open externally on each side in front of the genital apertures and in the mantle furrow. The sexes are separate in *Polyplacophora* and *Chaetoderma*, whereas the *Neomeniae* appear to be hermaphrodite. The single ovary and testis are alike in *Polyplacophora*, and are simple glands with a right and left duct opening posteriorly into the mantle furrow. The hermaphrodite gland of *Proneomenia* appears to be double. In it, in *Neomenia* and *Chaetoderma*, the genital duct or ducts open

into the pericardial cavity, and through it communicate with the nephridia. *Neomenia carinata* has been said to possess lateral male ducts with calcareous penes.

In *Chiton* the ova are impregnated in the pallial groove. Segmentation is total, and at first equal. There is a Veliger with a flagellum in the centre of the velar area, a pair of lateral eyes in the mantle furrow, and a foot-gland which aborts. The nerve-cords are formed from the ectoderm. Transverse dorsal furrows make their appearance, in which the cuticula thickens, and the thickenings are the rudiments of the shell-plates. There does not appear to be a shell-gland.

The sub-class *Isopleura* is divisible into three orders:—(1) *Polyplacophora* (*Chiton* and its allies); (2) *Neomeniae*, including the genera *Neomenia* and *Proneomenia*; and (3) *Chaetoderma*, with a single genus of the same name.

*Polyplacophora*. *Chitons of Adriatic*, Haller, Arb. Zool. Inst. Wien, iv. 1883; v. 1884. Haddon, Challenger Reports, xv. 1886. *Eyes and sensory organs*, Moseley, Q. J. M. xxv. 1885. *Nephridium, &c.*, Sedgwick, P. R. S. xxxiii. 1883; Van Bemmelen, Z. A. vi. 1883; cf. Haller, M. J. xi. p. 41. *Eggs and envelopes*, Sabatier, Revue Sc. Nat. Paris and Montpellier (3), iv. *Development*, Kowalesky, Annales Mus. Nat. Hist. Marseilles, i. 1883.

For other literature and that relative to *Neomeniae* and *Chaetoderma*, see Hubrecht on *Amphineura*, Q. J. M. xxii. 1882. This author is stated to be preparing a monograph of the group in the 'Fauna and Flora of the Gulf of Naples.'

## SUB-CLASS 2. GASTROPODA ANISOPLEURA.

Gastropoda, in which the primitive bilateral symmetry is retained in the head and foot, whilst the visceral dome with the mantle fold is twisted from behind round the right side more or less to the front, so that the ctenidia, anus, nephridial and generative pores are placed either on the right side of the body or more or less anteriorly, the primitive right ctenidium thus appearing on the left side of the anus or body. The visceral dome frequently continues to grow with a similar but spiral twist, and its surface, with the mantle, is generally protected by a more or less spiral shell. The primitive left ctenidium and left (? right) nephridium<sup>1</sup> usually atrophy. The genital gland and duct are single. A superficial secondary bilateral symmetry is sometimes acquired (*Natantia*, *Opisthobranchia*). The foot has commonly a pedal gland.

The foot is generally broad and flat, and sometimes much expanded. It is divided into a distinct pro- and meso-podium, and a metapodium in many Reptant *Azygobranchia* and all *Natantia*. The pro- and meso-

<sup>1</sup> So says Professor Lankester; but recent researches make it probable that the primitive right and not the left, nephridium atrophies. See p. 479 and note. The word 'primitive' implies the organs of the right and left sides before the occurrence of any spiral twist.

podium of the latter group are flattened laterally, and the mesopodium frequently carries a sucker, whilst the metapodium forms, as a rule, a large swimming tail. The metapodium often bears upon its dorsal surface in many *Azygobranchia*, even when not divided off from the mesopodium, a spiral and calcareous, or chitinous operculum, which closes the aperture of the shell when the animal is completely retracted within it. This operculum is sometimes present in the embryo *Opisthobranch*, but is always lost in the adult. Lateral lobes of the foot, extending for a greater or less extent along its sides, and known as epipodia, are present in some *Azygobranchia* and many palliate and a few non-palliate *Opisthobranchia*; and the cephalic hood or fold above the head, seen in many members of the last-named group, is perhaps an anterior extension of these folds. The foot is completely aborted in some of the non-palliate *Opisthobranchia*, e. g. *Phyllirhoe*. The visceral dome is not distinctly marked off in the order just named and in some *Pulmonata*. Its torsion is sometimes 'reversed,' and certain genera or species, e. g. the Whelk (*Buccinum undatum*) often show a great tendency to this reversal. The dome varies much in size and development, and is most marked in the Reptant *Azygobranchia* and some stylommatophorous *Pulmonata*. So too with the mantle fold. It may be aborted altogether in the adult of some *Opisthobranchia*, hence termed *Non-Palliate*, e. g. *Doris*, *Eolis*, *Phyllirhoe*, or become insignificant in size, as in some *Pulmonata* (*Limacidae*). It generally forms a low ridge, but is well developed when it incloses the ctenidia in a branchial cavity, which opens either to the right side or anteriorly. The aperture of this branchial cavity in most *Pulmonata* is reduced to a small contractile pore by the concrescence of the free edge of the mantle with the body wall. The edge of the mantle is often produced into variously-shaped processes, and is sometimes reflected over the edges of the shell when the animal is fully expanded temporarily, as in many *Streptoneura*, or permanently as in *Aplysia* among palliate *Opisthobranchia*.

The primitive shell-sac of the embryo appears to persist in some *Pulmonata*, and incloses in *Arion* a mass of crystals of Calcium carbonate, or a small shell as in *Limax*. The shell of *Clausilia* is also stated to originate within it in the first instance. But as a rule it disappears, or only contributes a minute portion to the shell, which is formed by the edges and surface of the mantle and visceral dome. The size of the shell is therefore correlated with the size of these two regions. Its shape is variable: sometimes plate-like, e. g. *Aplysia*; conical, as in the Limpets *Fissurella* and *Patella*; usually spiral. The axis of this spiral may be steep, or at various degrees of obliquity: almost horizontal, forming a disc-like shell in *Planorbis*. In some cases successive coils inclose one another more or less completely, e. g. *Conus* or *Cypraea*. The spiral twist follows that of the visceral dome, and is therefore usually right-handed or dextral: and it is rare for a left-

handed or sinistral twist to be normal in a given genus or species. The successive coils of the spiral are closely applied to one another as a rule, but the lower coils may become loose and straggling, e.g. *Siliquaria*, *Vermetus*; and in *Magilus*, when the animal becomes inclosed by the corals among which it lives, the shell may lose its spiral growth altogether. The adult of the Non-Palliate *Opisthobranchia* is devoid of any shell at all. The Veliger, however, possesses a small nautiloid shell, which is discarded during growth, and the same is true of the shell-less *Azygobranchia Natantia*. The first formed shell aborts in some cases, and a second shell, unlike the first, is then formed, e.g. *Marsenia* among Reptant *Azygobranchia*. The texture of the shell varies. It is often brightly coloured, and the coloration is derived from the glands at the edge of the mantle. Its anterior edge is sometimes produced into a spout-like notch, along and beyond which a grooved process of the mantle is capable of protrusion. This process is the siphon, and is characteristic of the carnivorous sub-order *Siphonochlamyda* of *Azygobranchia Reptantia*, e.g. the Whelk.

The ectoderm, or epidermis, consists of a columnar epithelium provided with a delicate cuticula, and which, where it is exposed, is often ciliated to a greater or less extent. It contains unicellular mucous glands, pigment glands, and glands the secretion of which is loaded with Calcium carbonate. The two latter kinds of glands are especially numerous on the edge of the mantle, where they secrete the colouring matter of the shell, its outer epicuticula, and the greater part of its calcareous substance. But the cells of the surface of the mantle and visceral dome also have the power of repairing injuries to the parts of the shell already formed. The mucous glands are sometimes large, and then lie in the sub-epidermic connective tissue. A series of transverse lamellae is developed in many *Streptoneura* to the right of the ctenidium on the roof of the branchial cavity. They constitute the hypobranchial gland, and secrete much mucus. In the genera *Purpura* and *Murex* the secretion, at first colourless, changes in sunlight to a purple or violet, used as a dye by the ancients, and known as 'Tyrian purple.' Specialised glands are found in connection with the foot, and may be distinguished into a suprapedal gland, which opens between the head and foot, e.g. *Helix*, *Succinea* among *Pulmonata*, *Vermetus*, *Cyclostoma* among *Azygobranchia Reptantia*; and a pedal gland, which opens on the surface of the foot itself, as in certain of the latter group, e.g. *Conus*, *Nassa*, *Bithynia*. Other special glands are the grape-like poison glands of *Aplysia* and *Dolabella*, which open near the genital aperture close to the osphradium, and the small glands on the inner surface of the mantle-edge which secrete a purple liquid in *Aplysia Camelus*, a colourless liquid in other species of the genus and its allies. In *Phyllirhoe* certain unicellular cutaneous glands exude a fatty phosphorescent secretion. The muscles are composed of long non-striated muscle-cells. The foot is



pre-eminently muscular, and certain of its muscles—the columellar muscles—connect the animal to its shell. The head, tentacles, buccal mass, and even in some instances the nervous collar surrounding the latter, have special retractor muscles, connected to or derived from the columellar muscles. Calcareous spicules are found in the dorsal integument of *Doris*, &c. among *Non-Palliata*. Thread cells (nematocysts) are found in sacs at the apices of the cerata or dorsal processes, in some *Non-Palliata*, e. g. *Eolis*, *Tergipes*.

The cerebral ganglia are sometimes closely approximated, sometimes far apart. The pleural and pedal ganglia usually lie below and at the sides of the buccal mass, but are fused together surrounding the aorta cephalica in stylommatophorous *Pulmonata*: and in the *Non-Palliata* the right and left ganglia appear to be fused with the corresponding cerebral ganglia, but remain connected by a slender loop beneath the oesophagus. In *Fissurella* and *Haliotis* (*Zygobranchia*), in *Turbo* (*Trochidae*) the pedal ganglia are replaced by two long cords extending down the foot, sheathed with ganglion cells and connected by transverse commissures. The pleural ganglia are only incompletely separated from these cords anteriorly. The ganglia or the cords replacing them are often of a deep orange colour. The cerebro-pedal and cerebro-pleural connectives are sometimes of great length, and distinct from one another; sometimes short, and contained within a common sheath. The two main pedal nerves are connected by transverse commissures in *Paludina* among *Azygobranchia* and some *Pulmonata* (p. 120). The two visceral nerves connected with the pleural ganglia are always united posteriorly, but the length of the loop thus formed and the distinctness of its two visceral and the single abdominal ganglia are variable. In one section of the *Anisopleura*, the *Streptoneura*, the posterior union of the visceral nerves, which are always long, is situated dorsally to the intestine, and the loop is therefore twisted with the torsion of the visceral dome, the right side of the loop passing above, the left below the intestine. In the other section, the *Enthyneura*, the union is situated ventrally to the intestine, and the nerves are consequently not twisted, and in this case the loop may be very short, yet the ganglia remain distinct, e. g. in *Limnaeus* among basommatophorous *Pulmonata*. A pair of buccal ganglia is invariably present, connected with the cerebral ganglia: but in *Fissurella*, *Haliotis*, and *Turbo* their connectives have been traced to the pleuro-pedal centres. Ganglia may also be present on other nerves.

Sensory cells with sense-hairs occur on the tentacles of the head, and of other parts of the body, and the body itself. A number of these cells sometimes form projecting 'gustatory' papillae. In *Fissurella* and certain species of *Trochus* lateral organs, composed of a central mass of sense cells with surrounding supporting cells, are found ventral to the tentacles of the mantle furrow. Special ganglia are situate at the bases of these lateral

tentacles, and ganglion cells beneath the lateral organs. A sensory organ known as osphradium lies near the ctenidium. It is present in the Limpet (*Patella*), and in some *Pulmonata*, e.g. *Limnaeus*, where the ctenidium is aborted. It consists of a patch of cylindrical ciliated cells, with an underlying ganglion, and is always supplied with a nerve from the visceral loop or ganglion. There are two osphradia in the *Zygobranchia*, one right, the other left. Gustatory buds have been detected in the oral cavity of *Fissurella* and *Trochus*. The eyes are usually two in number, situated one at the base of each cephalic tentacle, and sometimes raised on a papilla. In certain *Pulmonata*, hence *Stylommatophora*, they are placed at the tips of the two superior tentacles. In some *Non-Palliata*, e.g. *Eolis*, *Doris*, and the palliate Opisthobranch *Philine*, they lie upon the cerebral ganglia, and are then small in size. In *Patella* the eye is a cup-shaped depression, widely open; in *Haliotis*, some species of *Trochus*, nearly closed; in other *Anisopleura* quite closed. The retina is formed of a single layer of cells, differentiated into pigmented and non-pigmented. The latter are broadest at their bases, narrow at their inner ends, which are prolonged into a delicate rod. The former are broadest at their inner ends, which are furnished with rods, narrow at their bases, and they surround, in groups containing four to eight cells, each non-pigmented cell, the visual rod of which is enveloped by their rods. Both (?) kinds of cells are connected by basal processes with the fibres of the optic nerve, which spread over the back of the eye, and in many instances at least contain intercalated ganglion cells. In *Helix* there is a well-developed peripheral optic ganglion (Carrière). The open retinal capsule contains a vitreous body in *Haliotis*, (? *Patella*); the closed a vitreous body and a lens, which occupies the anterior part of the capsule. The former is soft, the latter more dense and slightly yellow; both are structureless. A vitreous body is said to be absent in stylomatophorous *Pulmonata* (Hilger and others)<sup>1</sup>. The internally-placed eye

<sup>1</sup> Carrière in his account (*Sehorgane der Thiere*, 1885) denies the existence of a separate lens in the eye, and thinks that when such a lens-like structure is traceable it is a differentiation of the vitreous body and nothing more. Hilger states that the lens stains only peripherally with such a re-agent as haematoxylin, but the vitreous body throughout its substance. The embryonal lens of *Paludina* is laminated concentrically, and finely striated in a radial direction. Carrière's account of the retina differs from that of Hilger's mainly in the fact that he regards the non-pigmented cells as secretory and forming the vitreous body.

The clear cells (*supra*) evidently correspond to Patten's retinophorae, the pigmented to his retinulae. The former cannot therefore be considered, as they are by Fraisse and Carrière, as supporting or secretory cells. Patten has investigated only the eye of *Haliotis*, and points out its strong resemblance to the invaginated eye of *Arca*. See under *Lamellibranchiata*. He finds typical retinophorae and retinulae present. The latter bear rods; their basal ends are long slender hyaline stalks, or *bacilli*. The rods of both kinds of cells pass over into the vitreous body which fills the optic cup, and is a clear nerveless fluid. Its outer part is dense and forms the lens. The vitreous body and lens represent the corneal layer of the cuticula. At the margin of the optic cup they pass together with the retinidial layer by gradual transition into the cuticula of the hypodermis. See *Mitth. Zool. Stat. Naples*, vi. pp. 614-19; and discussion, pp. 619-23; and for the explanation of terms, the note, p. 452 of this book.

of *Opisthobranchia* appears to be much simplified. The anterior epithelial cells of the closed retinal capsule are transparent, as is also the thin layer of connective tissue intervening between it and the superficial epithelium of the surface or cornea. In the *Natantia* the whole eye is inclosed within a capsule, to which it is attached by muscles. Certain species of *Onchidium* (*Pulmonata*), littoral marine slugs, possess a number of retractile tentacles ranged along the dorsum. Each tentacle bears two to three eyes. These eyes possess a lens composed of five cells, a retina in which the visual rods are turned externally, i.e. away from the lens, and an optic nerve which perforates the retina, the nerve-fibres being distributed on its inner surface. The two otolithic vesicles are usually in close apposition with the pedal ganglia, but in *Natantia* and *Non-Palliata* near the cerebral ganglia, from which their nerve is invariably derived. The capsule contains ciliated cells, and in some instances, at any rate, sense-cells. The calcareous otolith is either laminated and globular, or, as is most usual, consists of a mass of crystals.

The head is always very distinct, and bears one or two pairs of tentacles, which are invaginable in the Stylommatophorous *Pulmonata*. It is usually retractile, but there are exceptions, e.g. *Patella*. The buccal cavity is often armed with jaws, either a chitinous plate on its upper wall, e.g. terrestrial *Pulmonata*, or two, one on each side, opposed to one another, varying in shape and consistency, and best developed in *Azygobranchia*. The mouth-bearing region of the head is greatly elongated in the carnivorous *Azygobranchia*, e.g. the Whelk, forming a proboscis, which can be retracted within a sheath. In other *Azygobranchia* the mouth may be placed at the end of a non-retractile snout known as rostrum. The sac of the radula varies much in size, and is greatly developed in the Limpet (*Patella*). The radula itself is occasionally wanting, e.g. *Tethys* (*Non-Palliata*). The form and arrangement of its teeth vary considerably, and have been employed as classificatory characters (see note, p. 116). Salivary glands are usually present, to the number of one or two pairs, opening into the buccal cavity. Their shape and size are extremely variable. In *Dolium* and its allies among the carnivorous *Azygobranchia* the salivary secretion contains free sulphuric acid. Goblet cells are found in the buccal epithelium, sometimes collected into small groups. The oesophagus is often dilated into a crop, or has a lateral caecal crop attached to it (*Limnaeus*, *Planorbis*, *Buccinum*). The stomach is usually simple in form, but in some palliate *Opisthobranchia* it is constricted into three or four portions, which differ from one another in internal characters, and in *Non-Palliata* it is often prolonged as a single or double caecum behind the pylorus. A small pyloric caecum is found also in other instances. The intestine is usually long, and coiled among the lobes of the liver, but is simple and much shortened in *Non-Palliata*. Its termination is sometimes dilated. The

anus lies beneath the mantle fold, either on the right side or anteriorly. In *Non-Palliata* it is sometimes on the right side, but usually in or near the middle dorsal line, as e.g. in *Doris*. The stomach receives the ducts of the two branched glands known as liver. They are usually large, and often asymmetrical in point of size, especially when the visceral dome is large and spirally twisted. In some *Opisthobranchia* the liver is represented by a variable number of lobes, which open into a caecum extending backwards from the stomach, or by a number of simple or branched processes originating from the stomach and its single, e.g. *Eolis*, or double, e.g. *Antiopa*, caecum. These simple and branched processes extend, one into each of the cerata (*infra*) in the *Eolidia*, and in many instances the food passes into them 'as it does in Scorpions' (Lankester). It is also said that they open at their apices to the exterior, at least in some instances. A caecal gland or 'pancreas' is said to exist in some *Opisthobranchia*, e.g. *Doris*, *Aplysia*, opening into the stomach. An anal gland opens into the anus in *Purpura* and *Murex* among *Azygobranchia*.

The heart consists of a thick-walled ventricle and thin-walled auricle, the latter receiving the blood from the respiratory organs. The ventricle is pierced by the intestine, and has a double auricle in *Haliotis* and *Fissurella*<sup>1</sup>. The ventricle gives origin to an aorta, which soon divides into a cephalic and an intestinal branch. The degree to which these two vessels are developed is very variable. The former may be prolonged to the head, passing between the pedal and pleural ganglia (*Natantia*, *Pulmonata*), and the latter may form a rich network over the intestine and liver, as in the *Pulmonata*. Eventually the blood passes into the lacunar system of the coelome, but the size of the lacunae is very variable, and in the *Pulmonata* some of them may have a more or less vessel-like character. The blood passes to and from the respiratory organs in special channels, and the character of the efferent sinuses depends upon the mode in which those organs are disposed, e.g. in many ceratontous *Non-Palliata* there is a well-developed longitudinal sinus on each side the body, into which the blood returning from the cerata is collected. The heart is placed sometimes in front of, sometimes behind, the base of the ctenidia, and then the auricle lies either anteriorly or posteriorly in the body, with reference to the ventricle. Hence the terms prosobranchiate and opisthobranchiate. The blood consists of a colourless plasma with amoeboid corpuscles. In *Planorbis* (*Pulmonata*) the plasma is tinged with haemoglobin, and it contains haemocyanin in various *Streptoneura*, e.g. *Haliotis*, *Fissurella*, *Turbo*, *Murex*, and in *Helix* among *Pulmonata*<sup>2</sup>.

<sup>1</sup> In *Turbo* the pericardium is perforated, but not the ventricle; in *Neritina* neither. In these two genera and in *Nerita* the intestine is usually said to pass through the ventricle. Cf. Landsberg, Z. A. v. 1882.

<sup>2</sup> A pericardial gland in the form of lobes upon the auricle occurs in *Fissurella*, *Parmophorus*, *Haliotis*, *Turbo*, and *Trochus*, according to Grobben, Z. A. ix. 1886, p. 371.

The respiratory organs are represented either by ctenidia, or by the surface of the branchial cavity formed by the mantle, or else by secondarily formed processes of the body wall. Processes of every kind are absent, and the general surface of the body is respiratory in certain *Non-Palliata*—the *Haplomorpha*, e.g. *Phyllirhoe*. Two ctenidia are present only in the *Haliotidae*, and *Fissurellidae* among *Zygobranchia*. In all other *Anisopleura* there is but one. But in some *Azygobranchia* the osphradium is large, thrown into folds, and is generally taken for a second but reduced ctenidium (parabranchia). The single persistent ctenidium is on the left side of the anus, and therefore represents the original right ctenidium. The Limpets (*Patellidae*) among *Zygobranchia* have the two ctenidia quite rudimentary, forming the capito-pedal organs of Lankester. The single ctenidium of palliate *Opisthobranchia* is also lost in the *Phyllidiobranchia*. In both cases vascular lamellae or pallial gills are developed in the mantle furrow, forming a complete series in the former of the two groups (*Patellidae*), a right and left row in the latter. A circle of pinnate folds surrounds the anus in certain *Opisthobranchia Non-Palliata*, i.e. the *Pygobranchia*, e.g. *Doris*. It is probable that they are secondary processes, not true ctenidia, and in certain members of the same sub-order, as well as in the sub-order *Ceratonota* of *Non-Palliata*, cylindrical hollow processes of the body walls—the cerata—are developed, more or fewer in number, and extending in lateral rows on each side of the body. Into these cerata liver caeca may extend (*supra*). In one group of *Azygobranchia*—the *Pneumochlamyda*, e.g. *Cyclostoma*—and in the *Pulmonata*, the roof of the branchial cavity formed by the mantle has taken on a respiratory function, and is traversed by a network of vascular sinuses. In the genus *Ampullaria* (*Azygobranchia Holochlamyda*) from the fresh-waters of tropical America, Africa, and East Indies, one side of the roof of the branchial cavity is respiratory, but a ctenidium is present as well.

Two nephridia are found in some *Zygobranchia* (*Fissurella*, *Patella*), but not in others (*Haliotis*). One of the two—the left, i.e. the primitive right nephridium—is rudimentary. It appears to be the one that is aborted in other *Anisopleura*, and not the right (primitive left), as is generally maintained. In *Haliotis*, and still more in *Turbo*, where the organ is on the right side of the body, its duct crosses the intestine and opens on its left side. In other instances the organ itself appears to undergo a greater or less change of position<sup>1</sup>. The nephridium consists of a urinary chamber opening externally, of secreting and usually branched acini, the calibre of which is variable, and a canal which connects the pericardium and the urinary chamber. This chamber is primitively small, e.g. *Fissurella*, and

<sup>1</sup> The point is one which requires further research. It is possible that the *Anisopleura* do not all agree. See Haller, M. J. xi. 1886, p. 26. In *Paludina* the nephridial duct is to the right of the rectum, between it and the vagina.

lined by a ciliated secretory epithelium, but it is generally large and its epithelium non-secretory. In *Non-Palliata* it is a wide sac extending antero-posteriorly. In this group the secreting acini may be lost, e.g. *Phyllirhoe*, but they are as a rule branched tubes scattered along the edges of the chamber, e.g. *Bornella*. The acini are also branched in other instances, and often grouped into two lobes, anterior and posterior, of which the former may be lost (*Pulmonata*). They are either large or small; either free, e.g. *Fissurella*, or united by connective tissue; and are lined by a ciliated secretory epithelium, with either similar or dissimilar cells. In the latter case the two kinds of cells may be found, either side by side or confined to separate lobes. The differences relate to form and character of the excretory products. The urinary chamber either opens direct by a simple aperture, e.g. *Buccinum*, or by a papilla, or a long duct, e.g. some *Pulmonata*. The opening lies within the branchial cavity, either near the base of the gill, or, when a duct is present, near the anus. Its position seems to be somewhat variable.

The sexes are separate in the *Streptoneura*, but the *Euthyneura* are hermaphrodite, the male and female products ripening at different times (successive hermaphroditism). When a Gastropod is hermaphrodite, the sperm and the ova either develop in the same follicle of the gland, e.g. *Pulmonata*, or the sperm in a central capsule, into which open a number of smaller capsules containing ova, as in many ceratodontous *Non-Palliata*; or finally, as in *Elysia* (*Non-Palliata Haplomorpha*), there are two separate glands. The genital gland consists of simple or branched acini, and usually lies in or near the liver. It is often lobed or compact in form, usually single but sometimes double, e.g. hermaphrodite gland of *Phyllirhoe*, testis of *Paludina*. The efferent ducts are ciliated in some cases<sup>1</sup>. When the sexes are separate the vas deferens is usually a simple canal devoid of any accessory glands, e.g. *Natantia*. It either opens on the left side of the anus, and a ciliated furrow either leads to the base of the penis, e.g. *Murex*, *Natantia*, or is continued along it, e.g. *Strombus*, &c.; or it is continued onwards as a canal, and opens either at the base or at the apex of the penis, e.g. *Buccinum*. The penis, placed on the right side near the head, is rarely hollow and invaginable, usually solid and muscular. Accessory glands sometimes open upon it. The oviduct in the lower part of its course usually dilates into a uterus, the walls of which secrete albumen, or more rarely there is a specialised albumen gland, e.g. *Paludina*, *Natantia*.

<sup>1</sup> Professor Ray Lankester states ('*Mollusca*,' Encyclopaedia Brit. (ed. ix.) xvi. p. 645) that the *Zygobranchia* retain the archaic character of the absence of special genital ducts. 'The generative products escape by the larger nephridium,' i.e. the right. And Wegmann, in his monograph on *Haliotis*, maintains the same view; (*A. Z. Expt.* (2), iii. 1884, p. 340). On the other hand, Haller states explicitly that he has found a separate genital duct in both *Fissurella* and *Haliotis* (*M. J.* xi. 1886, p. pp. 10, 14). As to *Patella*, Harvey Gibson agrees in his lately published memoir with the statement of Professor Lankester. The *Zygobranchia* have no accessory sexual glands.

The vagina is always short, and there is in some instances an appended receptaculum seminis, e.g. *Paludina*, *Natantia*. The genital opening is usually at some distance from the anus. In hermaphrodite forms there is an hermaphrodite duct to the ovo-testis, which may remain outwardly undivided as far as the aperture, but has a partially divided cavity, as in *Aplysia* and most other *Opisthobranchia Palliata*. It usually divides, sooner or later, into separate male and female ducts. A ciliated furrow leads from the genital aperture to a hollow evaginable penis on the right side of the head in *Aplysia* and a few others. When the ducts are separate, the vas deferens ends in an evaginable penis, and has commonly an appended prostatic (?) gland. A vesicula seminalis is often present. The oviduct has a uterine section, an attached receptaculum seminis, and invariably an albuminiparous gland. The two apertures, male and female, open as a rule, except in aquatic *Pulmonata*, into a sexual cloaca, which lies either near the anus, or on the right side of the body, and in all *Pulmonata* far forwards, close to the head. Some *Pulmonata* and certain species of *Doris* possess a dart, attached in the former to the female, in the latter to the male, duct.

Two forms of spermatozoa are found in the same individual in various *Azygobranchia*, and of these one form only appears to fertilise the ovum in *Paludina*. In the hermaphrodite groups copulation may or may not be reciprocal. The ovum is small, and is usually devoid of a vitelline membrane. It is surrounded by a quantity of albumen, the surface of which hardens. In some of the *Pulmonata* there is a calcareous egg-shell, e.g. *Testacella*, *Helix*. In some *Azygobranchia*, e.g. *Paludina*, and some *Pulmonata* (e.g. *Clausilia*, *Pupa*), the ova develop within the uterus, but in most cases they are laid, either singly or in masses, contained sometimes in a fixed hard cocoon with terminal aperture, as in many *Azygobranchia*. One ovum only frequently develops in this case, the others serving as food material. The egg-masses are usually fixed to some object, except in the terrestrial *Pulmonata*. They are carried about attached to a float-like structure formed by the foot in *Ianthina*. Segmentation is unequal, but the degree of inequality depends upon the amount of food-yolk present. The hypoblast cells are sometimes of very large size, and two yolk cells persist for a long time in *Aplysia*. When the blastomeres are all relatively small, the gastrula is invaginate, e.g. *Paludina*; when the hypoblast cells are large, it is formed by overgrowth. There is a Trochosphere and Veliger stage. The velum is said to be absent in some *Pulmonata*. It usually becomes bilobed or multilobed, and is large in size in *Natantia*, and persists to a greater or less extent in the Opisthobranch *Tergipes* and the Pulmonate *Limnaeus*.

Most *Gastropoda Anisopleura* are marine; the basommatophorous *Pulmonata*, and some *Azygobranchia*, e.g. *Paludina*, *Neritina*, are fresh-

water; some of the last-named group are also found in brackish water, e.g. *Littorina*, whilst others, such as *Cyclostoma*, are, like the stylommatophorous *Pulmonata*, terrestrial. A few are parasitic: *Entoconcha mirabilis* inhabits the perivisceral cavity of a *Synapta* (*Holothurioidea*); in the genus *Eulima*, which lives upon *Holothurioidea*, some species are ecto-, others endo-parasitic. *Stylifer* is ecto- or pseudo-parasitically attached to *Holothurioidea*, *Echinoidea*, and *Asteroidea*. Some are entirely pelagic, as the *Natantia* and *Phyllirhoe*. The majority are reptant, but of these some few can swim, as does, e.g. *Oliva*, by means of the epipodia. The majority are vegetable feeders, the siphonostomatous *Azygobranchia* carnivorous. The *Anisopleura* appear in the primary rocks, the existing genera *Patella*, *Turbo*, *Natica*, and *Pleurotomaria* in the Lower Silurian. Though the number of fossil forms is great, the extinct genera are not numerous.

The *Gastropoda Anisopleura* are classified as follows (Ray Lankester):—

I. *Streptoneura* (= *Prosobranchia* minus *Placophora*). Visceral nerve-loop twisted; sexes separate.

(1) *Zygobranchia*. Both ctenidia persistent or aborted. A left rudimentary nephridium present in some instances. No accessory generative organs. The visceral dome relatively small; lying close upon the foot and co-extensive with its prolongation in an aboral direction. Marine.

*Ctenidiobranchia*, including *Haliotidae* and *Fissurellidae*; *Phyllidiobranchia*, including the *Patellidae* with secondarily developed gill-lamellae.

(2) *Azygobranchia*. Left ctenidium, with corresponding osphradium and right nephridium retained (see p. 479, and note). Osphradium often large and lamellate = parabranchiâ. Hypobranchial and adrectal gland often present. Shell usually large and spiral; operculum often present. Visceral dome large. Anus on the right side. Radular teeth vary much in form.

(a) *Reptantia*. Foot or mesopodium a creeping disc. Includes (1) *Holochlamyda*; with mantle edge entire; with mouth, as a rule, at the end of a non-introversible snout, i.e. rostriferous; vegetarian; marine, brackish, freshwater, or terrestrial, e.g. *Trochus*, *Ianthina*, *Paludina*, &c.: (2) *Pneumono-chlamyda*, no ctenidium; pallial chamber, a lung sac; rostriferous; terrestrial, e.g. *Cyclostoma*: (3) *Siphono-chlamyda*, a pallial siphon; <sup>shell</sup> always spiral; usually an operculum, horny, and lamelliform; rostriferous, or a proboscis; mostly carnivorous; marine, e.g. *Strombus*, *Cypraea*, *Conus*, *Murex*, *Buccinum*.

(b) *Natantia* (= *Heteropoda*). Pelagic; foot a swimming organ; carnivorous. *Atlantacea*, with large visceral dome and shell: *Carinariacea*, visceral dome greatly reduced; shell small, cap-like, hyaline; ctenidium projecting freely; mesopodium with a sucker, fin-like; metapodium pointed, forming posterior end of body: *Pterotracheacea*, no shell; visceral dome, an oval sac imbedded in the posterior dorsal region of body; mesopodial sucker absent in female.

II. *Euthyneura*. Visceral nerve loop not twisted, often very short; shell generally light, little calcified; often lost in adult; operculum often present in embryo but lost in adult; radular teeth usually fine and similar: anus not so far



forwards as in *Azygobranchia*, may become median and posterior; left ctenidium and right nephridium only retained (see p. 479, and note); ctenidium and mantle-fold sometimes lost. Hermaphrodite.

(1) *Opisthobranchia*. Visceral dome always small; shell rarely present; a nautioid shell in the Veliger stage. Foot large in archaic forms, and mantle-fold projecting over right side. Anus then placed far back beyond mantle-edge, behind the ctenidium, the free end of which is turned backwards. Heart in front of base of ctenidium. Epipodia commonly present and often reflected over shell or dorsal surface. Marine.

(a) *Palliata* (= *Tectibranchia*). Mantle-fold present. Includes (i) *Ctenidiobranchia*, a ctenidium present; shell, with rare exceptions, delicate, sometimes small or completely enclosed within the reflected mantle-edge; epipodia common, e. g. *Bulla*, *Aplysia*, *Pleurobranchus*; (ii) *Phyllidiobranchia*, ctenidium atrophied, replaced by a lateral row of lamellae on each side within the pallial fold, e. g. *Phyllidia*.

(β) *Non-Palliata* (= *Dermatobranchia*). Mantle atrophied in adult; and shell lost; body slug-like, visceral dome and foot co-extensive; anus usually median and posterior. Includes (i) *Pygobranchia*, ctenidium (?) a circler of pinnate processes round the anus; epipodial-fold may be large and simulate a mantle-fold; cerata sometimes present, e. g. *Doris*, *Polycera*; (ii) *Ceratonota*, ctenidium aborted; simple or branched cerata, into which liver processes usually pass; anus on right side, or dorsal and median: e. g. *Tethys*, *Eolis*; (iii) *Haplomorpha*, no ctenidium; no cerata; foot also sometimes lost; degenerate and small, e. g. *Phyllirhoe*, *Elysia*.

(2) *Pulmonata*. Ctenidium aborted; dorsal wall of branchial cavity formed by mantle, respiratory; osphradium on left side (*Planorbis*, *Auricula*) or right (*Limnaeus*); usually lost; visceral dome small and co-extensive with foot, e. g. *Limax*, *Arion*, or large and spirally twisted, e. g. *Limnaeus*, *Helix*. Includes (i) *Basommatophora*; eyes median at base of tentacles; male and female genital orifices separate but near one another; aquatic; e. g. *Limnaeus*, *Planorbis*, *Ancylus*, *Auricula*; (ii) *Stylommatophora*, eyes elevated on invaginable tentacles; shell either large or spirally coiled, or minute, or absent; edge of branchial fold of mantle always fused to neck, leaving a pulmonary aperture; mostly terrestrial, e. g. *Helix*, *Pupa*, *Clausilia*; *Testacella*, *Limax*, *Arion*; *Onchidium*.

See literature, pp. 109, 112, 118, 123, 283.

*Haliotis*, Wegmann, A. Z. Expt. (2), ii. 1884. *Patella*, Harvey Gibson, Trans. Roy. Soc. Edinburgh, xxxii. pt. 3, Session 1884-85; *development of*, Patten, Arb. Zool. Inst. Wien, vi. 1886. *Anatomical points in Fissurella*, *Haliotis*, *Trochidae*, Haller, marine *Rhipidoglossa*, M. J. ix. 1883. *Vermetus*, de Lacaze Duthiers, A. Sc. N. (4), xiii. 1860. *Pleurobranchus*, Id. op. cit. (4), ix. 1859; cf. A. G. Bourne, Q. J. M. xxv. 1885. *Non-palliate Opisthobranchia*, Bergh, Challenger Reports, x. 1884 (with lit. referred to); Trinchese, Atti Acad. Lyncei (3), xi. 1880-81; cf. British *Nudibranchiata*, Alder and Hancock, Ray Soc. 1845. *Onchidium*, marine, slug-like Pulmonate, Bergh, Challenger Reports, x. 1884, Appendix, p. 126; and M. J. x. 1885. *Structure and development of O. celticum*, Joyeux-Laffaie, A. Z. Expt. x. 1882.

*Glands of mantle margin in Aplysia*, Blochmann, Z. W. Z. xxxviii. 1883.

*Purple gland = hypobranchial gland of Purpura*, de Lacaze Duthiers, A. Sc. N.

(4), xii. 1859. *Sucker of Natantia* = *Heteropoda*, Niemic, Recueil Zool. Suisse, ii. 1885.

*Nerve eminences of Fissurella*, &c., *gustatory organs*, Haller, M. J. ix. 1883, pp. 44, 73. *Tactile bodies on tentacles*, Flemming, A. M. A. xxiii. 1884.

*Eyes of Onchidium*, Semper, Reisen im Archipel. d. Philippinen, (2), iii. Ergänzungsheft, 1877, and A. M. A. xiv. 1877.

*Histology of nervous system*, Haller, M. J. ix. 1883.

*On formation of ctenidium*, Osborn, Studies from Biological Laboratory Johns Hopkins University, iii. pt. i. 1884; *of Fasciolaria*, Id. ibid. pt. 3, 1886.

*Nephridia; structure, in marine Rhipidoglossa*, M. J. xi. 1886; *of Patella*, Cunningham, Q. J. M. xxiii. 1883; *of Aplysia*, Id. Mittheil. Zool. Stat. Naples, iv. 1883. See a note on function, Joliet, C. R. 97, 1883.

*Two forms of spermatozoa*, Von Brunn, A. M. A. xxiii. 1884; Z. A. vii. 1884. *Mimicry in Mollusca*, Osborn, Science, vi. 1885.

## BRANCH II. LIPOCEPHALA.

Mollusca with rudimentary prostomium. Eyes absent on the prostomial region of the adult. No odontophore or jaws.

### CLASS LAMELLIBRANCHIATA.

#### (*Conchifera; Pelecypoda; Elatobranchia*).

*Lipocephala* with very well-marked bilateral symmetry. There are two large mantle-folds, a right and left, each covered by one of the valves of the shell. An elastic ligament unites the two valves of the shell together in the median dorsal line. The foot is laterally compressed and usually sharp-edged. There are two pairs of labial tentacles. The gill-filaments usually undergo concrescence and form gill-lamellae. There are three pairs of ganglia, the cerebro-pleural, pedal, and visceral. The liver, auricles, nephridia, sexual glands are paired and symmetrical. Salivary glands and accessory organs of generation are wanting.

The valves of the shell are usually equivalve, but rarely equilateral as in some species of *Pecten*. Accessory pieces may be present in the median dorsal line as in *Pholas*. The valves may be small and cover the mantle-surface incompletely, and then the animal clothes its burrow in wood (*Teredo*) or sand (*Septaria*) with a calcareous lining. Or though free originally, they become fused at an early period into a continuous calcareous tube secreted by the general surface of the mantle, open posteriorly, and often anteriorly as in *Aspergillum* and its allies (*Gastrochaenidae*). In *Ostreidae* the right valve is firmly fixed to stones. The shell is often produced into processes or ridges formed by lobes of the mantle-edge; it is generally coloured by pigments derived from unicellular glands in the same region. The ligament must be regarded as a median

dorsal but uncalcified region of the shell. Calcareous interlocking and asymmetrical processes of each valve, placed at the <sup>an</sup> anterior end of the ligament, and known as hinge- and cardinal-teeth, unite the valves in many forms (see p. 125). The two mantle flaps or folds are often united indirectly at the posterior end of the ctenidial axis (p. 128); sometimes also directly for a greater or less extent of their ventral edges. The margin of each fold is thickened, muscular, and contractile, and often carries a number of tentacles on its inner surface. Its posterior region is often prolonged into two tubes or siphons, which may be of great extent and either free from one another for a greater or less extent, or united almost to their extremities. Of these siphons, the ventral is inhalent, the dorsal exhalent, the currents being caused by the action of cilia on the inner surface of the mantle, on the ctenidia and labial tentacles.

The foot, the sole organ of locomotion, is lost or rudimentary in the *Ostreidae* and some other families. It is typically ploughshare-shaped, and is used for burrowing in sand or mud, rarely disc-shaped and used for crawling as in *Arcadae*. It is bent upon itself and can be used for jumping in *Cardium*, *Trigonia*, and in *Solen* and its allies is a long cylindrical burrowing organ, which when rapidly contracted causes water to spurt out of the siphons and so propels the animal in the water. The *Pectinidae* swim by alternately opening and shutting the valves of the shell. The edge of the foot often contains a special gland, the byssus gland, which secretes a horny material in the form of filaments, by means of which the animal is attached to foreign objects. The gland is sometimes present in a rudimentary condition in the young animal, though aborted in the adult, e. g. *Anodon*.

The musculature of the body forms certain special muscles. These are, the muscles that close the valves of the shell or adductors; those that move the foot, protractor, anterior and posterior retractors; and the pallial muscles. The adductors are formed by transverse fibres, which pass from one to the other valve. In many forms there is one, the anterior, in the prostomial region, and a second, the posterior, at the hind end of the body, the former above the mouth, the latter below the anus. The anterior adductor may be absent altogether (*Monomya*), but may then be present in the embryo as in *Ostrea*. The protractor and anterior retractor of the foot are inserted close to the insertion of the anterior adductor, the posterior retractor near the posterior adductor (p. 125). They are paired, one on each side of the body, but the posterior retractors are united for a certain distance. The pallial muscles are retractors and compressors of the free edge of the mantle. The insertions of these muscles are the cause of 'impressions' on the inner surface of the valves. The impression of the pallial muscles, termed 'pallial line,' either follows the contour of the edge of the shell in its whole extent, or when the siphons are large curves

inwards forming a deep bay at the posterior end of the valves. These two conditions are known respectively as integro- or sinu-palliate.

The cerebro-pleural ganglia usually lie at the sides of the mouth connected by a dorsal commissure. They are sometimes fused dorsally (*Teredo*). The pedal ganglia are always closely united. Their size varies with the development of the foot and they are absent in the *Ostreidae*, but an infra-oesophageal cord passes from one cerebro-pleural ganglion to the other and thus represents the pedal system. The pedal connectives are sometimes excessively short and the ganglia approximated to the cerebro-pleural as in *Pecten*. The visceral ganglia are always large, their connectives long, and the two are closely united. They lie on the ventral surface of the posterior adductor muscle, and give off branches to the viscera. The two branches to the ctenidia are each connected with an osphradial ganglion, and when the siphons are large, e.g. *Solen*, *Mya*, there are siphonal ganglia developed on the siphonal nerves. Both cerebro-pleural and visceral ganglia give off pallial nerves, which traverse the margins of the mantle and may unite, e.g. *Ostrea*, to form a circumpallial nerve, or are resolved into a circumpallial plexus, e.g. *Anodon*. Nerve and plexus alike contain ganglionic centres. The chief ganglia are often orange coloured.

The tentacles or papillae developed on a greater or less extent of the margin of the mantle, and at the siphonal apertures in many *Lamelli-branchiata*, are probably tactile. Cells ending in sensory hairs are found upon them in *Pecten*, *Anomia*, &c., as well as on the margins of the mantle<sup>1</sup> (p. 137). Eyes provided with a lens are often found in the larva. They are two in number and lie at the base of the velum on each side of the oesophagus near the auditory sacs. *Teredo* has a row of such organs in front of the foot. But in the adult eyes are confined to the edges of the mantle and the siphons. They have the form of diffuse ommatidia, which are generally present and are sometimes the only kind to be found, e.g. *Ostrea*, *Avicula*, *Cardita sulcata*; or else the ommatidia are aggregate, and then the eye is either pseudo-lenticulate, evaginate, or invaginate. The first-named is found only in *Arca*; the retineum is slightly invaginate but the retinidial elements form a prominent convex lens. The evaginate type occurs in *Arca* and is the only kind in *Pectunculus*. There is an ommateum; the retinophorae are surrounded each by eight [retinulae, four forming an outer, four an inner row, and the retinophoral rods are prominent and convex at their outer extremities. The invaginate eye is met with in *Arca* as a simple pit; in *Pecten*, *Spondylus*, and *Cardium* the pit becomes a vesicle and closely resembles the Vertebrate eye. In *Arca* the pit is lined by a retineum, and the retinidial cuticula is thickened.

<sup>1</sup> For the structure of the hypodermis, the intercellular nerves, the plexus of nerve-fibrils in the inner layer of the cuticle, and the sense-organs of the tentacles in *Pecten*, see Patten, Mitth. Zool. Stat. Naples, vi. pp. 604-5, 662-5, with the figures given.

In *Pecten* the hypodermis and a thin layer of connective tissue constitute a transparent cornea over the eye, which is situated at the apex of a tentacle. The corneal hypodermic cells form a lens-like body in *P. pusio*. The hypodermis cells of the surface surrounding the cornea are deeply pigmented and are termed iris. Beneath the cornea is a mesoblastic cellular lens, convex internally and projecting into a blood-sinus. The optic vesicle, which is derived from an ingrowth of the hypodermis, has its anterior wall converted into a retina, in which the retinophoral rods are turned away from the light as in Vertebrata. Its posterior wall is transformed into a double-layered argentea, in which the cells are obliterated and a red coloured cellular tapetum. Between the argentea and the retinophoral rods is intercalated a thin hyaline vitreous layer secreted by the cells of the argentea (?). The vesicle is invested by a thin mesoblastic sac, which forms a septum between the lens and retina, a sclerotic external to the tapetum. The optic nerve is derived as in all *Lamellibranchiata* from the circumpallial nerve. It divides into two branches. One which spreads over the sclerotic is central; its fibres enter the optic vesicle near its rim and become the axial nerves of the retinophorae. The other is lateral; its fibres pass to the anterior surface of the retina, pierce the septum, and are distributed to the ganglion cells and between the retinophorae. *Spondylus* appears to agree closely with *Pecten*; but the structure is very much simplified in *Cardium*<sup>1</sup>. A pair of auditory sacs are usually present when the foot is well developed. They lie close to the pedal ganglion in connection with a nerve from it<sup>2</sup>. The central cavity contains a single calcareous otolith.

The mouth is anterior and ventral to the anterior adductor when present. It is elongated transversely, and both its margins, upper and lower, are formed by two prominent ridges which are prolonged laterally into the labial tentacles. These structures are ciliated, and often of great extent, thrown into folds or fringed. The anus is a projecting papilla placed dorsally to the posterior adductor muscle. The alimentary canal is ciliated throughout, and consists of a short oesophagus, a dilated stomach to which is often attached a caecum, and an intestine which is disposed in folds. The terminal section is straight, median, and dorsal, and usually passes through the ventricle, except in *Ostrea*, *Anomia*, and *Teredo*. On the crystalline style, see p. 133, *ante*. Two ducts open into the stomach, one on either side. They lead to a large branched gland, the liver, which with the genital glands surrounds the coils of the intestine. Calcareous cells are not present in the liver, only granular and ferment cells. The

<sup>1</sup> For the terms used in this description see the note, p. 452, *ante*; and for a full account, Patten, *op. cit.*

<sup>2</sup> This is the usual statement; but in *Anodonta* the nerve is said to be derived from the cerebro-pedal connective. See p. 138.

heart lies in a pericardium in front of the posterior adductor muscle, and very generally beneath the shell-ligament. The ventricle is single, except in *Arca*, cf. Plate vii. Fig. 3, p. 291. There are two auricles, usually separate but united medianly in *Ostreidae*. The ventricle gives origin to an anterior and posterior aorta. Fine vessels with an endothelial lining are found in the labial tentacles and the intestine. Otherwise the blood spaces are irregular spaces between the viscera and in the mantle. A muscular valve surrounds the large venous channel which brings the blood from the foot to the median infra-cardiac sinus, and by its contraction causes the foot to swell as it does in locomotion. A portion of the mantle appears to form a blood reservoir. The blood is colourless, and contains amoeboid corpuscles. Haemoglobin coloured corpuscles occur in *Solen* (*Ceratisolen*) *legumen* and *Arca Noe*. The admixture of water with the blood and the presence of pori aquiferi on the margins of the foot appear to be very doubtful. The coloured corpuscles of *Solen* do not escape even when the animal is strongly irritated and consequently contracted. 'The pericardial gland' (see p. 129) 'appears in two forms, (1) as lobes upon the auricles, (2) as caecal outgrowths of pericardial epithelium into the mantle at the anterior angles of the pericardium. The first form commencing with *Arca* leads through *Mytilus* and *Pecten* to *Ostrea*,' where it is degenerate, 'the second commences with *Unio* and leads to *Venus* and *Scrobicularia*' (Grobben). *Venus* has also rudiments of the gland on the auricles, probably the more primitive form. Concretions are usually to be found in the epithelial cells, which are sometimes ciliated as in *Arca* and *Mytilus*, but not in *Unio*, &c. The first form resembles that found in *Cephalopoda*<sup>1</sup>.

Each ctenidium or gill consists of a longitudinal axis, united for the greater part of its length to the walls of the body but free at its posterior extremity. It contains an afferent and efferent blood-channel, the former bringing blood from the nephridia through which it passes from the median infra-cardiac sinus, the latter conveying it back to the auricles. The ctenidial axis bears two rows of gill-filaments. These are simple and lamellate in *Nucula* and *Yoldia* (*Arcacea*), but are usually more or less tubular, and recurved or bent upon themselves, the outer row externally, the inner row internally. And then either the recurved portion is united to the direct portion by solid interlamellar junctions, and also laterally by interfilamentar ciliary junctions (*Arca Pectunculus*, *Mytilus*), or by the development of solid interfilamentar junctions, the lattice-like structure of the branchia seen in most *Lamellibranchiata* is attained. The recurved portions of the outer row of filaments generally unite with the mantle; of the inner row anteriorly with the body, posteriorly with the corresponding row of the opposite side, but they may be either free or united

<sup>1</sup> Grobben, Z. A. ix. 1886, p. 369.

in the region between. With the development of interlamellar and interfilamentar junctions the blood-channels cease to run for the most part in the filaments but follow the course of the junctions. At the same time the branchial cavity is divided into an infra- and a supra-branchial cavity by the union of the recurved portions of the inner filaments as described above, cf. p. 130, *ante*. The anus lies at the posterior extremity of the supra-branchial cavity, which is continued on into the exhalent siphon when present, the cavity of the inhalent passing into the infra-branchial chamber. The nephridia are always paired, and bent or folded upon themselves. The ducts open externally by well-marked pores, usually placed as in *Anodonta*, (p. 134, cf. Pl. vi.), and the two ducts usually communicate one with another near the external opening. The glandular portion of each organ generally communicates with the pericardium, but the ciliary currents are said to set outwards as a rule. The Oyster differs from other *Lamelli-branchiata* in the structure of the nephridia, see p. 291. The genitalia are paired branched glands terminating in round or cylindrical caeca in which the genital products are formed. The branches are intermingled with the branches of the liver, but may be partially (*Anomia*) or wholly contained in the mantle (*Mytilus*). The ducts open as a rule near the nephridial openings, or into a groove common to the two sets of apertures (*Ostrea*, *Arca*, *Pinna*, &c.), which may be converted (?) into a canal with a small opening (*Pecten*, *Lima*, *Spondylus*). The sexes are separate with few exceptions such as *Ostrea edulis*, *Cardium serratum*, in which male and female products are developed in the same caeca but at different times; or *Pecten*, *Aspergillum*, &c., in which the male and female parts of the gland are more or less separate, but both genital products ripen at the same time and the animals may therefore be self-impregnating. *Cyclas* and *Pisidium* are also hermaphrodite, but it is not certain to which group of the two described they belong. The spermatozoa find their way to the ova either in the water, or, what appears to be generally the case, in the mantle cavity, or in that of the outer gill. In *Kellia*, *Galeomma* and *Montacuta bidentata* the ova develop within the ovary, but it is not certain whether the animals are hermaphrodite and self-impregnating, or the spermatozoa pass up the genital duct. The ovum is enveloped in a membrane, which is sometimes (*Anodon*, *Unio*) a vitelline membrane, or is formed by the superficial hardening of an albuminous layer (*Scrobicularia*). It is attached to the wall of the ovary by a protoplasmic stalk. Hence the membrane is incomplete at this spot, which forms the micropyle when the ovum is detached. The ovum always remains connected with the envelope at the micropyle, but is separated elsewhere by an albuminous layer. Segmentation is unequal. The gastrula is either invaginate or formed by overgrowth. The velum of the Veliger is a circular ridge, and from the centre of the velar area arises a long flagellum. This is wanting in

many marine forms, e.g. *Ostrea*, and the velum itself is in some fresh-water forms reduced (*Anodon*, *Unio*, *Cyclas*) or absent (*Pisidium*). In the case of *Cyclas* and *Pisidium* development takes place in a special brood-pouch which is connected with the root of the inner gill-lamella on each side. The young bivalve appears to be nourished by a clear fluid secreted by the walls of this pouch, as are the young of *Anodon* (and *Unio*?) by a secretion from the gills.

*Pholas* is phosphorescent. The luminous matter is secreted by cells disposed in a band along the anterior edge of the mantle, in two spots at the base of the inhalent siphon and two bands along the same tube.

The *Lamellibranchiata* are mostly marine. They are either fixed or free and they occur associated in numbers. They feed on minute organisms suspended in the currents of water caused by the motion of the cilia, clothing the mantle surfaces, the edges of the gill-lamellae, and the labial tentacles. The living genera *Arca* and *Mytilus* appear in the lower Silurian, and there are large numbers of fossil forms known.

The class may be divided as follows:—

1. *Isomya*. Anterior and posterior adductor muscles of approximately equal size.

(i) *Integripallia*. Marginal attachment of the mantle to the shell not inflected to form a sinus; siphons not developed in some, present in most, e.g. *Arcacea*, *Trigoniacea*, *Unionacea*.

(ii) *Sinupallia*. Marginal attachment of the mantle to the shell inflected so as to form a sinus into which the pallial siphons can be withdrawn; siphons always present and large: e.g. *Myacea*, *Pholadacea*.

2. *Heteromya*. Anterior adductor (pallial adductor) much smaller than the posterior adductor (pedal adductor); siphons rarely present: e.g. *Mytilacea*.

3. *Monomya*. Anterior adductor absent in the adult; siphons never developed: e.g. *Ostreacea*.

For literature, see pp. 127, 131, 133, 138.

*Anomia*, de Lacaze Duthiers, A. Sc. N. (4), ii. 1854. *Aspergillum*, Id. A. Z. Expt. (2), i. 1883. *Mytilus*, Sabatier, A. Sc. N. (6), v. 1877.

*Eye*, Patten, Mitth. Zool. Stat. Naples, vi. 1886, with lit. quoted.

## PHYLUM ARTHROPODA.

*Coelomate Metazoa, with a bilaterally symmetrical body, composed of a series of somites, usually disposed in dissimilar groups; with a pair of hollow-jointed limbs attached to more or fewer of the somites; with a chitinous cuticle, and body-muscles not arranged in continuous layers, and a nervous system composed of a supra-oesophageal ganglion and a ventral chain of ganglia.*

The segmentation of the body is rarely lost. Successive somites are



connected to one another, either by a soft intersegmental membrane or by fusion. The somite itself may be ring-like, or consist of a dorsal plate, the tergum, and a ventral plate, the sternum, connected laterally by a soft pleural membrane, or more rarely by distinct pieces, a dorso-lateral epimeron and ventro-lateral episternum. These last named parts may sometimes be distinguished as regions when the parts of a somite are continuous, e.g. higher *Crustacea*. The tergum may occasionally be broken up secondarily, as in the thoracic somites of *Insecta*.

A head region is nearly always distinguishable. It consists of a prae-oral or pro-cephalic region, to which are fused a variable number of post-oral somites, and it then either remains distinct (*Insecta*, *Myriapoda*) or becomes continuous with a part or the whole of the thorax, forming a cephalo-thorax (*Arachnida*, many *Crustacea*). A thorax is not marked off in the *Myriapoda*. In *Insecta* it consists of three somites; in *Arachnida* it may be considered as consisting of four; in the higher *Crustacea* of eight, and of a variable number in the lower. The somites behind the thorax constitute the abdomen. This region is not specially differentiated in *Myriapoda*, but is clearly distinguishable in the other classes. The number of its somites varies much from class to class, and within the limits of the same class.

The *Insecta*, *Myriapoda*, and *Protracheata* carry upon the head a pair of sensory antennae, which are probably to be regarded as processes of the procephalic lobes, and not as homologous with the remaining appendages. The *Arachnida* possess a pair of prae-oral appendages in the adult, which are post-oral in the embryo. The first antenna of the *Crustacea* is probably post-oral, like the second antenna and remaining appendages. The appendage or limb is composed of a series of articulated joints, and in the *Crustacea* possesses typically a basal portion bearing an external and internal branch (exo- and endo-podite). The muscles moving the joints are contained partly within the limb itself, partly within the somite that carries it. One pair of limbs at least, and usually more, are modified to act as jaws. The external shape of the limb varies much, according to its function.

The body wall is composed of a chitinous cuticle, sometimes thin, sometimes thick and then laminated, and in *Crustacea* hardened by calcareous deposit. It is formed by an underlying and single layer of ectoderm or hypodermis cells. When the animal grows, this cuticle is shed or undergoes ecdysis at stated periods, and at the same time its internal extensions into the stomodaeum, proctodaeum, gland ducts, tracheae, and sometimes the tendons, are shed also. Beneath the hypodermis a thin basement membrane is nearly always to be detected. *Peripatus* (= *Protracheata*) alone has a continuous layer of circular muscles and bands of longitudinal muscles, all of which are non-striated. In

other Arthropoda the muscles are striated, and are disposed in separate fascicles. Ciliated epithelium is universally absent, except, perhaps, in the funnels of the nephridia, &c. of *Peripatus*. The integument is remarkably poor in glands. Connective tissue is variably developed, to the greatest degree, perhaps, in the higher *Crustacea*, in *Scorpio* and *Limulus* among *Arachnida*, and as a fatty tissue in *Insecta*.

The supra-oesophageal ganglion in its simplest form or archi-cerebrum innervates the eyes and special sense-organs of the head, as in the Arachnid *Limulus*. In other Arthropoda (Scorpions?) it is probably always fused with other ganglia, and is a syn-cerebrum. In *Insecta* it gives origin in addition to the nerves of special sense, to the stomato-gastric sympathetic system, and in most *Crustacea* to the nerves of both pairs of antennae (see p. 187) and to the stomato-gastric in part. The ganglia supplying the jaws are fused together into an infra-oesophageal ganglion, and the succeeding ganglia, typically one to each somite, frequently undergo greater or less concentration. Each ganglion consists of a right and left half, which are sometimes distinct, and only connected by transverse commissures (a few *Crustacea*). Successive pairs of ganglia are united by two longitudinal commissures, which may retain their primitive distinctness or become united in one sheath. The structure of the nervous system of *Peripatus* is unique among Arthropoda.

Eyes are confined, with two exceptions, to the head. The cuticle corresponding to the eye is thickened to form *one* or *many* lenses; hence mono- and poly-meniscous. The hypodermic cells beneath the thickened cuticle constitute the *ommateum*, and remain either in a *single* or form a *double* layer; hence mono- or diplo-stichous. The monostichous ommateum is said to be apostatic when cup-shaped, and epistatic when in close contact with the cuticle and following its curvature. In the diplostichous eye the anterior layer forms the vitreous layer. Its cells either retain their regular arrangement or become disposed in groups or vitrellae, which develop a transparent vitreous body. The posterior layer forms the retinal layer; when its cells are collected into groups or retinulae it is said to be retinulate. Each cell in a group generally forms a clear visual rod or rhabdomere. The rods belonging to a group of cells commonly fuse into a rhabdome. The retinal cells are often more or less pigmented. Pigment cells are also present between them, and between the vitrellae. They are derived from the hypodermis, or perhaps in some instances from intrusive mesoblast, hence the eye is auto- or exo-chromic. A mono-meniscous eye may be retinulate. In a polymeniscous eye a single lens-facet, a vitrella, and retinula constitute an 'element,' or the two latter, i.e. vitrella and retinula, an *ommatidium*. The vitreous cells retain the power of forming cuticle, since that structure is shed at each moult over the eye as elsewhere. In the higher *Crustacea*, in *Scutigera* among *Myriapoda*, and

in *Insecta*, there are special optic ganglia in connection with the retinal layer, but external and posterior to it. The eye of *Peripatus* is formed on the Annelidan and Molluscan type, not the Arthropodan<sup>1</sup>. Auditory organs exist in the shape of special hairs in various regions of the body-surface (*Araneidae*, many *Crustacea*, ? *Insecta*), lodged also in the higher *Crustacea* in special depressions or sacs of the cuticle. They also exist as closed vesicles, containing one or more otoliths, in a few *Crustacea* and Insectan larvae. Olfactory and gustatory structures have been described. Tactile hairs connected with nerves occur, at least in *Insecta*.

The digestive tract consists of a stomodaeum and proctodaeum, both lined by cuticle and invaginated from the ectoderm. They are connected by a mesenteron developed from the archenteron. Salivary glands in connection with the stomodaeum occur in *Myriapoda*, *Arachnida*, and to a very limited extent in *Crustacea*. The corresponding glands in *Insecta* belong to the oral cavity, not to the stomodaeum proper. The epithelium of the mesenteron is often partly glandular (*Insecta*), or the external surface carries either villiform glands or larger caeca, which are much branched and of great size in the higher *Arachnida* and *Crustacea*.

The coelome contains the blood and amoeboid blood corpuscles. Circulation of the blood may depend solely in the animal's movements, or

<sup>1</sup> The account in the text follows that given by Professor Lankester and Mr. A. G. Bourne. Patten has quite recently published some investigations on the compound polymeniscous eye of *Crustacea* and *Insecta* which, if confirmed, must considerably alter the conception formed of its structure. See *Mitth. Zool. Stat. Naples*, vi. 1886. His chief results are the following: (1) To each corneal facet coincides a group of two hypodermic cells, sometimes very difficult to detect. These cells are the true homologues of the so-called vitreous cells of the diplostichous eye, e. g. of the Spider. (2) The eye is an ommatium, composed of ommatidia, the constituent cells of which extend from the corneal hypodermis to the fibrous basement membrane. (3) Each ommatidium is made up normally of four retinophoral cells surrounded by several circles of retinulae. (4) The four retinophorae are equal in all respects to one another; their outer ends are expanded into a calyx, which lodges four retinidia (=vitreous bodies, *supra*), one to each cell; and these retinidia are placed axially instead of terminally, as in the Lamellibranch *Arca* and some Arthropoda. They vary much in consistency. The middle portions of the retinophorae are contracted, and fused into a slender hyaline 'style' in which the axial nerve is contained; their basal portions may or may not expand into a 'pedicel.' This pedicel contains transverse striated plates, which appear to act like the argentea and tapetum combined in the eye of *Pecten*. The base of the pedicel contracts and the four retinophoral cells again become separate. There appears, however, to be a closer connection between two of them. (5) The pigmented retinulae bear no rods; the cells of the outermost circle in the region of the calyx are lighter, and contracted basally into bacilli; the cells of the circle surrounding the style or pedicel are darker, and sometimes, if not always, seven in number. They are continued outwards as a hyaline sheath to the calyx. Between the bases of the bacilli and the style or pedicel there may be a number of irregular cells containing highly refractile granules or crystals, soluble in weak hydrate of potash solution, to which they impart a red tinge. Similar crystals may be present in the outermost retinulae. The style or pedicel of the retinophorae coincides with the rhabdome so-called in the text. Patten objects strongly to the terms 'vitellae,' 'retinulate,' 'auto-' and 'exo-chromic.' He believes that the corneal hypodermis is always present, and that the eye of *Peripatus* represents the primitive Arthropodan eye. For the definition of his terms, or of the terms as he uses them, see note, p. 452, *ante*. Points in the structure of the eyes upon which he lays stress are noted under the different classes of Arthropoda. The compound polymeniscous eye occurs also in the Lamellibranch *Arca*.

on rhythmic motions of the intestine (e.g. some *Copepoda* among *Crustacea*). A contractile heart, composed of a single chamber or many chambers, each with its pair of ostia, is generally present, and lies dorsally. The lips of the ostia form internal valves which prevent regurgitation. The heart is always open anteriorly, and, except in *Insecta* and *Myriapoda*, as a rule posteriorly also. The extent to which arterial capillary and venous channels are differentiated varies, but it is slight except in *Myriapoda*, and especially in *Scorpio* and *Limulus*, and the highest *Crustacea*. A pericardial sinus exists in the higher *Crustacea*, *Arachnida*, the *Myriapoda* and *Insecta*. In the three classes last named, it is dilated by a system of segmentally arranged alary muscles, which affect the heart only indirectly. The blood currents flow in constant directions.

Respiration may be cutaneous, i.e. effected by the general surface of the body, in the lower *Crustacea* and *Arachnida*; or branchiate, i.e. effected by processes developed from the surface of the body, or in connection with the limbs, as in most *Crustacea* and some *Arachnida*; or tracheate, and carrying air to all the tissues, as in *Insecta*, *Myriapoda*, most *Arachnida*, and the *Protracheata*. The tracheae are developed as internal growths from the hypodermis, lined by a chitinous cuticle, which is generally crenulated spirally in the tracheal tubes. The simplest form is seen in *Protracheata* as a depression of the integument, from which arises a bundle of tracheal tubes. The structure is much the same in *Myriapoda* *Diplopoda*. But as a rule the tracheal tubes branch and anastomose. The external apertures are known as stigmata. In certain *Arachnida* (e.g. *Scorpio*) the depression is large, and its walls disposed in leaf-like folds, tracheal tubes being absent. Such structures form the so-called lungs or lung-books. The tracheal system may become closed externally in aquatic forms, and then external processes of the integument, variously shaped, may be developed, in which tracheal branches ramify, as in the tracheal gills of some *Insecta*. Air enters and is expelled from the open tracheal system by contractions of the body walls and by diffusion. *Peripatus* has numerous tracheal pits; in other tracheate *Arthropoda* more or fewer of the somites possess each a pair of stigmata, the head alone excepted, on which they are very rarely present. It has been suggested that the tracheae represent modified glands (Moseley).

Excretory organs are present in *Crustacea* as (1) the two shell-glands, (2) the two antennary or green glands, (3) caeca of the mesenteron in *Amphipoda*, or of the proctodaeum in *Squilla*, whilst (4) in some instances the walls of the proctodaeum itself appear to be excretory. In tracheate *Arthropoda* the organs in question are tubular outgrowths of the proctodaeum known as Malpighian tubes, varying in number, shape, &c. Uric acid appears to be constantly found among the excretory products<sup>1</sup>.

<sup>1</sup> The coxal glands of *Arachnida* are possibly aborted excretory organs.

Arthropoda are very rarely hermaphrodite. The male is generally distinguished from the female by differences of size, colour, by the large development of special sense organs, or of copulatory and prehensile organs. The form of the testis and ovary is subject to much variation. The glands are typically paired, but the members of the pair may be fused. The ducts are also paired, but may fuse distally, and the sexual apertures are accordingly paired or single. They are placed in the thorax or abdomen, and are sometimes terminal. Accessory organs are frequently present, but vary in the different classes. The spermatozoa are commonly united into spermatophores by the secretion of the walls of the vasa deferentia, or of special glands. The ova vary in size. Secondary yolk is generally present, and is placed centrally (centro-lecithal ova). When the ovum segments, fission is consequently on the centro-lecithal type, and either regular, unequal, or superficial. But there are exceptions. Regular segmentation, with completely separate blastomeres, occurs in *Podura* among *Insecta*, and in the lower *Crustacea*, rarely in the higher. Telo-lecithal ova, with partial segmentation, are found in some *Crustacea* (parasitic *Copepoda*, *Isopoda*, *Mysis*) and in the Arachnid *Scorpio*, but it is possible that they are modified from the centro-lecithal type. In development, certain differences are observable between the *Crustacea* and tracheate Arthropoda, which make it possible that they may form two distinct phyla, or branches of a phylum which separated at a very early period (?). In the *Crustacea* the archenteron is usually and primitively invaginate; the mesoblast originates from the wall of the invagination, and forms a layer between the epi- and hypo-blast; the proctodaeum is formed before the stomodaeum, and these two parts are usually of great relative length as compared with the mesenteron. In tracheate Arthropoda the archenteron is not invaginated, and the mesenteron is derived from the yolk-cells; the mesoblast develops as a median thickening of the ventral plate, which divides into two bands. These bands in Spiders and *Myriapoda*, and perhaps in *Insecta*, divide into somites, with cavities continued into the limbs. The stomodaeum develops before the proctodaeum, and the mesenteron is relatively large. The proctodaeum gives origin to the Malpighian tubes. In the tracheate Arthropoda and higher *Crustacea*, a thickening of the blastoderm gives rise to a ventral plate, by the growth of which the body is subsequently formed. In the *Insecta*, and perhaps *Myriapoda*, this plate is marked by a median longitudinal mesoblastic groove, or by a keel-like thickening in Spiders. Groove and thickening alike are generally termed 'primitive streak,' and, like the structure so-called in Vertebrata, are probably the remnants of a blastopore.

Parthenogenesis occurs in some *Insecta* and *Crustacea*, and leads to a form of Alternation of Generations known as Heterogamy. Sexual dimorphism is very common in the two classes named. Some *Crustacea*

possess the power of casting off limbs ; all reproduce them when injured. A similar reproduction has been observed in some *Insecta*, *Myriapoda*, and Spiders. Mimicry of colour and shape is frequent, and in some *Crustacea* the expansion and contraction of pigment cells (chromatophores) may assimilate the tint of the organism to its surroundings. The life-history of a Crustacean is primarily, of an Insect secondarily, connected with a metamorphosis. In the higher *Crustacea* the metamorphosis becomes restricted or lost, in the higher *Insecta* more pronounced. There are but slight indications of similar changes in the other classes. Degraded forms, with regressive metamorphosis, are found e.g. in many parasitic *Copepoda* among *Crustacea*, *Linguatulina* among *Arachnida*.

There are five classes of Arthropoda usually recognised, the *Insecta* s. *Hexapoda*, the *Myriapoda*, the *Protracheata*, the *Arachnida*, and *Crustacea*, to which must be certainly added, as an independent group, the *Pycnogonidae* s. *Pantopoda*. The *Insecta* may perhaps have some relationship with the *Myriapoda* through the genus *Scolopendrella*. The class *Protracheata*, represented by the genus *Peripatus*, stands quite alone. But the three classes first-named agree together, and differ from the two last in having praeoral cephalic processes or antennae. The praeorally placed appendages of *Arachnida* and *Crustacea* appear to be postoral limbs, which have acquired a secondary praeoral position. It has been proposed in consequence to unite them under the common term *Acerata*. The majority of *Arachnida* are tracheate, and by some authorities the *Insecta*, *Myriapoda*, *Protracheata*, and *Arachnida* are therefore grouped together as *Tracheata*. But it does not appear certain that the tracheae of the four classes in question are homologous structures, and the *Arachnida*, as given below, include certain branchiate forms, viz. *Limulus*, and the extinct *Eurypterina* and *Trilobita*. The young *Limulus* has a singular resemblance to the extinct *Prestwichia*. Many *Trilobita* have a similar larval form, and it is possible that the Scorpions and *Eurypterina* may be traced back to the same type. There are however certain sub-groups the position of which is exceedingly doubtful. These are the *Linguatulina*, the *Tardigrada*, and *Acarina*. They are generally classed among *Arachnida*, and are retained in that position here. It is possible, however, that they may have to be separated, and this is especially the case with the *Acarina*, which are placed apart by Haller in a Class, *Acaroidea*.

There are many interesting points relative to the connection of the classes of Arthropoda and certain of their sub-groups which cannot be discussed in a short compass. Reference must be made to the authorities cited below.

Haller gives the following characters for the class *Acaroidea* (Z. A. iv. 1881, p. 386): "Wingless Arthropoda, usually of small size, respiring partly through the integument, partly by tracheae. Cephalothorax and abdomen as a rule indis-

tinguishably fused, seldom clearly separate, the line of division being usually indicated by a furrow. Each principal division of the body provided with two well-developed pairs of limbs. There are three pairs of jaws with a rudimentary upper lip and large under lip. The first pair of maxillae palpate, the second pair often rudimentary. The larva is hexapodous, the post-embryonal development frequently interrupted by a Deutovum stage.' Haller makes two orders, (1) '*Acarina atracheata*, Mites devoid of tracheae, respiring through the integument;' and (2) '*A. tracheata*, Mites provided with tracheae at least in the adult condition.'

It remains to be seen whether Haller's conclusions meet with acceptance and confirmation. The cuticular membranes cast off by some Mites in the course of development, and characteristic of the Deutovum and Tritovum stages, are by no means always developed. But if the mouth-parts really consist of three pairs, mandibles, first and second maxillae, and a palpate lower lip which represents a fourth pair of metamorphosed appendages, together with four pairs of limbs, then a Mite possesses two pairs of appendages not present in the adult Spider. But it should be borne in mind that there are in Spiders aborted embryonic limbs behind the last pair of legs, and the Scorpion actually retains two additional pairs in the genital operculum and pectinate appendages. See table, pp. 174-5. The *Acarina* might be regarded as a group of *Arachnida* with two additional pairs of limbs converted into mouth-parts, just as in the branchiate *Arachnida* there are five pairs of limbs in relation with the mouth in *Limulus*, four pairs in *Eurypterina* and *Trilobita*. Oudemans states that the fourth pair of ambulatory limbs is intercalated in the *Oribatiidae*, between the first and second pairs of limbs of the hexapod larva. Such a fact rather points to the conclusion that the hexapod stage has been secondarily acquired by the temporary suppression of a somite.

*Affinities of Arthropoda*, Kingsley, Q. J. M. xxv. 1885, p. 556 et seqq.; Oudemans, Tijdschrift der Nederland. Dierk. Vereen. (2), i. 1885, p. 37.

*Phylogeny of Arthropoda*, Balfour, Comp. Embryology, i. p. 451.

*Acaroidea*, Haller, Z. A. iv. 1881, p. 380.

*Eyes of Arthropoda*, Patten, Mitth. Zool. Stat. Naples, vi. 1886; Ray Lankester and A. G. Bourne, Q. J. M. xxiii. 1883.

## CLASS INSECTA.

### (Hexapoda.)

*Tracheate Arthropoda with the body divided into three regions, a head, thorax, and abdomen. The head carries a pair of antennae and three pairs of oral appendages, the thorax three pairs of jointed locomotor appendages, and in most instances one or two pairs of wings. Abdominal limbs are rarely present.*

The head shows no trace of segmentation and is sharply marked off from the thorax, to which it is moveably connected by a neck in the imago. It is also generally distinct in the larva except in some *Diptera*. The thorax consists of a pro-, meso-, and meta-thorax. The pro-thorax may be free, e.g. *Coleoptera*, many *Rhynchota*, but as a rule the three

somites are firmly united. The pro-thorax is generally small, the meso- and meta-thorax either equal in size or one larger than the other, the variations depending on the peculiarities, &c. of the wings. The thoracic somites, especially the meso- and meta-thorax, are rarely ring-like (*Apterygogenea*), but have well-developed tergal and pleural regions. The sternal region varies much in size. The abdomen consists typically of eleven somites, but the number may be reduced in certain groups, e.g. to ten in *Lepidoptera* &c., to nine or eight in many *Diptera*. The successive somites are connected by soft intersegmental membranes, which admit of contraction and expansion of the abdomen in respiration and of its distension by the sexual products. Each somite of the abdomen may have the form of a ring (*Apterygogenea*; *Plecoptera*), or may have a firm tergal and sternal plate connected laterally by soft pleural membranes. The shape of the abdomen varies much. The first somite may remain independent, e.g. *Dermoptera*, *Ephemeridae*, or it may lose its sternal plate whilst the tergal plate becomes connected to the meta-thorax, e.g. *Coleoptera*, *Trichoptera*, a change that may extend to more or fewer of the following somites. In *Hymenoptera* with a pedunculate abdomen the peduncle is formed by the contracted second, or second and third somites. The meta-thorax in *Macro-Lepidoptera*, *Diptera*, and *Rhynchota Homoptera* is so closely united to the first abdominal somite that in most instances it appears to be a portion of it, the meso-thorax being very large.

The head bears the antennae, mandibles, maxillae, labium or second maxillae. The antennae, processes as in *Myriapoda* of the procephalic lobes and not appendages, are borne on the margin of the head in front of the eyes in more primitive forms, or upon the vertex, i.e. summit of the head. They are jointed, and their length, shape, and other secondary characters are very variable. They lodge peculiar nerve-endings and appear to be olfactory in function. The mouth-parts may be similar in all stages of life and then either adapted for biting (*Menognatha*) or for sucking (*Menorhyncha*), or else in the larva they are adapted for biting, in the imago for sucking (*Metagnatha*), the change commencing in the pupal, and rarely affecting the larval, stage. The mandibles are one-jointed and never possess a palp, and are furnished in biting insects with a variously conformed biting or masticatory surface, whilst in sucking insects they may be reduced to a pair of stilets (i.e. are setaceous), e.g. *Rhynchota*, become rudimentary as in many *Diptera*, or even completely lost as in *Lepidoptera* with rare exceptions (see p. 150). The maxillae have a complicated structure when fully developed as in biting insects (see p. 140), and are provided with jointed palpi<sup>1</sup>. The two galeae are lengthened out, and

<sup>1</sup> Cf. Beauregard on Vesicant Insects, *Journal de l'Anat. and Physiol.* xxii. 1886, p. 95 et seqq.



each one forms one half of the antlia in *Lepidoptera*. In other sucking insects the maxillae may be reduced to stilets, e. g. *Rhynchota*, may be lost as in some *Diptera*, their palpi being either lost or preserved. The labium is formed from the second pair of maxillae. The basal joints of the limbs are united invariably, but the remaining parts may be more or less completely retained or lost. It possesses jointed labial palpi rarely absent. In the *Rhynchota* it is modified into a four-jointed tube containing the mandibles and maxillae. An upper lip or labrum, the nature of which is not quite certain, forms a chitinoid plate well-developed in typical biting insects, and lies transversely in front of the oral cavity in continuity with the head. It usually bears on its oral surface an internal process or epipharynx. The oral surface of the base of the labium also bears an internal process or hypopharynx, beneath which the ducts of the labial salivary glands open. The labrum and hypopharynx are produced into stilets in some *Diptera*, and the fleshy proboscis of certain members of this group (e. g. *Muscidae*) is formed from the hypopharynx and exterior surface of the labium. Varieties of detail in the structure of the mouth-parts are very numerous.

The mouth-parts are attached to the head by articulation as well as by muscles. In the *Collembola* (*Apterygogenea*) as in *Scolopendrella* (see p. 519) the mouth-parts, mandibles as well as maxillae, are retracted within the head. They project from the head in other Insecta either *forwards* in a direction prolonging the axis through the so-called occipital foramen, or *downwards* in a direction at right angles to it. The insect in the first case is said to be ortho- or pro-gnath, in the second hypo-gnath, and the distinction applies equally to larva and imago.

The thoracic limbs consist typically of a coxa, trochanter, femur, tibia, and tarsus. The trochanter may be subdivided into two parts or fused with the femur. The tibia is often armed with spines or calcaria, and the tarsus is composed of a series of joints, usually not more than five in number. The terminal joint bears two bent hooks or claws, between which are often lodged one, two, or three membranous pads or pulvilli. Hairs often clothe the under surface of the tarsal joints, and in jumping and climbing Insects certain of them are connected to glands and exude a sticky fluid. The form, size, &c. of the limbs depend upon the mode of locomotion of the insect, e. g. running, swimming, jumping, &c. In addition to limbs the meso- and meta-thorax in the majority of Insecta give origin dorsally to wings. The *Thysanura* and *Collembola* appear to represent a primitive group of Insecta in which wings have never been developed; hence *Insecta Apterygogenea*. Other Insecta may be designated *Pterygogenea*, and wingless forms such as the *Mallophaga*, *Siphonaptera*, &c. must be regarded as having lost their wings. The wings themselves are primarily thin membranous expansions composed of two membranes,

an upper and lower, originally separate; narrow at the base, where they are attached and supported by veins or nervures, spreading from the base in the thin membrane and dividing it into areae or cells of various shape and size and often characteristic pattern, hence reticulate (minutely divided); areolate (with largish cells). The veins are essentially thickenings of the two layers of membrane, in which (or in the larger of which) are lodged tracheae, nerves and tubular extensions of the coelome in which blood circulates. There is much variety in the shape, texture, clothing with hairs or scales, &c. of the wings. The two pairs when both are membranous may be alike in size and shape, e. g. most *Homoptera* among *Rhynchota*, or unlike, e. g. *Lepidoptera*. They may be retained in a flat expanded condition, e. g. *Odonata*, or may be folded longitudinally, e. g. hind wings of *Orthoptera*, and transversely as well, e. g. in the hind wings of *Dermaptera* and *Coleoptera*. The fore and hind wings may be connected together by retinacula, either a series of hooklets on the fore-edge of the hind wings in *Hymenoptera*, or a hook and bristle with a bundle of stout hairs in many *Lepidoptera*. The fore wings may be converted into wing covers for the hind wings and are then more or less tough and coriaceous as in the hemi-elytra of *Dermaptera* and elytra of *Coleoptera*; or the change of texture may affect the base only of the wing as in *Rhynchota Heteroptera*. The fore wings are represented by slender contorted processes in *Strepsiptera* among *Coleoptera* (see p. 511 note), and the hind wings into balancers=halteres in *Diptera*. The wings are absent in the larva and are formed during growth, and in *Metabola* (see *infra*, p. 508) make their appearance in the pupa stage.

The abdomen of the imago is limbless as a rule. Ventral processes however which appear to be the homologues of limbs are found on more or fewer of the somites in the *Thysanura* (*Apterygogenea*). And the cerci anales or cercopoda, a pair of jointed processes attached to the last somite in some Insecta, e. g. *Orthoptera*, are perhaps to be regarded in the same light. These cerci are transformed in *Dermaptera* into the anal forceps. Rudimentary abdominal limbs are found in the embryos of many Insecta, and may persist as 'prolegs' in the cruciform larva, on all the somites as in *Panorpa*, on eight somites as a maximum in the *Tenthredinidae* among *Hymenoptera*, or on five somites as a maximum in *Lepidoptera*. A pair of processes which appears on the ventral aspect of the seventh (or eighth) somite and two pairs similarly placed on the eighth (or ninth) are developed during growth in the female in many groups, and form either the ovipositor, or in aculeate *Hymenoptera* the sting. In the male, two (*Aeschna* among *Odonata*) or three pairs of processes are similarly developed from the ninth or tenth somite and become copulatory organs. These processes are commonly regarded as modified limbs, but the homology is doubtful (see p. 300). The limb-like processes developed

in Dipterous larvae are regarded by Brauer as *secondary* structures and not as homologues of true appendages.

The chitinoid cuticle is generally firm, but its texture varies in different orders and in different stages of life. Copper has been detected in it in *Coleoptera*. Calcareous hardening is rare. It is more or less marked by hexagonal areae and by various sculpturings (dots, pits, lines, &c.). It is frequently covered with hairs, and scales placed above fine pores. Tactile hairs of different shapes, connected basally with a cell and a nerve, are found on the integument of various soft-bodied and aquatic larvae and in certain parts of the imago, e.g. on the antennae, palpi of maxillae and labium, wings, halteres, tarsi. Thin spots of the cuticle with underlying cells in connection with nerves are found also on the palpi. Integumental glands are not common, but are found in various regions of the body, e.g. scent-producing glands sometimes connected with hairs; wax-producing glands distributed over the body, e.g. in certain *Aphidae* and *Coccidae* (*Homoptera*), or confined to the ventral surface of the abdomen in *Apis*; poison glands in connection with the sting in Aculeate *Hymenoptera* (Bees, Wasps, Ants), or with hairs as in some Lepidopterous Caterpillars, &c.

The supra-oesophageal ganglion supplies the antennae and eyes. It has a complicated structure in the imago, especially in the higher orders e.g. *Hymenoptera*. The infra-oesophageal ganglion innervates the oral appendages, glands of the mouth, &c., and represents at least three ganglia fused. The ventral chain consists of a series of ganglia. The last probably always represents two even in primitive forms with the ganglia separate, a condition most generally found in the eruciform larva. Fusion may take place between the meso- and meta-thoracic ganglia, between some or all the abdominal ganglia which may then become placed in the thorax (*Heteroptera*, some *Diptera*); but it is rare for the infra-oesophageal ganglion to unite with the fused thoracic and abdominal ganglia, as in the parasitic *Pupipara* among *Diptera*. The nervous system of the larva may be more or less concentrated and little differentiated, and may become less concentrated and more differentiated in the imago, e.g. *Musca*, *Myrmeleo*. As a rule however the imago possesses in the *Metabola* a more concentrated and specialised nervous system than the larva. There is a stomatogastric sympathetic system divisible into an azygos portion and a paired portion, conformed much as in the Cockroach (see p. 142-3) and derived from the supra-oesophageal ganglion. A respiratory sympathetic system regulating the closure of the stigmata, &c. originates from a nerve in relation with the dorsal aspect of the ventral chain (p. 149).

Few Insecta are blind, e.g. some subterranean and cave insects, &c. and some larvae. Eyes are restricted to the head and occur in two forms, the monomeniscous ocellus and the polymeniscous or so-called compound

eye. The ocellus is found in the larvae of orders with complete metamorphosis (*Metabola*) and the larval *Ephemeridae*, and in addition to faceted eyes in the imago of some orders, e.g. *Hymenoptera*, though wanting in others, e.g. *Dermoptera*. It is the only kind of eye present in *Collembola*, the *Pediculidae*, and *Siphonaptera*. The compound eye is present in the imago of all groups with the exceptions just named and in the larvae of *Ametabola* and *Hemimetabola* except *Ephemeridae*, though it may differ in detail from that of the imago. The number of ocelli present is not constant, but in the imago there are usually three. Of the polymeniscous eyes there are two, one on each side of the head. They vary much in size, are sub-divided in some Lamellicorn *Coleoptera* into two, e.g. in *Geotrupes*. So too in the male *Chloëon* (*Ephemeridae*), in which they are slightly stalked, especially the median halves. The ommateum of the ocellus is variably conformed. In the larval *Dytiscus* and *Acilius* (*Coleoptera*) it is monostichous and apostatic. The visual (retinal) cells possess visual rods at their inner ends, and the surrounding cells are pigmented at their peripheral ends, hyaline at their inner ends, which bend inwards horizontally over the visual cells. The structure requires examination in other larvae. In the ocellus of the imago the ommateum is diplostichous, the vitreous cells are generally small and flat, and the rods of the visual cells composed of two refractile plates covering the anterior (or inner) fourth of the cell. The shape and size of the lenses in the polymeniscous eye vary even sometimes in one and the same eye, e.g. in *Odonata*. The vitreous cells either persist in a uniform layer (the *acone* eyes of *Coleoptera* minus *Pentamera*, *Rhynchota*, *Tipularidae* among *Diptera*, *Dermoptera*), or are grouped into fours forming vitrellae, and then (1) surround a clear fluid or gelatinous cone (the *pseudocone* eyes of *Diptera Brachyura*, e.g. *Musca*), or (2) are reduced to feeble remnants inclosing a solid crystalline cone composed of 2-5 parts, the *eucone* eyes of other Insecta, including *Lepisma*. The visual cells are grouped to the number of seven into retinulae. In *acone* eyes one cell stands in the centre with the six others around, and the visual rods or rhabdomeres are contained one in each cell. In *pseudocone* and *eucone* eyes the seven cells are grouped round a central axis. The rhabdomeres in the former coalesce only anteriorly, in the latter throughout their whole length, into a rhabdome. Pigment cells lie between the vitrellae and retinulae separating the ommatidia from each other. So far as observations go the compound eye is autochromic. There are as a rule two optic ganglia, a peripheral and a central. Details vary much<sup>1</sup>. Auditory organs

<sup>1</sup> Patten draws attention to the following points (Mitth. Zool. Stat. Naples, vi. 1886): (1) As to the ocellus of the imago. The vitreous cells are, properly speaking, corneal hypodermis cells; the retinophorae are terminal; and the layer of visual cells is a retineum in which the retinidia of the retinophorae form a continuous layer. (2) As to the compound eye. It has the typical structure detailed in note, p. 452. In *Mantis religiosa*, the type which he examined, the retinidia = crystalline

appear to occur in two forms: (1) as vesicles containing some clear floating globules, found only in some *Diptera* in the posterior region of the abdomen in the larvae (*Tabanus*, &c.), or in the basal joint of the antennae of the imago; (2) as the chordotonal organs. The essential structure of these organs consists of a nerve ending in a ganglion, the cells of which are provided with terminal processes or end-organs, composed each of a terminal rod ('Endstift') variously conformed and inclosed within a sheath or 'scolopophore.' The end-organs are either connected directly to the hypodermis or indirectly by a lateral filament. They appear to occur in the larva as well as the imago, and in all orders of Insecta except *Thysanoptera*, where they have not been detected. They are found in groups of 2-200 in various parts of the body, antennae, palpi, legs, wings, in the halteres of *Diptera*, and upon the dorsal aspect of the abdomen. Among the *Orthoptera*, they are connected in *Acrididae* with a thin membrane, of which there are two, one on each side of the first abdominal somite; and in *Locustidae* and *Gryllidae* they lie in a special pit under a thin membrane on each side of the proximal ends of the tibiae of the fore limbs. The main trachea of the limb is dilated between the two organs. Cells furnished with a pointed projecting rod, and connected to a nerve, are found in various Insecta on the antennae, and on the palpi, and in various parts of the oral cavity, e.g. in the Bee. In the first two instances they are supposed to be olfactory, in the third gustatory in function.

Salivary glands, varying in shape, number, and structure, open into the oral cavity, the most important pair belonging to the labium. They appear to be developed close to the mandibles and *not* from the stomodaeum. Silk glands or sericteria open on the labium in the larvae of *Lepidoptera* and the *Tenthredinidae*, &c. among *Hymenoptera*. They are developed close to the inner side of the labial limbs. The oral cavity is closed in the larvae of *Dytiscus* and of *Megaloptera* among *Neuroptera* (e.g. *Myrmeleo*, *Chrysopa*) which suck up the juices of their prey through the perforated mandibles, in the imago of *Ephemeridae* and male *Coccidae* and *Aphidae*. In the last-named family, the male and perfect female *Phylloxera* are stated to want the digestive tract. The stomodaeum varies in complexity. It may dilate into a crop and the muscular walls of its posterior part become much thickened and the chitinous lining ridged and toothed, forming a gizzard (*Orthoptera*, some *Coleoptera*, &c.). It may be provided with a dilatation or so-called sucking stomach, attached by

cones are fluid, and the style (=rhabdome) of the four retinophoral cells does not expand into a basal pedicel. This last-named structure is perhaps more or less characteristic of nocturnal Insecta. The red light which is reflected outwards from it, is especially well seen in Moths. It is evident that Grenacher's acone eyes in particular will require re-examination in the light of Patten's researches.

a longer or shorter peduncle (imago of *Lepidoptera*, *Diptera*, many *Neuroptera*). The stomodaeal section is usually straight and traverses the thorax. The mesenteron and proctodaeum lie in the abdomen in the imago and are more or less convoluted, the coils being held in position by tracheae, fatty tissue, and nerves. The mesenteron or chylific stomach varies in length. Its anterior extremity may develop a few caecal tubes (many *Orthoptera*, *Plecoptera*). Its epithelium contains glandular cells, and its outer surface is sometimes beset with villiform glands (some *Coleoptera*). The proctodaeum does not communicate with the mesenteron in the larvae of aculeate *Hymenoptera*, some *Neuroptera* (*Myrmeleo*, *Hemorobiidae*), and *Pupipara* among *Diptera*. In the *Neuroptera* named it forms a silk gland. It is generally of some length and its calibre varies in different regions. The short posterior dilated section or rectum is generally, especially in the imago, provided with 2-6 longitudinal ridges richly supplied with tracheae. These ridges become of functional respiratory importance in the larval *Odonata*, in which water is taken into and expelled from the rectum rhythmically. The anus is terminal in the last abdominal somite.

Excretory organs or Malpighian tubes open into the commencement of the proctodaeum, rarely into the end of the mesenteron as in *Thysanura*, *Termes*, &c. They arise from the proctodaeum as one or two pairs of outgrowths, but their number may be subsequently increased by budding. The full number present may be small (2-8) or large (30-50 or more, e. g. 150 in *Apis*). Hence Insecta may be designated as *Oligo-* or *Poly-nephria*. They may branch, and they open into the proctodaeum separately or united in bundles with a common aperture.

The coelome is more or less filled by the viscera and fat-body when present. The latter is always plentiful in the larva, and persists to a variable degree in the imago. It is a tissue composed of fat-containing cells richly supplied with tracheae. The blood is colourless or yellowish, tinged with green in vegetable-feeders, or sometimes reddish. In the larva of *Chironomus* (*Diptera*) it is deeply coloured with Haemoglobin. The blood corpuscles are amoeboid<sup>1</sup>. The heart is placed dorsally in the abdomen. It consists in the imago usually of eight chambers with lateral valved ostia. The anterior end gives off an aortic trunk which extends to the head. The posterior end is closed, and but rarely gives off vessels. The organ is suspended by muscular filaments to the terga, and lies in a pericardial sinus limited ventrally by the alary muscles, the contraction

<sup>1</sup> Von Wielowiejski distinguishes three types of blood-cells in Insecta. (1) Fatty cells, constituting the fat body; they are grouped together, are rarely bi- or multi-nuclear, and their protoplasm is filled with fat drops. (2) Oenocyths, multi-nucleate cells with slightly coloured protoplasm and containing but few granules, tied to the smallest tracheal capillaries. (3) Pericardial cells, which differ much in character but are known by their position in the pericardial system. Z. W. Z. xliii. 1886.

of which dilates the sinus and affects the heart indirectly. The sinus is partially filled by pericardial cells and connective tissue, and the blood enters it between the alary muscles. There is a ventral sinus of similar structure and similarly pulsatile; open in front and behind, and lodging the nerve-chain.

Respiration is tracheal. The majority of Insecta are holopneustic, i. e. possess open stigmata. Each stigma leads into a single tracheal stem, rarely into several. A pair of stigmata lie in the head (? prothorax) of *Smyntaurus* (*Collembola*), and there are in the embryo Lepidopteron three pairs in the same region. Otherwise stigmata are restricted to the thorax and abdomen. The latter possesses eight pair as a maximum, but the number may be reduced. There may be a pair on the prothorax, e. g. *Lepidoptera*, Coleopterous larvae; a pair on the meso- and meta-thorax, e. g. *Hymenoptera*; or on the pro- and meta-thorax, rarely on all three (*Siphonaptera*). The stigmata lie in the thorax above the base of the limbs, in the abdomen, either in the soft pleural membrane or between successive somites, and are either freely exposed or concealed, e. g. by the elytra in *Coleoptera*, or the overlap of the somites in *Hymenoptera*. In various aquatic larvae and some imagines of *Heteroptera*, e. g. *Nepa*, there is a posterior pair of stigmata to which air is brought by a simple or split tube. The stigmatic aperture consists either of a simple slit with a surrounding chitinous ring (e. g. *Heteroptera*); or of a number of apertures leading into a common tracheal stem (Dipterous larvae and pupae); or it is provided with more or less prominent lips, and may then be protected by hairs, e. g. *Coleoptera*, *Lepidoptera*. The commencement of the trachea is closed by a special apparatus of chitinous structures and muscles controlled by the nervous system. The tracheae are frequently connected close to their origin from the stigma by lateral longitudinal trunks; they branch and anastomose, and the finest branches are distributed to the muscles, nerves and other viscera. In insects of great powers of flight the branches have vesicular dilatations. The system of tubes is lined throughout by a chitinoid membrane, plain in the dilatations, crenulated spirally in the tubular portions<sup>1</sup>. The crenulations disappear in the ultimate tracheal capillaries, which either end in certain cells contained in the coelome or in the investing membranes of the muscles and other organs. When the tracheal system becomes completely closed, the Insect is said to be apneustic (larvae of *Ephemeridae*, most *Odonata*,

<sup>1</sup> Packard states (Amer. Naturalist, xx. 1886, p. 440) that the spiral appearance is deceptive. The apparent spiral lines or 'taenidia' of the tracheal membrane ('endotrachea') are due to the fact that the outer cell layer ('ectotrachea') proliferates during the formation of the tracheal tube, and forms an inner layer of endotracheal cells (or nuclei?). These inner cells lengthen out into parallel band-like processes which unite laterally, constituting the lining intima. The median portion of each band persists as a taenidium.

of the *Plecoptera*, *Trichoptera*, and of *Corethra* among *Diptera*). In this case the rectum is respiratory (*Odonata*); see *supra*. Or leaf-like processes are appended to the end of the abdomen (*Agrionida*, among *Odonata*); or similar leaf-like, filamentous, or tufted processes are attached laterally to more or fewer of the abdominal somites (*Ephemeridae*, *Calopterygidae* among *Odonata*, *Trichoptera*, *Sialidae* among *Neuroptera*); or to the thorax (*Plecoptera*), and then they are often retained by the imago side by side with the stigmata<sup>1</sup>. These *tracheal gills* rise close to the rudiments of the stigmata, which appear to be always present. There is a longitudinal tracheal trunk from which tracheae pass off to the gills on one side, the viscera on the other. The condition of an apneustic insect has been secondarily acquired.

The sexes are separate. Hermaphroditism when it occurs is due only to malformation. The male differs in size, shape, &c. from the female. The genital rudiments develop into a series of ovarian tubes s. ovarioles, or testes. The latter are very variable in number and shape, and the same statement is true also of the ovarian tubes. The anterior extremities of the ovarioles are prolonged into filaments, the filaments belonging to one side unite, and the common filament thus formed is attached to the dorsal aspect of the abdomen or thorax. There are two oviducts and two vasa deferentia. The latter sometimes dilate to form vesiculae seminales. In the *Ephemeridae* the two male or female ducts open separately, the former on the ninth abdominal somite in connection with one or two copulatory organs, the latter between the seventh and eighth somites, on the ventral aspect. The male ducts are similarly arranged in *Dermoptera*, but in the genus *Forficula* the terminal portion of one duct alone persists. In other Insecta the external genital apertures are single, and there is an azygos portion invaginated from the integument constituting the vagina in the female, or ductus ejaculatorius in the male, the terminal portion of which is generally an intromittent organ. Accessory female organs in connection with the vagina are the bursa copulatrix and seminal receptacle, and other glands by which the ova are fixed to some foreign object or enveloped in a cocoon or case. The male possesses glands which unite the spermatozoa into spermatophores as well as others of unknown function. The female aperture lies either between the seventh and eighth or in the eighth somite of the abdomen; the male aperture in the ninth or tenth. In *Lepidoptera* the oviduct opens on the same papilla as the anus, but the entrance to the bursa copulatrix is in its normal position on the eighth somite. The two structures are connected internally (see p. 160). The male copulatory organ in *Odonata* is placed upon the second abdominal somite, and therefore far in front of the sexual aperture. For the ovipositor see p. 500.

<sup>1</sup> Two branchiate Lepidopterous larvae are known.



The ovum is invested in a tough shell or chorion produced by the epithelium of the ovarian tube. This chorion is pierced by at least one pore or micropyle through which the spermatozoon enters as the ovum passes down the vagina. A fold of the blastoderm over the ventral plate gives origin in the majority of Insecta to two embryonic membranes, an outer *serous* envelope and an inner amnion.

A few Insecta are viviparous. The *Tachinae*, some *Oestridae* among *Diptera*, some *Staphylinidae* among *Coleoptera*, the *Strepsiptera* (note p. 511) produce larvae; the *Pupipara* among *Diptera* pupae which are nourished in the larval condition by a special gland; and certain generations of *Aphidae* among *Homoptera*, young which closely resemble the parent. Parthenogenesis occurs normally among certain groups, and then the female possesses either complete sexual organs (*Psyche*, *Solenobia* (two sp.) among *Lepidoptera*; *Coccidae* among *Homoptera*; certain *Cynipidae*<sup>1</sup>, and *Tenthredinidae* among *Hymenoptera*; *Gastrophysa Raphani* among *Coleoptera*<sup>1</sup>), or the ovaria and ducts are perfect but accessory organs wanting (*Aphidae* among *Homoptera*). Voluntary parthenogenesis occurs in the queen Bees, Humble Bees, and Wasps, among *Hymenoptera*; occasional parthenogenesis among *Lepidoptera*, as also in the worker Bee, Wasp and Ant which are dimorphic females with rudimentary ovaria and ducts. The offspring produced are of the male sex in the Bees, Wasps (and Ants?); of the female in *Psyche*, *Solenobia*, *Coccidae*, *Aphidae* and *Cynipidae*, but males make their appearance at last. In some *Tenthredinidae* the offspring belong to the male sex, in others to the female, whilst in others again the brood is mixed male and female. The parthenogenetic *Aphidae* except *Chermes* and *Phylloxera* are viviparous. In the *Cynipidae* there is as a rule only one such generation, but many in *Aphidae*, *Coccidae*, *Psyche* and *Solenobia*. Paedogenesis or the production of ova by the immature animal is rare, and is in Insecta always parthenogenetic. In the larvae of certain *Diptera* (*Heteropeza*, *Miastor*) the cells of the genital rudiment develop into larvae which feed on the parent and burst their way out through the cuticle; and the pupa of a *Chironomus* (*Diptera*) produces ova at a very early period which are laid just before or as soon as the imago becomes free. The *Strepsiptera* are said by Von Siebold to afford another instance of its occurrence.

The Insect at birth is always minute in size. Growth is accompanied by moults or ecdyses, and in many instances by changes, variable in degree, in the structure of the antennae, eyes, mouth-parts, body-somites, and internal organs, making a metamorphosis more or less complete. Accordingly Insecta may be described as *Ametabola*, *Hemimetabola*, and *Metabola* (or *Holo-metabola*<sup>2</sup>). In the *Ametabola*, the young insect or

<sup>1</sup> It is not stated if the organs are complete in these instances.

<sup>2</sup> These terms are defined here in a sense which differs somewhat from that generally given to

larva resembles its parent in most respects, except in the number of antennal joints, of facets in the eye, absence of wings, and want of maturity of the sexual organs. In the *Hemi-metabola*, the larva may differ notably from the adult in the structure of the antennae, eyes, mouth-parts, shape and disposition of the body-somites, especially the thorax, as well as in the absence of wings and in internal structure. It is aquatic and possesses special contrivances for respiration. The characters of the adult may be acquired gradually or quickly. In the *Metabola*, three well-marked stages are distinguishable, larva, nymph or pupa, and imago. The larva may be Campodeiform, or eruciform (see p. 150), with or without limbs; its antennae differ much from those of the adult; its eyes are ocelli; its mouth-parts may be similar (not identical) or very dissimilar to those of the adult. It passes into a pupa-stage, which becomes the imago in one, rarely in two moults. The pupa is quiescent for the whole or part of its existence (p. 152), and profound changes take place leading to a re-construction more or less complete of organs external as well as internal, together with the development of structures peculiar to the imago (wings, genitalia). In a few instances (*Mantispa* among *Neuroptera*, *Meloidae* among *Coleoptera*) there is a hyper-metamorphosis. The first larva is Campodeiform, the second more or less eruciform. Much variety in the details of metamorphosis are noticeable.

Alternation of Generations is coupled with parthenogenesis, and is known in this case as Heterogamy. Dimorphism is common, and falls under several heads:—(1) sexual when the male and female differ markedly, a form of dimorphism sometimes connected in *Lepidoptera* with change of locality: (2) seasonal when the imago produced at one time of the year differs from that produced at another—seen in the summer and winter broods of some *Lepidoptera*: (3) functional, e. g. winged and apterous viviparous *Aphidae*, the small female or worker in the colonial *Hymenoptera* (Bees, Wasps, Ants) or the arrested male and female workers and soldiers among the *Termitidae* (White Ants<sup>1</sup>).

Some *Coleoptera* are phosphorescent, and the light is produced by special organs lodged in the head (*Elateridae*) or in the abdomen (*Lampyridae*). Some insects live in colonies, e. g. the social *Hymenoptera* (Bees, many Wasps, Ants), the White Ants, some Lepidopterous larvae. A great variety of structures are found, made for protection during pupation or for rearing the young. Many insects possess the power of emitting sounds, caused by the friction of external parts or of special organs (*Cicada* among *Homoptera*), by the motion of the wings in flight, by the

them, but accords with Brauer's views as to Classification (*infra*) and the results of recent researches. Compare the general works cited p. 146.

<sup>1</sup> Complementary 'kings and queens' are also met with in this family.

passage of air through the stigmata or through the mouth (Death's Head Moth).

The majority of Insecta are terrestrial, some are aquatic in the larval and adult condition, or in one or the other. They feed on vegetable and animal matters living or dead, and some few are parasitic (*Siphonaptera*, *Mallophaga*, &c.). The oldest known fossil Insecta are genuine *Orthoptera* (*Blattidae*, *Phasmidae*, *Mantidae*), genuine *Neuroptera* (*Sialidae* in Devonian strata), and *Rhynchota Homoptera* (*Fulgoridae*), which differ from living forms only in genus or even, looking at generalised generic characters, belong to genera still living (*Brauer*). A *Blatta* has been found in Silurian, *Coleoptera* in Carboniferous strata; *Hymenoptera*, a Lepidopteron, *Heteroptera* and *Diptera* occur in the Solenhofen Slates (Oolitic).

The following classification is taken from Brauer (Systematisch Zool. Studien, SB. Akad. Wien, xci. Abth. I, 1885). It is based upon recent advances in anatomy and embryology. Italics, &c. have been employed, and the mode of numbering the paragraphs altered. A small addition has also been introduced in *Rhynchota* (B. 8), and a slight change made in C.\* *Oligonephria*, section b, in order to make it tally obviously with section a. The terms have been explained and used in the foregoing text.

I. *INSECTA APTERYGOGENEA* (= *Collembola* and *Thysanura*).

II. *INSECTA PTERYGOGENEA*.

**A. Menognatha ametabola and hemimetabola.**

\* *POLYNEPHRIA*.

(a.) genital orifices of the male, or of both sexes double; or single either by loss of one, or by the union of the two: ducts without chitinoid lining.

1. Ametabola. Wings very dissimilar; fore wings short, corneous; hind wings folded longitudinally and transversely. Antennae filiform; mouth-parts distinct. *Dermaptera* (Earwigs).

2. Hemimetabola. Larva aquatic; imago with wings never folded; hind wings the smaller or lost; antennae subulate; mouth-parts rudimentary. *Ephemera* (May flies).

(b.) genital orifice single; vasa deferentia and oviducts united to a common duct lined by chitin.

3. Hemimetabola. Larva aquatic; imago with sub-equal wings not folded, reticulate; antennae subulate; male copulatory organs remote from sexual aperture; prothorax small. *Odonata* (Dragon flies).

4. Hemimetabola or perennibranchiate. Larva aquatic; imago with hind wings often folded; longitudinal veins predominant; antennae filiform; prothorax broad; wings sometimes wanting. *Plecoptera* (= *Perlariae* or *Orthoptera Amphibiotica*).

5. Ametabola. Very generally winged; hind wing dilated, folded longitu-

dinally from the base, sometimes folded transversely; fore wings more or less coriaceous, reticulate, or modified in various ways. *Orthoptera* (Cockroaches, Leaf Insects, Walking Sticks, Grasshoppers, Crickets, *Embidae*?).

\*\**OLIGONEPHRIA*.

6. Ametabola. Wings none, or four equal and caducous, or unequal similar, with either predominant longitudinal veins or areolate. *Corrodentia* (White Ants, *Psocidae*, *Mallophaga* = Bird-lice).

7. Ametabola. Wings four, fringed, very narrow, or wanting; antennae on the vertex; tarsal claws obsolete; mandibles setaceous. *Thysanoptera* (*Thrips* and its allies).

**B. Menorhyncha ametabola and metabola<sup>1</sup>.**

8. No maxillary palps; labial palps transformed into a spurious labium, generally jointed; mandibles and maxillae setaceous, forming with the labium a sucking apparatus; wings either absent or four in number, similar or dissimilar, veined or areolate. *Rhynchota* (= *Hemiptera*), includes *Homoptera* with similar wings, *Coccidae*, *Aphidae*, *Cicadidae*, etc., and *Heteroptera* with dissimilar wings, e.g. Bugs, Water Scorpions, &c., and the Lice or *Pediculidae*.

**C. Menognatha and Metagnatha metabola.**

\**OLIGONEPHRIA*.

(a) wings alike, veined; or hind wings rudimentary or transformed or wanting: metathorax either equal to or less than mesothorax. = *Petanoptera* (Brauer).

*i. Menognatha.*

9. Wings, four, reticulate, similar; labial palps 3-jointed, joints free; maxillae free; pupa with distinct mandibles; larva Campodeiform, menognathous, or Ant-lion-like and metagnathous. *Neuroperta* (*Megaloptera*, e.g. Ant-lion, Lace-winged Fly; *Sialidae*).

10. Wings, four, similar or absent; labial palps 3-jointed, with basal joints connate; maxillae long, connate with the labium, with lobes free; pupa with distinct mandibles; larva eruciform. *Panorpatae* (Scorpion-flies).

11. Wings, four, similar, subequal; or the hind wings very often folded longitudinally from the base, the broader and with longitudinal veins predominant; mandibles rudimentary; maxillae connate with labium, all but lost; palps distinct or caducous; pupa with distinct mandibles; larva sub-eruciform. *Trichoptera* (Caddis-flies).

*ii. Metagnatha.*

12. Wings, four, covered with scales; hind wings sometimes folded; fore wings rarely folded from the base (*Pterophoridae*); longitudinal veins predominant; mandibles lost, rarely distinct; galeae of maxillae forming the antlia; labial palps very generally of large size, free; pupa metagnathous, rarely mandibulate; larva mandibulate, eruciform. *Lepidoptera* (Butterflies, Moths).

13. Wings, two, hyaline; never folded, with predominant longitudinal veins; hind wings transformed into halteres, very seldom lost; maxillary palps free or

<sup>1</sup> The male *Coccidae* alone are metabola.

lost ; labial palps transformed into a labella ; hypopharynx setaceous ; larva apodous or with false (i. e. secondary) feet ; mandibulate or metagnathous ; no labial palps ; pupa metagnathous. *Diptera* (Two-winged Flies).

14. Wings, none ; mandibles long, with serrated edges ; maxilla short, with 4-jointed palp ; labial palps 4-jointed, approximated at the base ; labrum distinct ; no hypopharynx ; pupa metagnathous ; larva apodous, mandibulate, with obsolete labial palps. *Siphonaptera* = *Aphaniptera* (Fleas).

(b.) wings dissimilar, metathorax much larger than mesothorax.

15. Menognatha, rarely metagnatha ; fore wings coriaceous, rarely lost ; hind wings membranous, folded longitudinally and often transversely, or wanting ; longitudinal veins predominant ; larva mandibulate, Campodeiform or eruciform, with or without legs ; pupa mandibulate. *Coleoptera* (Beetles).

\*\**POLYNEPHRIA*.

16. Menognatha and metagnatha ; wings four, similar, membranous, very often areolate, or caducous, or absent ; fore wings the larger ; mesothorax the larger ; pupa mandibulate, with maxillae sometimes transformed ; larva mandibulate, eruciform, with or without legs. *Hymenoptera* (Gall-flies, Saw-flies, Ants, Bees, &c.).

*Note.* The *Strepsiptera* are included by Brauer and others among the *Coleoptera*. Prof. Westwood is still of opinion that they should be retained as a separate order. They are ento-parasitic on various Bees and Wasps. The male is free, has small twisted fore wings, longitudinally folded hind wings, and a large metathorax. It is metagnathous. The mandibles are reduced, the maxillae connate with the labium, their palpi 2-jointed. The female is blind, vermiform, and never quits the host. There is a dorsal canal, by which the male effects impregnation. The ova develop in the coelome ; the Campodeiform larvae escape by the dorsal canal. They are carried by a Bee or Wasp to its nest, where they bore into a grub, and are transformed into apod vermiform larvae. The male pupa is coarctate (p. 153), and perforates one of the abdominal intersegmental membranes of the Bee pupa, protruding only the head, as does also the female. See von Siebold, A. N. ix. (1), 1843 ; Id. 'Paedogenesis,' Z. W. Z. xx. 1870.

See lit. pp. 146, 151, 156, 161.

INSECTA APTERYGOGENEA. See pp. 299-300. *Ventral tube and copulation of Collembola*, Reuter, Ent. Tidskr. i. 1880, and Zool. Record, 1884, Insecta, p. 277 ; cf. Lemoine, C. R. French Assoc. xi. 1882 ; *development*, Lemoine, op. cit. with lit. quoted.

INSECTA PTERYGOGENEA.

*Ephemeridae*, Eaton, Monograph, Tr. L. S. (2), iii. 1884-5 ; *larvae*, Vayssière, A. Sc. N. (6), xiii. 1882 ; *development of Chloeon*, Lubbock, Tr. L. S. xxiv. 1864, xxv. 1866 ; *vessels to caudal setae*, Zimmermann, Z. W. Z. xxxiv. 1880.

*Odonata* : *mouth-parts*, Gerstaecker, 'Morph. Orthoptera Amphibiot.' Festschr. Natf. Freund. Berlin, 1873 ; *larvae*, Dufour, A. Sc. N. (3), xvii. 1852 ; *of Aeschna grandis*, Amans, Rev. des Sc. Nat. Montpellier (3), i. ; *tracheae of larva*, Hagen Z. A. iii. 1880.

*Plecoptera* : *Pteronarcys regalis*, Newport, Tr. L. S. xx. 1851 ; Gerstaecker, op. cit. under *Odonata* ; Id. 'Vorkommen von Tracheenkieme, &c.' Z. W. Z. xxiv.

1874; *Pteronarcys*, Hagen, Stet. Ent. Zeitung, xxxviii. 1877; *Perla maxima*, Imhof, Inaug. diss. Arau, 1881; *Hermaphrodite Perla*, ♂, Brandt, Z. A. i. 1878.

*Orthoptera*, cf. p. 146. *Sound apparatus of Cricket*, Pierce, Amer. Naturalist, xiii. 1879. *Migratory Locust of Rocky Mountains*, Riley, Packard, Thomas, Reports U. S. Entom. Commission, 1878, 1880; *generative organs of class*, Berlese, Atti Accad. Rom. (3), xi. 1882; *Embiidae*, Hagen, Canad. Entom. xvii. 1885.

*Corrodentia. Termitidae*, F. Müller, J. Z. vii. 1873, ix. 1875; Hagen, Linnaea Entom. x. 1855, xii. 1858, xiv. 1860; Id. Proc. Boston Soc. xix. 1878, xx. 1881; Hubbard, *ibid.* xix. *Termes lucifugus*, Lespès, A. Sc. N. (4), v. 1856. *Infusorian parasites*, Leidy, Journal Acad. Nat. Sci. Philadelphia, viii; Saville-Kent, A. N. H. (5), xv. 1885. *Mallophaga*, Grosse, Z. W. Z. xlii. 1885; Taschenberg, Nova Acta, 44, 1883; and *Pediculidae*, Piaget, 'Les Pédiculines,' Leyden, 1880, Suppl. 1885; Giebel, 'Insecta Epizoa,' Leipzig, 1874. *Psocidae*, Kolbe, J. B., Zool. Sect. Westf. Vereins, 1879-80; Hagen, Psyche, iii. 1881; Id. Stet. Entom. Zeitung, xliii. 1882, xlv. 1883 (Pl. in xliii); *head*, Burgess, Proc. Boston Soc. xix. 1878; Kolbe, Berlin Entom. Zeitung, xxviii. p. 177; *sexual organs, dimorphism*, Bertkau, A. N. 49 (1), 1883.

*Thysanoptera*, Heeger, SB. Akad. Wien, ix. 1852. Brit. Mus. Catalogues, 'Homoptera,' iv. 1852, p. 1049 et seqq., Pls. v.-viii.

*Rhynchota; proboscis*, Wilde, A. N. 51 (1), 1885; Witlaczil, Z. A. ix. 1886. *Homoptera: Aphides*, Buckton, Ray Soc. 4 vols. 1876-83; Lichenstein, 'Les Pucerons,' Montpellier, pt. i. 1885 (in progress); *migrations, &c.*, Id. 'De l'évolution biol. des pucerons, et du *Phylloxera* en particulier,' Paris, 1883; Id. A. N. H. (5), iii, v, vi, viii, xi, xii, xiii, xiv, xv; Kessler, Nova Acta, xlvii. (3); *dimorphism*, Witlaczil, Dk. Akad. Wien, xlvi. 1884: cf. Buckton, *op. cit.* ii. p. 121, and A. N. H. (5), xv. p. 273; *anatomy*, Witlaczil, Arb. Zool. Inst. Wien, iv. 1882; *development*, Witlaczil, Z. W. Z. xl. 1884; Will, Arb. Zool. Zoot. Inst. Wurzburg, vi. 1883. *Coccidae*, Witlaczil, Z. W. Z. xliii. 1886. Comstock, Report Dep. Agric. U. S. A. 1880. ♂ *Aspidiotus Nerii*, Schmidt, A. N. 51, (1), 1885. *Psyllidae*, Witlaczil, Z. W. Z. xlii. 1885; Löw, Verhandl. z. b. Ges. Wien, xxxi. 1881; *British sp.*, Scott, Entom. M. Mag. xix. 1882; *Palaeartic*, Löw, *op. cit.* xxxii. 1882. *Cicada, sound apparatus*, Lloyd Morgan, Middlemis, Nature, xxxiii. 1885-6. *Pelagic Hemiptera*, Buchanan White, Challenger Reports, viii. 1883. *Pediculidae: Phthirus*, Graber, Z. W. Z. xxii. 1872; *Haematopinus tenuirostris*, Ströbelt, A. N. H. (5), xi. 1883. See also 'Piaget' and 'Giebel' under *Corrodentia Mallophaga*.

*Neuroptera: larvae of Ant-lion*, Redtenbacher, Dk. Akad. Wien, xlvi. 1884; *structure of mouth-parts*, Dewitz, Berlin Entom. Zeitung, xxvi. 1882, p. 61. *Sialidae: Corydalis*, Haldeman and Leidy, Mem. Amer. Acad. iv. 1849; Saunders, Canad. Entom. vii. 1875; Riley, Rep. Ins. Mo. 1877; cf. Wood-Mason, P. Z. S. 1884; and *Chauliodes*, Riley, Canad. Entom. xi. 1879; *nervous system*, Krauss, Psyche, iv; *Raphidia*, Waterhouse, Trans. Entom. Soc. i. 1836. *Hemeroptera: Mantispa*, Brauer, Verhandl. z. b. Ges. Wien, xix. 1869; *Osmylus*, Id. A. N. 17 (1), 1851; Hagen, Linnaea Entom. vii. 1852. *Coniopteryx*, Schlectendahl, J. B. Ver. Zwickau, 1882.

*Trichoptera: Monograph*, McLachlan, 1874-80, Suppl. 1884. *Marine Caddis-worms*, Id. J. L. S. xvi. 1883; cf. Zool. Record, 1883, Insecta, p. 123. *Cases of Brazilian sp.*, F. Müller, Z. W. Z. xxxv. 1881. *Development*, Patten, Q. J. M. xxiv. 1884.

*Panorpatae*: *Fanorpa*, *Bittacus*, Brauer, Verhandl. z. b. Ges. Wien, xiii. 1863, p. 307; xxi. 1871, p. 106.

*Lepidoptera*, cf. pp. 151, 156, 161. *Larvae of British Butterflies and Moths*, Buckler, edd. by Stainton, Ray Soc. i. 1886. *Abdominal somites of Caterpillar*, Packard, Amer. Naturalist, xix. 1885; *extra limbs in Caterpillar of Lagoa*, Id. *ibid.*

*Diptera*, *mouth parts*, Hansen, Nat. Tidskrift (Schiödte), (3), xiv. 1883; Becher, Dk. Akad. Wien, xlv. 1882; *of Musca*, Kraepelin, Z. W. Z. xxxix. 1883. *Larvae*, Brauer, Dk. Akad. Wien, xlvii. 1883; *chordotonal organs of*, Bolles Lee, A. M. A. xxiii. 1884. *Metamorphosis*, Beling, A. N. 48 (1), 1882. *Halteres*, Bolles Lee, Recueil Zool. Suisse, ii. 1885.

*Siphonaptera*: Kraepelin, '*Pulicidae*,' A. N. H. (5), xiv. 1884; Taschenberg, 'Die Flöhe,' Halle, 1880. *Index to species*, Ritsema, Zeitschrift f. Ges. Natw. (Giebel), 53, 1880. *Sarcopsylla*, Schimkewitsch, Z. A. vii. 1884; A. N. H. (5), xv. 1885.

*Coleoptera*, *larvae*, Schiödte's papers in Nat. Tidskrift (3), i. 1861-xiii. 1883. *Meloidae* (anatomy), Beaugard, Journal de l'Anat. &c. xxi. 1885; xxii. 1886. See under *Hypermetamorphosis, infra*. *Nervous System of Oryctes nasicornis*, Michels, Z. W. Z. xxxiv. 1880.

*Hymenoptera*, *British Phytophagous*, Cameron, Ray Soc. 2 vols. 1881-4 (in progress). *Ants, Bees, Wasps, Habits of Social Hymenoptera*, Lubbock, Internat. Series, 50, 1882. *Agricultural Ant of Texas*, McCook, Philadelphia, 1879; *Honey and Occident Ants*, Id. 1882; Moggridge, 'Harvesting Ants,' &c. 1873; Suppl. 1874. See also Belt, 'Naturalist in Nicaragua,' 1874; Bates, 'Naturalist on the river Amazons,' 1863, i. p. 23; ii. pp. 95. 350. *Sting of Ant*, Dewitz, Z. W. Z. xxviii. 1877; cf. Id. op. cit. xxv.; *of Bee*, Kraepelin, Z. W. Z. xxiii. 1873; cf. Carlet, Bull. Soc. Entom. Fr. (6), iv. 1884; C. R. 99, 1884. ♂ *copulatory organs of Bombus*, Radoszowsky, Bull. Mosc. lix. (1). *Larval food and salivary glands of Apis*, Schiemenz, Z. W. Z. xxxviii. 1883<sup>1</sup>.

*Fossil Insecta*, Zittel, Handbuch der Palaeontologie, Abth. i., Palaeozoologie, ii. pt. 5, 1885; cf. Brauer, SB. Akad. Wien, xci. Abth. 1.

See lit. pp. 146, 151, 156, 161.

*Glands opening externally, with lit.*, Dimmock, Psyche, iii. 1882. *Sensory organs; integumental*, Leydig, Z. A. ix. 1885; *gustatory*, Will, Z. W. Z. xlii. 1885; *in Coleoptera*, Gazonnaire, C. R. 102, 1886. *Smell in Bees*, Schiemenz, Z. W. Z. xxxviii. p. 126. *Eye*, Patten, Mitth. Zool. Stat. Naples, vi. 1886. *Auditory organs*: (1) *vesicular*, Grobben, SB. Akad. Wien, lxxii. Abth. 1, 1875; Graber, A. M. A. xvi. 1879; (2) *chordotonal*, Graber, A. M. A. xx. xxi. 1882; Lee, A. M. A. xxiii. 1884.

*Midgut*, Frenzel, A. M. A. xxvi. 1885.

*Female genital armature*, de Lacaze Duthiers, A. Sc. N. (3), xii. 1849; xiv. 1850; xvii. xviii. 1852; xix. 1853. *Ovipositor of Locusta viridissima*, Dewitz, Z. W. Z. xxv. 1875, p. 176.

*Regeneration of lost parts*, Newport, Ph. Tr. 134, 1844, p. 288.

*Parthenogenesis*: von Siebold, 'Beiträge,' &c. Leipzig, 1871; Id. 'True Parthenogenesis' (transl. by Dallas), London, 1857; Leuckart in Moleschott's Unter-

<sup>1</sup> For the remarkable parasite *Platypsylla*, found on the Canadian Beaver, which is perhaps a Coleopteron, see Westwood, Thesaurus Entom. Oxon., Clarendon Press, 1874, p. 194, Pl. XXXVII. 1 and 2; Leconte, P. Z. S. 1872. And for the parasitic Rhynchote *Polycetenidae* found on a Bat (*Molossus*), see Westwood, op. cit. p. 197, Pls. XXXVIII-XL.

suchungen, Frankfort a. M. iv. 1858. *Of Tenthredinidae*, Cameron, Brit. Phytophagous Hymenoptera, Ray Soc. i. p. 25. *Of Cynipidae*, Adler, Z. W. Z. xxxv. 1881 (cf. A. N. H. (5), viii.) *Of Gastropacha* (Coleopteron), Osborne, Nature, xx. 1879; xxii. 1880. *Of a Trichopteron*, Id. op. cit. xxii. *Of Chironomus Grimmii*, Schneider, Zool. Beiträge, i. (3) 1885.

*Occasional parthenogenesis*, cf. Gerstaecker, Bronn's Klass. und Ordn. des Thierreichs, v. Abth. i. p. 164.

*Paedogenesis of Ceccidomyidae*, Wagner, Z. W. Z. xiii. 1863; Meinert (transl. by von Siebold), Pagenstecher, Z. W. Z. xiv. 1864; Ganin, Z. W. Z. xv. 1865; Leuckart, A. N. 31 (1), 1865 (cf. A. N. H. (3), xvii.); Mecznikow, Z. W. Z. xvi. 1866, p. 407; Schneider, Zool. Beiträge, i. (3), 1885, p. 272.

*Hyper-metamorphosis: of Mantispa*, Brauer, Verhandl. z. b. Ges. Wien, xix. 1869; *of Meloidae*, Riley, Amer. Naturalist, xii. 1878; cf. xvii. pt. 2, 1883, p. 790; Lichtenstein, A. N. H. (5), i. 1878; iv. 1879; Beaugregard, A. N. H. (5), xvi. 1885; Id. C. R. 101, 1885; Newport, Tr. L. S. xx. 1851; Fabre, A. Sc. N. (4), vii. 1857.

*Phosphorescence: Luciola*, Emery, Z. W. Z. xl. 1884; Id. Arch. Ital. Biol. vii. 1886; *of Cucuyo (Elateridae)* Heinemann, A. M. A. xxvii. 1886. *Lampyridae*, Wielowiczski, 'Studien,' &c. Z. W. Z. xxxvii. 1882. *Non-luminosity of Fulgoridae*, Champion, Proc. Entom. Soc. 1883, pp. xx. xxi.

*Dimorphism: Seasonal*, Weismann, 'Studies in Theory of Descent' (transl. by Meldola), London, 1880-82; Scudder, 'Butterflies,' New York, 1881; *Sexual*, Wallace, 'Contributions to Natural Selection,' London, 1870, p. 130; Mansel Weale and Trimen, Trans. Entom. Soc. 1874 (specimens in Hope Collection, Oxford Museum); Trimen, *ibid.* 1881.

*Mimicry: Bates*, 'Lepidoptera of Amazons,' Tr. L. S. xxiii. 1862; Trimen, 'African Butterflies,' *ibid.* xxvi. 1870; Wallace, op. cit. *supra*, p. 45; F. Müller 'On *Ituna*,' Trans. Entom. Soc. 1879, p. xx.

*Variation induced by Isolation*, Weismann, 'Einfluss der Isolirung auf die Artbildung,' Leipzig, 1872.

*Insects in relation to Flowers*, Darwin, 'Insectivorous Plants,' London, 1875; Geddes, under same title, Encyclopaedia Britannica (ed. ix.), xiii. 1881; Kerner, 'Flowers and their Unbidden Guests' (transl.), London, 1878; H. Müller, 'Fertilisation of Flowers' (transl.), London, 1883.

*Genealogy of Insects*, cf. lit. p. 162.

## CLASS MYRIAPODA.

*Terrestrial tracheate Arthropoda, with a head, followed by a series, usually numerous, of similar somites: with a pair of antennae, mandibles, and maxillae. Limbs 6-7 jointed, ending with a claw.*

The body is elongate, and of nearly the same diameter throughout, and either flattened dorso-ventrally or cylindrical. In the *Archipolypoda* it appears to have been fusiform. The head is generally somewhat flattened. The numbers of somites in the body varies from five (*Eupauropus*) to some hundreds in the *Geophilidae* (*Chilopoda*). In *Chilopoda* the head is



followed by a large 'basilar segment,' usually stated to be composed of three or four fused somites<sup>1</sup>. The remaining somites are either all similar, or some are smaller than others and partially concealed by them, and each somite consists of a single tergal and sternal plate united at the sides by a soft pleural membrane. In *Diplopoda* the tergal region makes frequently (e.g. *Iulidae*) at least three-fourths of a circle, or when flattened dorso-ventrally it has lateral expansions (e.g. *Polydesmidae*). To each tergum corresponds a pair of sterna, one in front of the other, and the first somite has the tergum expanded anteriorly and it may then conceal the head completely (*Eupauropus*) or partially as in many others.

The antennae are 7-jointed in *Diplopoda*, and sometimes lodged in grooves of the head. They are long and many jointed in *Chilopoda*. In *Pauropoda* (*Diplopoda*) the last joint of the antennae is bifid and the organ is terminated by three long jointed appendages. The mandibles have a broad masticatory surface in the vegetable-feeding *Diplopoda*, a toothed margin in the carnivorous *Chilopoda*, in some of which a rudimentary palp is said to exist. The maxillae in the former group are represented by a four-lobed plate derived from a single pair of limbs in the embryo; in the latter each maxilla consists of a palp and bilobed median process. The *Polyzonidae* (*Diplopoda*) have the jaws united to form a sucking tube. The first pair of post-maxillary appendages in *Chilopoda* is limb-like, the bases of the limbs in contact, as is the case in the second pair, the limbs of the 'basilar segment,' which form the stout curved poison claws. The poison gland is lodged in the two last joints and opens on the convex side of the apex. The third pair of limbs (which have no corresponding tergum) is leg-like and sometimes wanting (*Lithobius*, *Scutigera*). The remaining somites bear a single pair of jointed limbs, the last pair being usually long and turned backwards. The first two or three somites in *Diplopoda* may carry a single pair of limbs, of which the first pair are shorter and turned forwards and sometimes modified in the male; or there are two pairs to every somite in *Eupauropus*, as there are in the middle and posterior somites of other members of the class. The third somite is apodous in *Iulidae*, and the seventh in the male carries one pair of limbs and the copulatory organ. The limb is usually 7-jointed, the terminal joint being a claw.

The chitinoid cuticle is generally thick and firm in the terga and sterna. Hairs are sometimes well developed in *Diplopoda*, e.g. *Polyxenidae*, in which they are aggregated in bundles. Bundles of spines occur in the extinct *Protosyngnatha*, and in the extinct *Archipolypoda* six longitudinal rows of spines or tubercles. The majority of *Diplopoda* possess a longitudinal lateral series of *foramina repugnatoria*, the apertures of glands secreting a mal-odorous fluid. In *Fontaria* sp.? (*Diplopoda*) the secretion contains a ferment and a substance which breaks up into hydrogen

<sup>1</sup> Cf. Balfour, Comp. Embryology, p. 325.

cyanide and oil of bitter almonds. In *Glomeris* the secretion is sticky and probably serves to retain the animal in a rolled up condition when it falls. *Geophilus Gabrielis*, a Chilopod, has a ventral series of glands, in which a large number of tubules open on a perforated plate. The use of the red secretion is unknown<sup>1</sup>.

The nervous system consists of a supra- and a sub-oesophageal ganglion with a ventral chain. The number of ventral ganglia corresponds as a rule to the number of somites, and the *Diplopoda* have two to each tergal ring. The ganglia supplying the appendages of the 'basilar segment' in *Chilopoda* are fused together. *Siphonophora* (*Diplopoda*), the *Geophilidae*, and *Cryptops* (*Chilopoda*), are blind. *Scutigera* among *Chilopoda* has a poly-meniscous eye on each side of the head, other Myriapoda have a number of monomeniscous eyes grouped together in the same position. *Iulus* and *Glomeris* among *Diplopoda* are stated to have a monostichous ommateum, and the *Chilopoda* a diplostichous, though the vitreous layer is evanescent. The eye is apostatic or cup-shaped, but the layer of vitreous cells does not share in the invagination. The visual rods at the sides of the cup are directed inwards more or less horizontally, and there are no pigment cells between the visual rods whether at the sides or base of the cup. Each visual cell is said to support many visual rods in the *Diplopoda*. *Scutigera* has a reticulate ommateum, and the visual cells secrete rhabdomeres surrounding a conical vitreous body<sup>2</sup>. Sensory hairs are found upon the antennae, and the apical joint of those organs in some *Diplopoda* is furnished with sensory structures very similar to the structures found in Insecta. A cavity opens externally in *Scutigera* between the mandibles and maxillae, and one or more cavities beneath or near the eye in some *Diplopoda*. Their function is unknown, but the presence of hairs within the cavity of *Scutigera*, and of a single moveable hair in the cavities of *Polyxenus lagurus*, point perhaps to that of hearing.

The digestive tract has a short stomodaeum with salivary glands<sup>3</sup>, a long straight mesenteron, disposed however in a single longitudinal fold

<sup>1</sup> One of the English *Scolopendridae* discharges a phosphorescent fluid on irritation. Some *Chilopoda* possess two phosphorescent spots upon the head (Belt, Naturalist in Nicaragua, 1874, p. 141).

<sup>2</sup> The corneal hypodermis (=vitreous cells) is perhaps always present in development. The horizontal position of the visual rods or of those placed near the rim of the cup may be due, as suggested by Patten, either to the collapse of a vesicle through the action of reagents, or to the lamination of a vitreous body. The rods (=retinidia) of the basal cells in the eye of *Lithobius*, as figured by Grenacher, appear to be terminal, and to constitute a retineum. The conical vitreous body of *Scutigera* is probably to be interpreted as a compound retinidium surrounded by several circles of retinulae. See Patten's general remarks on the Arthropod eye, pp. 665-688, Mitth. Zool. Stat. Naples, vi. 1886; and for significance of terms, p. 492 of this book and the note p. 452. The structure of the Myriapod eye needs re-examination.

<sup>3</sup> The Myriapod 'of the division *Sugentia*' (= *Folyzonidae*) 'of Brandt,' mentioned by Belt, op. cit. *supra*, p. 140, which discharges a viscid fluid over its prey, is a species of *Peripatus*: see Moseley, A. N. H. (5), iii. 1879, p. 265.

in *Glomeris* and *Sphaerotherium* (*Diplopoda*), beset with short glandular tubules, and a short proctodaeum. The anus is terminal, and in *Diplopoda* is inclosed between two valves borne by the last somite. There is a dorsal heart composed of a series of chambers (two to each somite in *Diplopoda*), with valved lateral ostia and inclosed in a pericardial sinus formed by a horizontal membrane, and furnished with alary muscles as in Insecta. Each chamber gives off one pair, or in *Diplopoda* two pairs, of lateral arteries. There is an anterior aorta which sends forward a cephalic vessel, and two lateral vessels which form an oesophageal ring and unite ventrally into a vessel which lies dorsally to the nerve cord and runs backwards. A single pair of stigmata opens in the pleural membrane of all or certain somites in *Chilopoda*, with the exception of the genus *Scutigera*, which has a single median dorsal stigma to each somite. In the *Diplopoda*, on the contrary, each somite carries two pairs of stigmata, opening ventrally, one at the base of each pair of limbs; but in *Glomeris* the three first pairs of stigmata belong each to a separate somite. The stigma in *Diplopoda* and in *Scutigera* leads into a chamber or 'tracheal sac,' from which originate bundles of simple tracheal tubes. *Glomeris*, however, is an exception. Each of its tracheal sacs gives origin to two branching trunks. Large tracheae, which branch and anastomose both longitudinally and transversely, arise from each stigma in *Chilopoda* a group in which the lining cuticle and spiral line are well marked. It is possible that the *Archipolypoda* possessed a pair of branchial appendages, situated ventrally on each somite. A single pair of urinary or Malpighian tubes opens into the proctodaeum in *Diplopoda*, two pairs in *Chilopoda*.

The sexes are separate. The ovary is generally a single tube, rarely double as in *Craspedosoma* (*Diplopoda*). There are two oviducts in *Diplopoda*, one or two in *Chilopoda*. Cement glands and receptacula seminis open either into the oviduct itself or, as is more usual, into the genital orifice. The testis also may be a single tube, or as in some *Diplopoda* (certain *Glomeridae* and *Iulidae*) two tubes connected by transverse anastomoses. The vasa deferentia, like the oviducts, may be single or double, and are always provided with accessory glands. In *Diplopoda* the two genital apertures are in connection with the basal joint of the second or third pairs of limbs. In *Chilopoda* there is a single posterior aperture. *Iulus* has a copulatory organ on the seventh post-cephalic somite; *Sphaerotherium* three pairs of copulatory appendages between the last pair of ambulatory limbs and the anus; and the corresponding organs in *Glomeris* are similarly placed. The *Scolopendridae* possess a short penis. *Scolopendra* is viviparous, other Myriapoda lay their eggs in earth, &c. The young *Pauropus* is hexapodous, so too *Lithobius*<sup>1</sup>. Some of the *Diplopoda* have an hexapodous stage, in which however the three pairs of limbs are not on

<sup>1</sup> Haase states, however, that it has eight limb-bearing somites.

consecutive somites. The majority of *Chilopoda* appear to possess the full number of limbs at birth. It may be noted that the embryo of *Diplopoda* develops one or two (*Iulus*) cuticular envelopes.

A sound-producing apparatus is found in the Chilopod *Eucorybas Crotalus* and in *Sphaerotherium*. In the former the fourth joints of the last pairs of limbs are expanded and leaf-like, and are rubbed together by the animal. In the latter, ridges on the outer side of the middle joint of the second and in *S. retusum* also of the first pair of copulatory organs in the male work against sharp points on the inner aspect of the last tergum. There is a limited power of reproducing lost parts of the appendages.

Extinct groups of Myriapoda appear in Carboniferous strata in America. Of these *Archipolypoda* belonging to the *Diplopoda*, the *Protosyngnatha* to the *Chilopoda*.

The *Myriapoda* are divisible into two orders.

1. *Diplopoda* (= *Chilognatha*). Body cylindrical or semi-cylindrical, with two pairs of feet to the middle and posterior somites; generative apertures on the basal joints of the second or third pairs of limbs.

2. *Chilopoda*. Body as a rule flattened dorso-ventrally; a 'basilar segment'; second pair of post-oral limbs forming powerful poison claws; one pair of limbs to each somite.

The two pairs of limbs, two ganglia, two stigmata, &c., to each somite in *Diplopoda* appear to arise not from fusion but from imperfect division of the somite. Cf. Balfour, *Comp. Embryology*, i. p. 234.

'Myriapoda,' Moseley, *Encyclopaedia Brit.* (ed. ix.) xvii. Latzel, 'Die Myriopoden der Oesterreichisch-Ungarnischen Monarchie,' 2 vols. 1884. Cf. *On Morphology of Chilopoda*, Haase, *Z. A.* viii. 1884; and *On Myriapoda*, Packard, *A. N. H.* (5), xii. 1883.

*Pauropoda*, Ryder, *American Naturalist*, xiii. 1879.

*Fossil Myriapoda*, Zittel, *Handbuch der Palaeontologie*, Abth. i. *Palaeozoologie*, ii. pt. 5, 1885.

*Anatomy of Sphaerotherium*, G. C. Bourne, *J. L. S.* xix.

*Sense organs of Antennae*, Bourne, op. cit. *supra*; von Rath, *A. M. A.* xxvii. 1886; *Antennal hairs*, Sazepin, *Mém. Acad. Imp. St. Petersburg* (7), xxxii. 1884; *Sensory cavities*, Bourne, op. cit. *supra*; Tömösvary in *Naples Zool. Jahresbericht*, 1884, pt. ii. p. 132; in *Scutigera*, Heathcote, *Q. J. M.* xxv. 1885; cf. Haase in *Schneider's Zool. Beiträge*, i. 1885.

*Hydrogen cyanide, &c. in Fontaria*, Weber, *A. M. A.* xxi. 1882; *Guldensteeden-Egeling*, *Arch. f. Physiol. (Pflüger)*, xxviii. 1882; Cope, *American Naturalist*, xvii. pt. 1. p. 337, 1883. *Sticky Secretion in Glomeris*, Dewitz, *Biol. Centralblatt*, iv. 1884-85.

*Pharynx of Scutigera*, Haase, op. cit.

*Respiratory organs of Chilopoda and Symphyla*, Haase, op. cit.

*Genital organs and development in Geophilus*, Sograff; see *Naples Zool. Jahresbericht*, 1883. pt. ii. p. 90.

*Regeneration of lost parts*, Newport, Ph. Tr. 134, 1884.

*Scolopendrella* (= *Symphyla*) is placed by Packard with the *Thysanura* among Insecta. Its mouth-parts are sunk into the head as in *Collembola* and *Campodea*; but there are many discrepancies in the accounts of its anatomy, and at present it is perhaps better to leave its position undefined. There is of course nothing intrinsically improbable in the existence of an Insect with very similar somites and fully developed jointed abdominal limbs. Packard, *American Naturalist*, xv. 1881; Wood Mason, *A. N. H.* (5), xii. 1883; Ryder, *Proc. Amer. Nat. Soc. Philadelphia*, 1881; Grassi, *Atti R. Accad. Sc. Torino*, xxi. 1885; Latzel, *op. cit. supra*.

## CLASS PROTRACHEATA.

### (*Onychophora*, *Peripatidea*.)

*Tracheate Arthropoda with soft, worm-like bodies, a pair of antennae, and a series of paired imperfectly jointed limbs. Tracheal stigmata numerous and scattered; nephridia or segmental organs present. A single genus Peripatus.*

The body is not segmented, and is flat ventrally, convex dorsally. The ringed antennae are large. There is a buccal cavity inclosed by soft lips and containing the first pair of limbs, which are 2-clawed and act as jaws. The second pair of limbs form the oral papillae placed at the side of the mouth, at the summits of which open the receptacles of the slime glands. The remaining limbs are placed at equal distances as far as the posterior extremity of the body. The number of pairs varies in the different species (from 14-30)<sup>1</sup>. In *P. capensis* the limb is originally 5-jointed, but in the adult the jointing becomes obscure. In all the species it is terminated by two chitinous claws. A pair of anal papillae by the side of the genital aperture appears to represent the last pair of limbs, as in some specimens of *P. capensis* they possess the two typical claws.

In *P. capensis* there is a delicate cuticle, a single layer of ectoderm (hypodermis) cells; an outer layer of circular muscles; an inner layer of longitudinal muscles arranged in five bands, two dorsal, two lateral, and three ventral; and a layer of transverse, i. e. dorsoventral muscles placed obliquely and dividing the coelome into three longitudinal cavities, a median containing the digestive tract, slime glands, and genitalia, and two lateral containing the salivary glands, nerve cords, and in the male the last enlarged pair of crural glands. The limbs contain a separate division of the coelome which lodges the crural glands and nephridia. The middle compartment

<sup>1</sup> Ernst states (*Nature*, xxiii. p. 447) that a young *Peripatus* (? *P. Edwardsi*) possessed at birth 29 pairs of feet, the adult 31; consequently new pairs of feet must be added during growth. He also observed a skin cast by the young animal. The fact that there are jaws and claws in reserve points to the probability of a moult occurring from time to time. For observed variations in the number of feet, cf. Moseley, 'On the Species of *Peripatus*,' *A. N. H.* (5), iii. 1879, p. 263.

of the coelome is lined by an endothelium. The surface of the body is covered with papillae. Closed capsules prolonged externally into a spine, lined by hypodermis cells and supplied by a nerve, are found in the primary papillae. They are very numerous on the antennae, lips, oral papillae, and certain regions of the ventral surface of the feet, and are probably tactile in function. The muscles, with the exception of those attached to the jaws, are unstriped.

The nervous system consists of a pair of supra-oesophageal ganglia united medianly, of commissures surrounding the pharynx, and a pair of widely separated ventral nerve-cords united dorsally and posteriorly by a fibrous commissure above the anus. The two cords are united across the middle ventral line by numerous transverse commissures. The antennary nerves arise from the supra-oesophageal ganglia, those for the jaws from the oesophageal commissures. The cords give off numerous lateral nerves, those for the feet being especially stout. The transverse commissures give off nerves to the skin. There is a ventral layer of ganglion cells more especially aggregated at the origin of the nerves to the feet. The sympathetic system consists of two nerves rising from the supra-oesophageal ganglia and running dorsally on the walls of the pharynx and oesophagus, where they unite. The eyes are paired, and lie dorso-laterally, one at the base of each antenna. They are formed as invaginations from the nervous thickenings of the prae-oral lobes of the embryo. The vesicle thus formed lies just below the skin. Its anterior cells become somewhat flattened, its lateral and especially its posterior cells elongated, forming visual cells. These cells are pigmented at their outer ends; at their inner they are clear, i. e. bear retinidia, and touch the oval gelatinous lens, which must be formed originally by secretion from the cells. There is an optic ganglion. This eye resembles that of *Chaetopoda* and *Gastropoda*<sup>1</sup>.

The digestive tract consists of the buccal depression above mentioned, a muscular pharynx into which opens ventrally and posteriorly the common duct of the two salivary glands, a narrow oesophagus, all lined by the chitinoid cuticle; of a wide mesenteron stretching nearly the whole length of the body, and a short rectum lined by cuticle and opening by a terminal anus. The rectum has an external circular and an internal longitudinal layer of muscle fibres. The position of these layers is reversed in the other sections of the tract. A dorsal blood-vessel or heart in the shape of a muscular tube with a pair of valved ostia to each somite of the body lies in a pericardial cavity, closed below by a horizontal septum and placed between the two dorsal muscle bands. It gives off no vessels. A delicate ventral vessel lies externally to the circular layer of muscles. There is

<sup>1</sup> Patten considers that it represents the primitive eye of the Arthropoda, from which other forms have been derived by abbreviation of development.

a double row of stigmatic apertures on either side the median dorsal line, and similar rows on either side the median ventral line; other apertures are found on the anterior and posterior aspects of the feet, at their base, on the dorsal aspect of the head, and a single large median ventral aperture in front of the mouth. Each stigma leads into a pit dilated internally, from which proceed bundles of unbranched extremely minute tracheal tubes, lined by a cuticle which has a faint transverse striation. They are distributed to the muscles, viscera, nervous system, &c. A nephridium opens ventrally near the base of each foot. It consists of a vesicle opening externally; a coiled tubular portion; and a terminal funnel (?ciliated) which opens into the section of the coelome in the foot, from which it is stated to be differentiated (cp. the Elasmobranch excretory system). The three first pairs of nephridia are rudimentary, the fourth and fifth enlarged and somewhat peculiar. The sexes are separate. The male has a pair of testes, each with a prostatic gland. The two vasa deferentia unite, and then receive terminally the ducts of a pair of tubular accessory glands. The ovary is single, but divided by a longitudinal vertical septum into two halves. The two oviducts dilate into uteri in which the embryo is developed. They unite in a terminal vestibule. The generative aperture is ventral and in front of the anus. The filiform spermatozoa are united into rodlike spermatophores, which the male attaches to the body of the female in any region. Segmentation is complete. The blastopore in *P. capensis* is elongated and divides, forming both mouth and anus. The young differ at birth from the adult only in size and colour.

*P. Edwardsi* differs in some respects from *P. capensis*. Crural glands are absent in the female, present in the male only on the 7-8 pairs of praegenital limbs. Bean-shaped vesicles to which muscles are attached and nerves distributed are lodged on the dorsal aspect near the claw of each limb. A pair of glands open ventrally in the male, one on either side of the anus (? = accessory male organs of *P. capensis*). The stigmata are irregularly scattered. There are no anal papillae. The sexual aperture lies in the penultimate somite between the last pair of limbs. The prostate gland of Moseley is the real testis and gives origin to the spermatospores, which undergo development in the dilated portion or testis of Moseley. The united portion of the vasa deferentia is divisible into three regions, an anterior in which the sperm collects, a middle in which the spermatophore is formed, and a terminal, the muscular ductus ejaculatorius. The spermatophore is about  $1\frac{1}{2}$  inch (= 4 cm.) long, has several envelopes, and contains the agglutinated spermatozoa in 3-5 dilations. The female organs consist of two ovaries, each connected by a ligament to the pericardial septum; of two oviducts, which communicate anteriorly and have each a funnel-shaped aperture into the coelome, and carry a horseshoe-shaped receptaculum seminis communicating at each

end with the oviduct; and two uteri, with a single short muscular vagina. Ciliated epithelium is found in the ducts of the receptaculum, and in the section of the vas deferens that secretes the spermatophore.

In *P. Novae-Zelandiae* the tracheae are said to branch. The end of the male duct is exceedingly muscular (=penis?), and contains unicellular glands in its walls. There is a spermatophore (Moseley).

The various species of *Peripatus* are found at the Cape of Good Hope, in Australia and New Zealand, in Central and South America, and the West Indies. They live under stones, in rotting wood, &c. in moist places, are nocturnal in habit, and feed on insects, &c., which they ensnare by the ejection of slime from the oral papillae. Their distribution and anatomy point to an extreme archaic origin.

Moseley, 'Myriapoda,' Encyclopaedia Britannica (ed. ix), xvii; Balfour, Q. J. M. xxiii. 1883 (with lit.); Gaffron, Schneider's Zool. Beiträge, i. 1885. *Eye*, Carrière, 'Sehorgane der Thiere,' 1885, p. 121. *Development*, Sedgwick, Q. J. M. xxv. 1855; xxvi. 1886; von Kennel, Arb. Zool. Zoot. Inst. Wurzburg, vii. 1885; viii. (1), 1886.

#### CLASS ARACHNIDA.

*Tracheate or branchiate Arthropoda with a cephalothorax bearing 4-6 pairs of ambulatory limbs, and an abdomen either segmented or unsegmented and sometimes divisible into two distinct regions, an anterior mesosoma, and a posterior metasoma, with a post-anal telson or spine.*

The head is rarely distinct from the thorax (some *Acarina*), or the thorax broken up into three clearly separate somites (*Solifugae*). In tracheate forms the abdomen may be soft, unsegmented, and separated by a constriction from the cephalothorax (*Araneidae*), or else united to it (*Acarina*). It is scarcely represented in *Tardigrada*. It possesses six somites in *Phalangidae*, in the remaining groups nine to twelve. Of these the first seven in *Scorpionidae* or nine in *Thelyphonus* (*Pedipalpi*) are broad, while the other five (*Scorpionidae*) or three (*Thelyphonus*) are contracted. Among branchiate forms *Limulus* (*Xiphosura*) has the mesosoma and metasoma fused and the original segmentation lost; the *Eurypterina* possess twelve distinct somites, whilst the *Trilobita* have a mesosoma containing 1-26 somites, and a metasoma or pygidium with somites undifferentiated. The telson is present in *Xiphosura* and *Eurypterina*, and in the *Scorpionidae*, where it forms the 'sting' and incloses a poison gland. In *Thelyphonus* it is represented by a long jointed filament, and in *Araneidae* by a small caudal lobe or anal valve. The *Linguatulina* differ remarkably from other Arachnida, and have an elongated ringed body, sometimes flattened, with an anterior pair of sensory papillae, and two pairs of chitinoid hooks placed anteriorly close to the mouth.



A well-developed chitinoid piece—the camerostome (the hypostoma so-called, in *Trilobita*?)—overhangs the mouth anteriorly. The sternal region in the thorax is variously developed or suppressed in the different groups. The posterior part or metasternite develops in *Limulus* into the two lobes or chilaria which lie behind the last pair of cephalothoracic limbs.

In the tracheate forms the appendages of the cephalothorax are as follows:—a pair of falces or chelicerae post-oral in development, prae-oral in the adult, composed of 1 to 3 joints, and terminated by a claw or pincer-like chela (*Scorpio*, &c.) or else represented by a pair of stilets (some *Acarina*); a pair of palpi (pedipalpi) or chelae usually large, the basal joints of which are well developed, inclosing the mouth (and stilets when present), and terminated either by a claw or chela, or by a copulatory apparatus in the male Araneid<sup>1</sup>; four pairs of limbs, generally elongated, ambulatory, and terminated by claws, to which adhesive lobes or discs may be added in some *Acarina*<sup>2</sup>. The number of joints in the limbs is variable, usually 6-7; and there may be a well-formed tarsus (*Solifugae*). The coxal joints of the two first pairs of ambulatory limbs are in relation with the mouth in *Scorpionidae* and *Phalangida*. The abdomen has appendages only in *Scorpionidae*, the first pair forming a minute genital operculum, the second the pectines or combs, organs probably of touch. The remaining six pairs of abdominal limbs present in the embryo Scorpion abort. Abdominal limbs are present to the number of four pairs in the embryo Spider, but abort at an early period.

Among branchiate forms *Limulus* has a pair of 3-jointed prae-oral chelicerae, the *Eurypterina* homologous appendages which are sometimes non-chelate. *Limulus* has five pairs of post-oral cephalothoracic limbs, the *Eurypterina* and *Trilobita* four pairs, of which the last are the most powerful. The coxae of these limbs surround the oral depression, and are therefore masticatory. *Limulus* has six pairs of limbs on the abdominal mesosoma, of which the first pair fuse to form a genital operculum, as in *Scorpio*; whilst the remaining five are lamellate and carry externally on their posterior surfaces a series of close-set branchial folds. The two first

<sup>1</sup> During the development of some *Acarina* the embryonic chelicerae and pedipalpi fuse into a proboscis. At a later stage, after an ecdysis, the stilets and palpi grow out from the proboscis, and are presumed to be the homologues respectively of the chelicerae (or mandibles as they are sometimes termed in the *Acarina*) and pedipalpi. Haller states that the *Acarina* possess four pairs of mouth-parts, a pair of mandibles, a first and a second pair of maxillae, the second often rudimentary, and a labium usually palpate. As an adult Mite also possesses four pairs of ambulatory limbs, the last of which Haller regards as abdominal, it has two pairs of limbs in addition to those present in a Spider. A Spider however has embryonic limbs, lost in development; and rudiments of two extra pairs are present in the Scorpion, as the operculum and pectinated appendages. See pp. 496-7 *ante*, and table, pp. 174-5.

<sup>2</sup> Kramer holds, as do some other authorities, that the two last pairs of limbs belong to the abdomen in *Acarina*. See his paper on 'Segmentation of the Mites,' A. N. 48 (1), 1882 (A. N. H. (5), x). The abdomen in the Mite in question (*Alycus roseus*?) has nine somites.

abdominal somites in *Eurypterina* are covered by a flap (? genital operculum), and probably bore branchiae. In *Trilobita* the somites of the mesosoma and the unsegmented metasoma (pygidium) have slender jointed limbs furnished with a short external jointed epi- or exo-podite. Two straight or spirally coiled branchial filaments are attached externally to the base of the limb, and appear to resemble closely the branchiae of certain species of *Cyamus* (Crustacea *Amphipoda*).

The chitinoid cuticle is thick and dense in *Limulus*, *Scorpio*, &c., delicate in *Linguatulina*. There are cutaneous glands in *Linguatulina* and some *Acarina*. The *Solifugae* are covered with thick-set hairs, and in *Acarina* cuticular hairs or processes may attain a great development. The *Araneidae* and *Pseudoscorpionidae* possess silk glands. In the former group they are very numerous, and open on the apices of 4-6 spinnerets placed in front of the anus: their secretion is used to form the web and attach the ova. In the latter they open near the genital outlet on the second abdominal somite<sup>1</sup>.

The supra-oesophageal nervous centre supplies the eyes and integument: it is connected at the sides and behind the oesophagus to a single nerve mass in *Linguatulina*, *Acarina*, *Araneidae*, *Pedipalpi*, and *Solifugae*, from which pass off nerves to the limbs, &c. In *Araneidae* the posterior nerve to the abdomen has often a ganglionic swelling at the junction of that region to the cephalothorax. In *Scorpionidae* there is a ventral cord with seven ganglia, the first of which corresponds to the fifth abdominal somite, the preceding parts, including the chelicerae, being supplied from the sub-oesophageal nerve-mass. In *Limulus* there is an oval oesophageal collar with 3-8 transverse commissures, which supplies the appendages of the cephalothorax, the chilaria, and the genital operculum, and an abdominal cord which gives off five groups of nerves to the branchial feet, the last pair supplying the metasoma and post-anal spine as well. A stomatogastric system exists in *Araneidae*, *Scorpionidae*, and *Phalangida*. Eyes are absent in *Linguatulina* and some *Acarina*. They are present in other Arachnida, and vary in number from two (*Acarina*, *Tardigrada*) to twelve. They are often grouped in a characteristic manner. In Spiders they are arranged in 2-3 rows across the cephalothorax dorsally and anteriorly. The *Scorpionidae* and *Xiphosura* have a pair of central dorsal eyes, and one (*Xiphosura*) or more pairs placed near the lateral margin of the cephalothorax. The lateral eyes in *Scorpionidae* and

<sup>1</sup> In a few Spiders a chitinoid plate, the cribellum, lies in front of the spinnerets. It is perforated by the ducts of innumerable glands. Its presence is correlated with that of the calamistrum, a single or double row of long wavy hairs on the dorsal aspect of the penultimate tarsal joint of the fourth pair of ambulatory limbs. One of the calamistra is rapidly vibrated over the cribellum, and draws out the secretion from the glands in the form of threads, used to strengthen the web, to assist in forming the cocoon for the eggs, and sometimes perhaps in making a domicile. See Bertkau, A. N. 48, 1, 1882.

all the eyes of *Limulus* are monostichous; the central eyes of the former group and other Arachnids, so far as known, diplostichous. With the exception of the lateral eyes of *Limulus*, which are polymeniscous, or more probably composed of a number of distinct ocelli, Arachnidan eyes are always monomeniscous. Vitellae are absent. The eyes of *Limulus* and Scorpions are retinulate. Each retinula in the central eyes of the latter consists of five cells surrounding a five-fluted rhabdome. The grouping of the cells is not so distinct in the lateral eyes. In *Limulus* the central eyes have groups of five retinular cells, but the grouping is sometimes quite irregular; the lateral eyes have retinulae with ten cells, each retinula corresponding to a single lens (*supra*). Curious differences of structure have been observed in certain Spiders between the anterior and posterior eyes of one and the same set<sup>1</sup>. In *Araneidae* auditory hairs occur on the palpi, tibiae and tarsal joints, and a sensory organ, probably olfactory or gustatory, on the anterior surface of the basal joint (=maxilla) of the palpi or second pair of limbs.

The digestive tract takes a straight course. The stomodaeum is muscular in *Linguatulina*. The part that traverses the oesophageal nerve collar is generally contracted, the anterior oral end as well as the posterior end being frequently dilated, and in the *Araneidae* (and others) the latter forms the 'sucking stomach.' Salivary glands, paired or unpaired, are generally present. They are absent in *Limulus*. The mesenteron is of considerable length. Its thoracic portion in *Araneidae* is furnished with five pairs of caeca which enter the bases of the limbs. It has lateral tubular outgrowths or glands, sometimes forked or ramified, and then forming a continuous (?) mass in *Scorpionidae* and *Limulus*. The numbers

<sup>1</sup> The differences in question are e.g. in *Epeira* that the visual cells or retinophorae of the anterior eyes are very numerous and slender, and their retinidia terminal; of the posterior eyes relatively few, stout, and their retinidia distinctly axial, whilst the retinophoral nuclei are consequently situated to the outer side of the retinidia, as in the polymeniscous eyes of Insecta and Crustacea. There can be little doubt that the retinidia of the posterior eyes are compound, and probably double as in Mollusca. In *Lycosa* and *Salticus* the ommatium of the posterior eyes is feebly concave, and does not extend laterally as far as do the vitreous cells. The outer ends of the retinophorae in *Lycosa* are swollen, and contain the nuclei; whilst in *Salticus* they are lengthened out and bent horizontally, so that the nuclei form a circumferential layer. Graber states that the vitreous cells = corneal hypodermis, are present in the lateral eyes of Scorpions. Patten regards the eyes of *Limulus* and *Scorpions* as of a peculiar type altogether, and as divergent in the same direction, *Limulus* more than *Scorpions*. They start with the fusion of a number of ocelli, which is not the case with the compound eyes of other Arthropods. It may be noted that the basement membrane of the hypodermis extends across the eye beneath the corneal hypodermis (=vitreous cells) in the eyes of Spiders, the central eyes of Scorpions, and of *Limulus*. In the last-named there are also a number of intrusive connective tissue elements. Lankester and Bourne figure the hypodermic basement membrane as passing beneath the lateral eyes of *Limulus* and Scorpions. In Spiders a membrane also extends in a similar way beneath the eye, and is stated to be continuous with the hypodermic basement membrane. The rhabdomes in Lankester and Bourne's account of *Limulus* and Scorpions would correspond on Patten's view to the vitellae so called of Insecta, &c. See note, p. 452, where Patten's terms are explained.

of these glands vary. The proctodaeum varies in length and size. Its rectal end is dilated in *Araneidae*, and with the exception of *Linguatulina* and *Limulus* its anterior end is provided with a pair of Malpighian or renal tubes, which are often branched. The anus is ventral at the base of the telson in forms which possess that structure, in others it is terminal and more or less ventral according to the shape of the tergal region of the abdomen. The food of Arachnids is liquid, either the juices of plants (some *Acarina*) or of animals; but *Limulus* feeds upon soft worms, &c., which it sucks into its wide pharynx and there crushes.

The coelome is more or less filled by the contained viscera, and in the higher forms by an abundant connective tissue as well as muscles of the appendages, &c. An *entosternite* or chitinous fibro-cellular plate much resembling cartilage, lies between the anterior extremity of the digestive tract and the central nervous system. Muscles are attached to it. It has been found in *Apus* among Crustacea, but its presence and large size is characteristic of Arachnida. In *Scorpio*, *Mygale* (*Araneidae*), in *Phalangidae*, *Galeodes* (*Solifugae*), and *Limulus*, a paired ductless *coxal* gland lies in the thoracic region; in the first-named in relation with the coxae of the last pair of limbs, in *Mygale* and *Limulus* with the coxae of the last four pairs of limbs. It has been found also in other Spiders; and in *Atypus*, two apertures, one at the base of the first pair of legs, the second at the base of the third pair, exist in connection with it. So too in *Scurria*, where a reservoir for the secretion is appended close to the aperture. In the young *Limulus* there is an aperture on the coxae of the fifth pair of limbs. The *Oribatidae* among *Acarina* have a very similar gland, which perhaps opens externally.

The blood-plasma contains haemocyanin in quantity, and is blue-coloured when oxygenated in Scorpions (*Androctonus*) and *Limulus*. It contains amoeboid corpuscles. A heart is absent in *Linguatulina* and *Acarina*, except some *Gamasidae*, in which a single-chambered heart with long aorta and bivalved inlets lies in the posterior part of the abdomen. A three-chambered heart with three pairs of lateral valved ostia is found in *Araneidae* and *Phalangidae*. It is eight-chambered in Scorpions and *Limulus*. It lies within a pericardium or sinus in the two last-named, and in some Araneids at least, into which open venous passages bringing back blood from the respiratory organs. Alary muscles are attached to this pericardium. There is an anterior aorta which supplies the eyes and limbs, and in Scorpions gives off two vessels which surround the oesophagus and unite into a median artery running backwards dorsally to the ventral nerve-cord. In *Limulus* the corresponding vessels *ensheath* the oesophageal nerve-collar as well as the nerves which it gives off and the ventral cord. The heart has a posterior aorta in *Araneidae* and *Scorpionidae*. Lateral vessels are given off from the base of the anterior

aorta, from each chamber of the heart, and from the posterior aorta in *Scorpionidae*: lateral vessels also exist in some *Araneidae* (*Epeira*). In *Limulus* there are four pairs of such vessels, which unite at their external ends into a lateral longitudinal trunk on each side. These two trunks fuse posteriorly, and are continued backwards as a single vessel. The capillary system is well developed in *Scorpionidae* and *Limulus*. The venous blood passes to the respiratory organs from a median ventral sinus. Respiration is cutaneous in *Linguatulina*, some aquatic and parasitic *Acarina*, and *Tardigrada*. There is a pair of stigmata leading to a tracheal system of tubes between the third and fourth pair of limbs in most *Acarina*, between the last pair of limbs in *Phalangidae*, and behind the fourth pair of limbs in *Solifugae*. Stigmata in other Arachnida are confined to the ventral aspect of the abdomen. One pair on the third to the sixth somite inclusive in Scorpions lead into long sacs with foliated walls. The *Pedipalpi* have similar structures on the third and fourth somites, and among *Araneidae* there are either two pairs of such sacs (*Mygale*) or the second pair lead into a system of tracheal tubes. Some *Araneidae* possess in addition a single stigma in front of the spinnerets leading into two branched or four simple tracheal stems. There are two pairs of abdominal stigmata leading to tracheae in the *Pseudoscorpionidae*, and also in the *Solifugae*. *Limulus* is branchiate, and the respiratory organs consist of parallel leaf-like folds borne upon the posterior faces and near the outer edges of the last five pairs of abdominal limbs.

The *Tardigrada* are hermaphrodite, and possess an azygos ovary and two testes which open into the proctodaeum. The testis may be unpaired or paired, the ovary always unpaired, in *Linguatulina*, but the vasa deferentia and oviducts are double. The latter open into a long vagina or uterus, in which the ova develop into embryos; its aperture lies on the ventral aspect in front of the anus. The former are terminated each by a copulatory cirrus which can be protruded from the single anteriorly placed male aperture. The *Acarina* and *Phalangidae* have as a rule a ring-like testis and ovary. The fertile portion of the glands may be more or less extended or restricted. The single genital aperture is on the abdomen ventrally and anteriorly, even between the last pair of limbs in some *Acarina*. The *Phalangidae* possess a protrusible copulatory organ and ovipositor. In the *Scorpionidae* the two testes consist of two, the single ovary of three, longitudinal tubes, united by cross anastomoses. The ducts open by a single aperture at the base of the operculum on the first somite of the abdomen. The testes of the *Araneidae* are two in number, tubular, with the termination of the tube sometimes dilated into vesiculae seminales. They open between the stigmata. The ovaries are usually two also, but they sometimes unite into a ring (*Segestria*, *Oletera*): the oviducts fuse into a single vagina. The testis and ovary of *Limulus* are retiform;

the ducts are double, and open separately on the posterior aspect of the operculum or first pair of abdominal appendages. The Scorpion has a copulatory organ at the end of each vas deferens, whilst in *Limulus* the spermatozoa are shed into the water. The male Spider retains the sperm in a special receptacle developed on the inner aspect of the last joint of each palpus. This structure consists of a chitinoid protecting envelope which often assumes complicated forms, open at the apex and lodging a coiled tube. From this apparatus the sperm is transferred to the female receptacula. Accessory glands, vesiculæ seminales, and receptacula seminis are often found except in *Limulus*. The receptacula seminis (rarely single) possess in most *Araneidae* independent openings in front of the female genital aperture.

*Phrynus (Pedipalpi)* and the *Scorpionidae* are viviparous<sup>1</sup>. The *Tardigrada* lay their ova in their cast-off skin; the *Araneidae* as a rule and the *Pseudoscorpionidae* carry their ova about attached to the abdomen. The ovum of the Scorpions is telolecithal; of others centrolecithal. The mode of segmentation in the latter case varies. The young Arachnid is as a rule hatched in a form resembling the adult. The *Acarina* however are often at first hexapodous; and in some instances the young octopod animal differs from the adult in colour, presence of hairs, &c., and passes through an inert stage<sup>2</sup>. The embryo *Pentastomum taenioides* lives encysted in the liver or lungs of the rabbit: it moults and acquires two pairs of hooks and a ringed abdomen, and then wanders about in its host, and may become encysted a second time. When devoured by the dog or wolf it becomes adult in the nasal fossae and frontal sinuses.

Certain *Acarina*, e. g. *Demodex*, are parasitic, as are the *Linguatulina*. The *Phalangidae* and *Solifugae* are nocturnal. The *Araneidae* are terrestrial for the most part. Some *Acarina* are aquatic, *Limulus* marine, as were the extinct *Eurypterina* and *Trilobita*. A Scorpion has been found in Silurian strata, and a Phalangid in the Solenhofen slates (Mesozoic); Spiders occur in amber. A Xiphosuran is found in the upper Silurian, *Limulus* in the Solenhofen slates: the *Eurypterina* extend from the upper Silurian to the Lower Carboniferous period; the *Trilobita* from Cambrian to the same period, but are chiefly Cambrian and Silurian.

<sup>1</sup> In *Sphaerogyna ventricosa (Acarina)* development is intra-uterine, and the female gives birth to adult males and females, which are fecundated at birth; Laboulbène and Megnin, Journal de l'Anat. et Physiol. xxi. 1885.

<sup>2</sup> This stage known as *Hypopus* appears to be the heteromorphous nymph or immature octopod form of *Tyroglyphus* and some allied genera. It has typically a large covering carapace; the fourth pair of limbs armed with long setae; mouth-parts rudimentary; the ventral integument soft and furnished with suckers, especially at the posterior end of the body. The special use of this stage, which passes by an ecdysis into the ordinary adult, appears to be the transport and dispersal of the species. See Michael, J. L. S. xvii. 1884, and Journal Roy. Micr. Soc. (2), v. 1885, p. 22 et seqq.

The Arachnida are classified as follows :—

A. Tracheate groups.

1. *Linguatulina* : parasitic, worm-like, elongated, body ringed ; *Pentastomum*.
2. *Acarina* : abdomen united to cephalothorax ; oral appendages adapted to biting, or piercing and sucking ; mostly tracheate ; minute. *Demodex*, *Sarcoptes*, *Tyroglyphus*, *Hydrachna*, &c.
3. *Tardigrada* : no abdomen ; four pairs of short limbs ; oral appendages adapted for piercing and sucking. Hermaphrodite. Minute, aquatic. *Arctiscon*, *Macrobotus*, &c.
4. *Araneidae* : abdomen soft, unsegmented ; falces with a poison-gland ; 4-6 spinnerets ; 2-4 lung-sacs. *Mygale*, *Cteniza*, *Tegenaria*, &c.
5. *Phalangidae* : abdomen as a rule with six somites, broad and applied to cephalothorax ; falces with a didactyle claw or chela ; limbs long and slender ; tracheate. *Phalangium*, &c.
6. *Pedipalpi* : abdomen with 11-12 somites ; falces clawed ; pedipalpi clawed (*Phrynus*) or chelate (*Thelyphonus*) ; first pair of limbs slender and elongate ; four lung-sacs. *Phrynus*, *Thelyphonus*.
7. *Scorpionidae* : abdomen composed of a seven-segmented mesosoma and five-segmented metasoma, with telson armed with a poison-gland ; both oral appendages chelate ; second pair large ; four lung-sacs. *Androctonus*, *Buthus*, *Scorpio*, &c.
8. *Pseudo-scorpionidae* : abdomen broad and flat, with 10-11 somites ; pedipalpi chelate ; tracheate. *Chelifer*, *Obisium*, *Chthonius*, &c.
9. *Solifugae* : head and thorax separate ; thorax of three separate somites ; abdomen with nine somites ; falces chelate ; palpi limb-like, tracheate. *Galeodes* (= *Solpuga*).

B. Branchiate groups = *Poecilopoda* of Wallcott.

1. *Xiphosura* : cephalothorax shield-shaped ; meso- and meta-soma fused ; first pair of oral appendages chelate ; coxae of the five pairs of cephalothoracic limbs masticatory ; six pairs of mesosomic limbs ; a telson. *Limulus*, *Belinurus* (fossil).
2. *Eurypterina* s. *Merostomata* : extinct ; abdomen with twelve somites and a broad telson ; first pair of oral appendages sometimes non-chelate ; four pairs of cephalothoracic limbs surround mouth ; no abdominal limbs. *Eurypterus*, *Pterygotus*, *Hemiaspis*, &c.
3. *Trilobita* : extinct ; a cephalothorax ; a segmented mesosoma and unsegmented metasoma (pygidium), both bearing limbs ; no prae-orally placed appendages, but four pair of cephalothoracic limbs surround the mouth. *Calymene*, *Phacops*, *Asaphus*, &c.

'Arachnida,' P. Cambridge, Encyclopaedia Britannica (ed. ix.), ii. 1875 ; Packard, Study of Insects, Salem, 1872 ; Murray, Economic Entomology, S. Kensington Handbooks, 1877 ; Blanchard, 'Arachnides,' L'organisation du Règne animal, Paris, 1860 ; Zoological position of Class, Kingsley, Q. J. M. xxv. p. 556.

*Linguatulina*, P. J. Van Beneden, A. Sc. N. (3), xi. 1849 ; Leuckart, Bau der Pentastomen, Leipzig, 1860.

*Acarina*, see pp. 496-7, ante. Classification, cf. Michael, *Oribatidae*, Ray Soc. i. cap. 4 ; *Demodex*, Mégnin, Journal de l'Anat. et Physiol. xii. 1877 ; *Sarcoptidae*,

Fürstenberg, 'Krätzmilben der Menschen,' &c. Leipzig, 1861; *Sarcoptides psoriques*, Mégnin, Revue et Magasin de Zoologie (3), v. 1877 (some plates in vi. 1878). *Sarcoptides plumicoles*, Trouessart, Paris, 1885; Robin et Mégnin, Journal de l'Anat. et Physiol. xiii. 1877; Haller, Z. W. Z. xxxvi. 1881. *Tyroglyphidae*, Michael, Journal Roy. Micr. Soc. v. 1885; Nalepa, SB. Akad. Wien, xc. pt. 1. 1884; Haller, Z. W. Z. xxxiv. 1880. *Glyciphagus*, Michael, J. L. S. xix. *Gamasidae*, Kramer, A. N. 48. (1), 1882; Michael, J. L. S. xv. 1881. *Argas (Ixodidae)*, Laboulbène and Mégnin, Journal de l'Anat. et Physiol. xviii. 1882. *Phytoptidae*: *Phytoptus*, Thomas, Zeitschrift f. Ges. Natw. (Giebel), 33. 1869; *Galls*, Id. op. cit. 49. 1877; Nova Acta, xxxviii. 1876; Schlechtendal, Zeit. Natw., 55, 1882; 56, 1883. *Trombidiidae*: *Trombidium* (and lit.), Henking, Z. W. Z. xxxvii. 1882; Donnadieu, Recherches pour servir à l'histoire des Tétraniques, Paris, 1875 (Ann. Soc. Lin. Lyons, xxii). *Hydrachnidae*, Kramer, A. N. 41. (1), 1875. *British Oribatidae*, Michael, Ray Soc. i. 1884.

*Tardigrada*, Greeff, A. M. A. ii. 1866; *Echiniscus*, Schultze, *ibid.* i. 1865.

*Araneidae*, see pp. 303, 304. *Classification*, see Thorell, A. N. H. (5), xvii. 1886 (with lit.). *Spiders of Great Britain*, P. Cambridge (systematic list), Tr. L. S. xxx. 1875. *Trap-door spiders*, Moggridge, 1873, and Suppl. 1874. *Mouth-parts*, Croneberg, A. N. 46 (1), 1880; Bertkau, A. N. 36 (1), 1870. *Spinnerets of Epeira*, Oeffinger, A. M. A. ii. 1866. *Respiratory organs*, Bertkau, A. N. 38 (1), 1872. *Generative organs*, Id. op. cit. 41 (1), 1875; *male palps*, see also Emerton, Proc. Boston Soc. xvii. *Seasonal dimorphism*, Karsch, Bertkau, Z. A. viii. 1885. *Development*, Balfour, Q. J. M. xx. 1880. *Regeneration of lost parts*, Blackwall, Brit. Assoc. Reports, 1844. *Stridulating organs*, Campbell, J. L. S. xv. 1881.

*Phalangidae*: *Classification* (with lit.), Simon, 'Arachnides de France,' vii. 1879; cf. Id. Ann. Soc. Entomol. Belg. xxii. 1879. *British sp.*, Meade, A. N. H. (2), xv. 1855. *Anatomy*, Rössler, Z. W. Z. xxxvi. 1882; Loman, Bijdrage tot de Anat. der Phalangiden (Diss.), Amsterdam, 1881. *Genital organs*, H. de Graaf, Sur la structure des organes genitaux des Phalangiens, Leiden, 1882 (Z. A. iii. 1880).

*Pedipalpi*, Karsch, A. N. 45 (1), 1879; 46 (1), 1880; Butler, A. N. H. (5), iv. 1879. *Phrynus*, Butler, A. N. H. (4), xii. 1873; *Thelyphonus*, Id. (4), x. 1872, and xii. 1873.

*Scorpionidae*: *Classification*, Thorell, A. N. H. (4), xvii. 1876; Atti Soc. Ital. xix. 1876. *Anatomy*, Ray Lankester, Q. J. M. xxi. 1881 (under *Limulus*); xxiii. 1883; xxiv. 1884; Tr. Z. S. xi. *Poison apparatus*, Joyeux-Laffuie, A. Z. Expt. (2), i. 1884; Dufour, 'Histoire anatomique' Mém. présentées par divers savants à l'Acad. des Sciences, xiv. 1856. *Lung-books*, Ray Lankester, Q. J. M. xxv. 1885.

*Pseudoscorpionidae*, Stecker, A. N. 41 (1), 1875 (lit. and distribution); L. Koch, Übersichtliche Darstellung des Europ. Chernetiden, Nürnberg, 1873.

*Solifugae*, Karsch, A. N. 46 (1), 1880. *Poison-glands*, Croneberg, Z. A. ii. 1879. *Anatomy*, Dufour, C. R. 46, 1858.

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*Trilobita*, Wallcott, Bull. Mus. Harvard, viii. 1880-81; Id. Science, iii. 1884; Salter, Monograph, Palaeont. Soc. 1863-83; Woodward, Monograph, Palaeont. Soc. 1883-84.

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## CLASS CRUSTACEA.

*Aquatic Arthropoda with cutaneous or branchiate respiration: with two pairs of antennae, a limb-bearing thorax, either free or united more or less to the head, and as a rule a segmented abdomen which may or may not carry limbs.*

The variety of external forms in this class is very great. The head appears to consist of five fused somites, denoted by the presence of two pairs of antennae, a pair of mandibles, and two pairs of maxillae. The number of somites in the thorax and abdomen of *Entomostraca* is extremely variable. In the *Malacostraca* the former has eight, the latter six somites with a telson, except in *Nebalia (Leptostraca)*, where there are eight. And of the eight thoracic somites, one (*Thoracostraca*), three or four (*Cumacea*), five (*Stomatopoda*), or all (*Decapoda*) may be united to the head to form a cephalothorax. The somites of the abdomen may fuse as in some *Isopoda*; or the abdomen may be rudimentary, e.g. *Cirripedia* and *Laemodipoda (Amphipoda)*. In the *Ostracoda* the body is not segmented at any time; and in some fixed or parasitic forms segmentation may become obscured or lost, though in some instances shown by the presence of limbs.

Each somite is typically ring-like or cylindrical as in *Copepoda*, but it may be flattened dorso-ventrally or laterally. In many cases certain somites, or all of them as in most *Thoracostraca*, develop a lateral pleural process, extending outwards above the articulation of the limbs. A process or fold formed by the edges of the last cephalic somite constitutes the shield of *Apus*, the mantle (with or without calcareous pieces) of the *Cirripedia*, and the bivalve shell of *Nebalia*. United pleural processes of

the fused somites of the thorax form the branchiostegite of *Podophthalmata* and the bivalve shell of the *Estheridae* (*Branchiopoda*), *Cladocera*, and *Ostracoda*. In the last-named group and in *Nebalia* a special transverse muscle closes the shell upon the body.

The first antenna is primitively uniramous, and retains this character in *Phyllopoda*, *Ostracoda*, and *Copepoda*; but during growth it generally becomes two or three branched. It is minute in *Cladocera* and terrestrial *Isopoda*. In the *Cirripedia* its second joint carries a disc in connection with which is the aperture of a cement gland. The animal is attached by its means to some foreign object, whilst the head dilates into a broad base or elongates into a peduncle. The other appendages of the head and body are primitively biramous, except in the *Ostracoda* and the appendages of the thorax in *Arthrostraca*. The second antenna may become uniramous, or the outer branch may be reduced to a scale or squame (many *Thora-costraca*). It is minute in *Apus* and is lost in all *Cirripedia* and *Hyperidae* (*Amphipoda*). The mandible is reduced to the basal masticatory portion in *Phyllopoda* and *Cumacea*. In other groups the reduction may be temporary, and there are developed subsequently a number of small joints which form the *palp*. In many parasitic suctorial Crustacea the mandibles form a pair of stylets, inclosed in a more or less complete sheath constituted by the so-called upper and lower lips. The maxillae vary much in character, but are generally more or less expanded or foliaceous. The outer and inner branch (=exo- and endo-podite) of the second maxilla are separated in *Copepoda* so as to appear like independent limbs, whilst in *Cladocera* the appendage is aborted. In the Copepodan families *Calanidae* and *Pontellidae* both first and second maxillae closely resemble the biramous *Nauplius* appendage. The first maxillae, like the mandibles, are stylets in *Argulus*, whilst the second are converted into large sucking discs. Both pairs of maxillae want the exopodite in *Isopoda*.

The thorax is always limb-bearing; the abdomen bears none in *Entomostraca*, but does so with few exceptions in *Malacostraca*. The primitive type of limb is probably that of the *Copepoda*, which closely resembles the *Nauplius* appendage. It has a basal stem carrying a more or less jointed or lamellate exo- and endo-podite. Such a limb is seen in the thoracic appendages of *Cirripedia* and of the *Schizopoda* among *Malacostraca*, and is generally found in the abdominal region. The Phyllopod type of appendage, seen also but in a more primitive state in *Nebalia*, with its branchia and external respiratory plate, and its series of internal lobes or endites, is probably an adaptation of the Copepodan limb. The exopodite is lost in the ambulatory thoracic limbs of *Arthrostraca* and *Decapoda*. Of the eight pairs of thoracic limbs in *Malacostraca* the first pair in *Arthrostraca*, the three first in *Decapoda*, and the five first in *Stomatopoda* are modified into foot jaws or maxillipeds. *Apus* (*Branchiopoda*)

is remarkable for having more than one pair of limbs on the posterior thoracic somites. The abdominal limbs, when present, with the exception of the last pair, never attain the same locomotor importance as do the thoracic. The last somite of the abdomen in *Entomostraca* carries a pair of *furcae anales*, variable in character, between which the anus opens. In *Malacostraca* the furcae and the somite which bears them are modified into an azygos plate or telson with the anus placed on its ventral surface.

The chitinous cuticle is thin and delicate, or thick, laminate, and calcified. Glands are found in various positions opening on the integument, the limbs, upper lip, round the mouth, where they may have an amylolytic function (many *Isopoda*); or on the under surface of the abdomen (*Decapoda*), or the lamellae of the brood-pouch (some *Isopoda*), when the secretion probably serves to attach the ova. In some *Cladocera* (e. g. *Sida*) there is a nuchal gland, by means of which the animal can attach itself to some foreign object. A similar gland is present in the young Branchiopod, but is more or less aborted subsequently, and it exists as the dorsal organ in the embryo Arthrostracan.

The nervous system resembles that of other Arthropoda in its general features. The commissural cords connecting the supra- and infra-oesophageal ganglia are sometimes of great length. The first-mentioned ganglion supplies the eyes, the first antennae, and, except in certain *Phyllopora*, the second antennae as well. In the order named the second antennae are innervated (? in all) by a pair of ganglia situated on the oesophageal commissures, and the right and left halves of the post-oral ganglia retain their independence and are united by transverse commissures. In other orders the halves are as a rule united closely; the ganglia supplying the oral appendages are fused into an infra-oesophageal ganglion, and concentration may proceed to such an extent that all the post-oral ganglia become united into a single mass (*Decapoda Brachyura*)<sup>1</sup>. A stomatogastric system originates in *Apus* from the first post-oral pair of ganglia; in the *Decapoda* from ganglia on the oesophageal commissures which are probably homologous with the first post-oral ganglia of *Apus*, and additional factors may be derived in the group last mentioned from the supra-oesophageal ganglion<sup>2</sup>.

<sup>1</sup> According to Claus (*Organismus der Phronimiden*, Arb. Zool. Inst. Wien, ii. p. 52) the nerves of the second antennae originate from the oesophageal commissures in the *Phronimidae*, but whether the corresponding nerve-centres are supra- or infra-oesophageal in position is a point he did not determine. In some *Isopoda*, the right and left halves of the thoracic ganglia, and of the abdominal also when distinct, are more or less separate, and connected to one another by transverse commissures (Huet, *Journal de l'Anat. et Physiol.* xix. p. 305).

<sup>2</sup> A nerve with ganglion cells intercalated from place to place has been observed by Claus in *Phronimidae* running on the dorsal aspect of the heart (op. cit. *supra*, p. 40). So too in *Stomatopoda*, in which a ganglion cell corresponds to each pair of ostia (Claus, 'Circulation of *Stomatopoda*,' op. cit. v. 1884, p. 11). In the same order a ganglion lies just above the epistoma (loc. cit. p. 12). Huet has recently investigated the sympathetic system of *Isopoda*. He detected an azygos nerve

Eyes are absent in some Crustaceans which live subterraneanly. They are confined to the head, but in the *Euphausiidae* (*Schizopoda*) accessory eyes or luminous organs (?) occur on the coxae of the second thoracic limbs, on the bases of the penultimate gills, and between the four first abdominal limbs. The eye is lost during development in *Cirripedia*, and many parasitic *Copepoda*. In some free living families of the last named order, e. g. *Cyclopidae*, there is an azygos median eye, composed of a ventral and two dorsal pigment plates imbedding a number of refractile cells. This azygos eye, which is found in the *Nauplius* form of all Crustacea, may persist as a rudiment in some *Branchiopoda* and those *Copepoda* which like the *Pontellidae* and *Argulus* possess the two laterally-placed compound eyes found in all other Crustacea. These lateral eyes may however fuse in the course of development as in *Cladocera*, and the *Cypridae* and *Cytheridae* among *Ostracoda*. In the *Cladocera* they also become inclosed in a sinus by the growth of an integumental fold. The eye is moveable in *Cladocera*, in the Ostracode *Cypridinidae*, and the *Argulidae*; mounted on a fixed stalk in the Branchiopod genus *Branchipus*, on a moveable stalk in *Podophthalmata*. The compound eye has the usual Arthropodan structure. The corneal cuticula is faceted in the *Malacostraca*, and the corneal lenses in *Isopoda* are of great size, but in other Crustacea the cuticula is of even thickness. A distinct layer of hypodermis cells intervenes between the vitellae and corneal cuticula in *Isopoda* and *Amphipoda*. The crystalline cones are composed of two segments in *Isopoda*, *Amphipoda*, and *Schizopoda*; of five in *Cladocera*; of four in other Crustacea; the retinulae are five in number in *Estheridae* (*Branchiopoda*), the *Cladocera*, and *Amphipoda*, seven in other Crustacea with possibly the exception of the *Schizopoda*. The *Malacostraca* possess four distinct ganglionic swellings in the course of the optic nerve. The 'eye-elements' are remarkably distinct from one another in *Cladocera*, *Isopoda*, and some *Amphipoda*. In the *Isopoda* they are separated by intervening pigmented hypodermis cells. The Copepodan family *Corycaeidae* differ in the structure of their eyes from all other Crustacea. A large soft lens lies immediately beneath the corneal cuticula, and the crystalline cone with the ommateum is situate at some considerable distance behind it<sup>1</sup>. Olfactory setae are generally found on the first antennae,

running from one to the next succeeding ganglion of the ventral cord, as described first by Rathke, as well as two recurrent nerves, derived one from each of the two posterior terminal nerves, and supplying the walls of the digestive tract. But he did not find the azygos 'ganglion frontale' of Leydig, placed in front of the supra-oesophageal ganglion to which it is connected; nor yet the dorsal intestinal nerve of the same observer, or of Lereboullet (see pp. 306-10, op. cit. in note 1).

<sup>1</sup> The *Phronimidae* among *Amphipoda* possess four eyes evidently formed by the division of the two eyes of other Amphipods. The pair on each side of the head are supplied by branches of the same nerve; and in *Gammarus pulex* the single eye on each side is constricted laterally. The

The *Podophthalmata* possess auditory organs, either open sacs provided with auditory hairs and inclosing foreign bodies as otoliths and placed in the basal joint of the first antenna in the *Decapoda*, or closed sacs containing a laminated otolith and situate in the endopodite of the swimmeret as in many *Schizopoda*. Auditory hairs are said also to occur on other parts of the body in the groups named.

Mouth and digestive apparatus are wanting in the *Rhizocephala* among *Cirripedia*, and the animal is attached to its host by branching processes which spring from its head and penetrate among the viscera. The tract is rudimentary in *Proteolepas* and many male *Cirripedia*. In other *Crustacea* the mouth lies between the mandibles and has an upper lip or epistoma, and a lower lip or metastoma<sup>1</sup>. The latter is often bilobed, and is known in that case as paragnatha. In *Euphausia* and perhaps in *Malacostraca* generally the paragnatha are derived from the basal part of the first maxillae. The stomodaeum or oesophageal section of the tract is well developed and often dilated posteriorly. The dilatation in higher *Crustacea* is generally provided with chitinous and sometimes calcified plates and teeth, differentiations of the cuticular lining. The mesenteron has no cuticle and corresponds with the archenteron. It varies in length and is rarely convoluted, and is furnished with glandular caeca. These caeca may be short and simple, variable in number, or large branched organs as in *Decapoda*. The proctodaeum is long in the higher *Crustacea*, short in the *Entomostraca*, and is lined by cuticle. The anus is posterior, and may be dorsal (*Copepoda*) or ventral (*Malacostraca*).

The coelome is filled to a variable degree by the muscles of the somites and limbs and the viscera. It contains a blood-plasma in which amoeboid corpuscles are suspended. The plasma is sometimes tinged red by a colouring matter, either haemoglobin (some *Phyllopoda* and *Cypris*) or tetronerythin. In other instances, e.g. *Homarus*, *Squilla* (*Decapoda*), it contains haemocyanin or haemochromogen. A heart may be absent (some *Ostracoda* and *Copepoda*, *Cirripedia*?). It is placed in the thorax

nuclei of the retinulae in *Amphipoda* are situated in the bases of the cells, which are distinctly separated from their outer parts. The nerves to the refractile cells of the *Cyclops* eye either unite with their internal pointed ends (Grenacher) or with their outer ends (Hartog).

Patten has examined the eyes of certain *Decapoda*, (*Penaeus*, *Palaemon*, *Galathea*, *Pagurus*), especially those of the first-named, in great detail. They have the typical structure given in note p. 452, *ante*. Pedicels are present in all; and in *Galathea* the two hypodermis cells corresponding to each corneal facet are modified into a contractile iris. In *Branchipus Grubii* Patten finds that the retinophorae are grouped in fours; the corneal cuticula is not faceted; the corneal hypodermis cells indefinite in arrangement. There are no pedicels, and the outermost set of bacillate retinulae absent. The somatic eyes of *Euphausia* are held by Sars to be luminous organs (Challenger Reports, xiii. 1885, *Schizopoda*, pp. 70-72). Patten considers that they have the essential structure of eyes. They possess an extremely thick laminated argentea behind the retina (cf. Mitth. Zool. Stat. Naples, vi. 1886, p. 685 et seqq.).

<sup>1</sup> Unicellular salivary glands are often found in the epistoma, or when that structure is small as in *Phronimidae*, surrounding the oesophagus. See on *Astacus*, p. 185.

and is a simple oval sac with two venous inlets and a short anterior aorta in *Cladocera*, some *Ostracoda* and *Copepoda*. It is long, thoracic in position in *Amphipoda*, abdominal in *Isopoda*; long and extending from the thorax into the abdomen in *Stomatopoda*; short in *Podophthalmata*, where it lies in the thorax. It lies in a pericardial sinus in *Arthrostraca* and *Thoracostraca*, with which it communicates by four paired ostia in *Isopoda*, three, but sometimes fewer in *Amphipoda*: by a large anterior pair and twelve smaller posterior pairs in *Stomatopoda*: and in the *Podophthalmata* by two pairs in *Mysis* and three pairs in *Decapoda*. It usually gives off in the higher Crustacea one or more anterior vessels to the eyes and antennae, lateral to the glands of the mesenteron and posterior into the abdomen: and in the *Stomatopoda* the posterior part gives off thirteen lateral pairs of vessels. The system of vessels is especially well developed in *Isopoda*, where the heart gives off lateral vessels to the feet. The anterior aorta in *Arthrostraca* forms a peri-oesophageal vascular ring, from which in *Isopoda* a sub-neural vessel is continued backwards giving off lateral branches. The venous blood-spaces are limited by connective tissue in *Arthrostraca* and *Decapoda*. In the three parasitic Copepodan genera, *Lernanthropus*, *Clavella*, and *Cyonus* (= *Congericola*), there is a special system of tubes containing a plasma with haemoglobin in solution. Respiration may be partly cutaneous as in *Copepoda* and *Cirripedia*. The bivalve shell of *Cladocera*, *Ostracoda*, and *Nebalia* is penetrated by the blood currents. But in most *Crustacea* organs of respiration exist in the shape of appendages to the thoracic limbs (*Branchiopoda*, *Cladocera*, *Leptostraca*, *Amphipoda*, *Decapoda*); to the abdominal limbs (*Stomatopoda*); and sometimes to the wall of the thorax itself (*Decapoda*), though in this case it is probable that their position is secondarily acquired. The endopodite of the abdominal limbs, with the exception of the first pair which form an operculum, is respiratory, thin, and transversely folded in *Isopoda*: and in the genus *Tylos* belonging to this order a special process of the four anterior pairs of abdominal feet bears cross folds with linear slits, which lead to branched air sacs. The inner wall of the branchiostegite in *Decapoda* is very thin, and probably respiratory, and in some land crabs there are vascular growths of the branchial chamber. The exopodite of the thoracic limbs in many instances, e.g. *Phyllopoda*, or of the second maxilla (*Decapoda*), forms a broad plate which keeps a current of water in constant motion. A rhythmical opening and shutting of the anus, admitting and expelling water, and thus constituting an anal respiration, takes place in *Phyllopoda*, *Branchiopoda*, and *Cladocera*, in *Copepoda*, *Astacus*, some *Nauplii* and *Zoaeae*, and is probably very general.

Excretory organs exist as the shell gland of *Phyllopoda* and *Copepoda* which opens close to the second maxilla: the antennary gland aborted in the two orders named during development, but persistent in *Malacostraca*,

except *Stomatopoda*, and opening on the basal joint of the second antenna: and in *Amphipoda* as one or two glands generally said to open into the anterior end of the proctodaeum, but in reality it appears opening into the posterior end of the mesenteron (Spencer). A pair of glandular excretory (?) sacs open close to the anus in *Stomatopoda* (Claus).

The sexes are united in the majority of *Cirripedia*: and in the *Cymothoidae* (*Isopoda*) the sexual organ of the young animal is male, of the old, female in function. In a few *Cirripedia* minute cirriped-like 'complemental' males are found on the hermaphrodite animal. In *Scalpellum vulgare* the male is not like a Cirriped, nor is it in the few instances where the sexes are separate, e.g. *Sc. ornatum*. In many *Copepoda* the animal is sexually mature before it is adult. The sexual organs vary much in character; they may be paired or azygos, and if paired may be united across the middle line, e.g. *Decapoda*. They lie generally in the thorax, sometimes in the abdomen, e.g. *Stomatopoda*, *Pagurus*. The ducts are as a rule double, each with its separate aperture. This aperture is variously placed in the thorax or abdomen in *Entomostraca*<sup>1</sup>, but in the *Mala-costraca* the male apertures open on the coxae of the last or eighth thoracic feet, the female on the coxae of the sixth, or else on the sterna of the corresponding somites. In the *Cirripedia* a long penis terminates the abdomen. Accessory glands are rarely present, e.g. the gland which secretes the capsule of the ovisac in *Copepoda*. Receptacula seminis are occasionally found as in most *Copepoda*. Parthenogenesis occurs in *Artemia* and *Apus* among *Branchiopoda*; in the *Cladocera* (so-called summer ova) and in some *Ostracoda* (certain species of *Cypris*<sup>2</sup>). The offspring belong to the female sex. In *Cladocera* males are eventually produced, and this is probably the case in *Ostracoda*, in *Artemia* and *Apus*, but has not been proved to occur. The male generally differs from the female in size, e.g. in parasitic *Copepoda* where it is minute; in greater development of organs of special sense; in the presence of organs modified to retain the female; or of accessory efferent organs, e.g. the two first pairs of modified abdominal feet in *Decapoda*: and in the absence of special contrivances to retain the ova, e.g. brood lamellae, such as are attached to more or fewer of the thoracic limbs in *Arthrostraca* and *Mysis*.

The spermatozoa are vibratile in *Cirripedia*: so too in *Ostracoda* after they have entered the female ducts<sup>3</sup>. In other Crustacea they are non-motile and are in *Decapoda* furnished with processes. They are generally united into spermatophores either by the secretion of the wall of the vasa deferentia or more rarely of special glands. The ova vary much in size,

<sup>1</sup> The oviducts of *Cirripedia* open at the base of the first pair of limbs, the most anterior position known in Crustacea.

<sup>2</sup> *Candona* is parthenogenetic in late autumn; so too *Cypris vidua*.

<sup>3</sup> The sperm shows amoeboid motion in the Cladoceran *Polyphemus*, but not in other members of the order. See Zaccharias, Z. W. Z. xli. 1885.

and in the quantity of secondary central yolk present. They are relatively largest when development is delayed or unaccompanied by metamorphosis. There is often a vitelline membrane and sometimes a specially secreted shell. The ova are rarely laid: they are attached by *Cypris* and *Argulus* to foreign bodies; deposited by the *Stomatopoda* in the burrows which they inhabit; left to float in a specially modified portion of the shell—the ephippium—as ‘winter’ ova by the *Cladocera*. They are generally carried about by the female, e.g. attached to the abdominal feet as in *Decapoda*; within the shell above the abdomen as in *Cladocera*; in a secreted ovisac, as by most *Copepoda*; or in a sub-thoracic brood-pouch by *Arthrostraca*.

Development is rarely direct (*Cladocera* with the exception of *Leptodora* and certain Land-crabs), and in those instances where it is apparently direct or abbreviated (*Arthrostraca*), traces of metamorphosis are to be found, e.g. the larval membrane shed *in ovo* when the two pairs of antennae and the mandibles are formed in *Oniscus* and other *Isopoda*: or as soon as the blastoderm is established, as in *Amphipoda*. The metamorphosis may be well-marked but intra-ovular, e.g. *Mysis*, *Nebalia*. The majority of *Entomostraca* quit the egg as a *Nauplius*, an unsegmented larva provided with three pairs of appendages, the first uniramous, the two others biramous, which correspond to the first and second antennae and mandibles respectively of the adult. The second pair often has a basal masticatory hook, and is innervated from a post-oral ganglion. There is a median eye. Somites and appendages are formed by subsequent growth accompanied by ecdyses. Among *Malacostraca* the Schizopod *Euphausia* and Decapod *Penaeus* have a *Nauplius*-stage. The latter passes through a *Zoea*- and a *Mysis*-stage into the adult. The Decapod *Lucifer* starts as a *Meta-Nauplius* with the rudiments of the two pairs of maxillae and the first maxillipeds, in addition to the *Nauplius* appendages: its ally *Sergestes* as a *Protozoea*, in which all these limbs are well-developed, and a cephalothoracic shield and unsegmented abdomen are present as well. Most other *Decapoda* are hatched in a later stage known as *Zoea*, in which the second and third maxillipeds and a segmented abdomen devoid of limbs are present. The thorax is short, not segmented, but contains a ganglionic mass pierced by the sternal artery. There is an azygos *Nauplius*-eye in addition to the stalked paired eyes. The *Zoea* like the *Nauplius* acquires secondary characters. Many *Decapoda* pass through a *Mysis*-stage, i.e. with biramous natatory feet on the thorax, a stage in which the lobster (*Homarus*) is hatched. Development is still more abbreviated and becomes almost direct in some forms, e.g. *Astacus*. The larva of the *Stomatopoda* is known as *Alima* and *Erichthus*; of the *Palinuridae* (*Decapoda*) as *Phyllosoma*. The true Crabs (*Decapoda Brachyura*) pass through a stage, *Megalopa*, resembling certain Hermit crabs.



A few *Amphipoda*, *Isopoda*, and *Decapoda* are terrestrial. The *Branchiopoda* are exclusively found in fresh water or in brine: one or two *Cirripectida* occur in brackish waters. Other *Cirripectida*, like the *Leptostraca*, *Cumacea*, and *Stomatopoda*, are exclusively marine. Representatives of other orders are both marine and fresh water: the majority of *Schizopoda* and *Decapoda* however are marine<sup>1</sup>. Several *Cirripectida*, many *Copepoda*, and some *Isopoda* are parasitic. Polymorphism has been observed among male *Arthrostraca*, principally in *Amphipoda*. A development of colour in connection with reproductive activity is seen in some *Cladocera*. Phosphorescence occurs among marine *Copepoda* (e.g. *Sapphirina*), *Ostracoda*, and in the *Euphausiidae* among *Schizopoda*. The majority prey upon animals or plants. The genus *Estheria* is found in the Devonian strata: other supposed *Phyllopoda*, e.g. *Hymenocaris*, from Silurian and Carboniferous strata, may be allied to *Leptostraca*. The shells of *Ostracoda* occur in most formations. *Cirripectida* date from the Inferior oolite: *Arthrostraca* from Devonian strata: *Decapoda* from the Coal measures.

The Crustacea may be classified as follows (Claus):—

A. ENTOMOSTRACA: small, simply organised; number of somites and of appendages very variable.

1. *Phyllopoda*: body elongated, generally well segmented, with a shield-shaped or lateral bivalved shell, and at least four pairs of lobed and lamellate natatory feet.

(a) *Branchiopoda*, which are large sized; with well segmented bodies, and 10–20 or more feet with well-developed branchiae. *Branchipus*, *Artemia*, *Apus*, *Limnetis*, *Limnadia*, *Estheria*.

(β) *Cladocera*, which are small, laterally compressed with a bivalve shell and large natatory biramous second antennae. *Sida*, *Daphnia*, *Moina*, *Bosmina*, *Polyphemus*, *Leptodora*, &c.

2. *Ostracoda*: small, with unsegmented body; seven pairs of appendages, and a rudimentary abdomen; all inclosed by a bivalve shell. *Cypridina*, *Cythere*, *Cypris*, &c.

3. *Copepoda*: elongated; generally segmented; no shell of any kind, and 4–5 pairs of biramous thoracic feet; and five-jointed abdomen. Often parasitic, and then degenerate; e.g. *Cyclops*, *Chondracanthus*, *Caligus*, *Lernaea*, *Argulus*, &c.

4. *Cirripectida*: fixed; body not clearly segmented; inclosed in a fold of the integument, generally strengthened by calcareous valves; as a rule five pairs of biramous thoracic feet; hermaphrodite; e.g. *Lepas*, *Scalpellum*, *Balanus*, *Sacculina*.

B. MALACOSTRACA. Head composed of five, thorax of eight, and abdomen of six somites.

<sup>1</sup> A peculiar Ostracode, *Elpidium Bromeliarum*, has been found by Fritz Müller in the water retained by the leaves of Bromeliads in Brazil. It is not found in any of the streams, ponds, &c., around. See Nature, xxii. 1880, p. 55. The Amphipod *Phronima* makes a 'house' for itself out of a *Pyrosoma*, a *Salpa*, or even the Siphonophoran *Abyla* (Mayer, Mitth. Zool. Stat. Naples, i. 1879, p. 46).

1. *Leptostraca* (= *Nebalia*): bivalve shell; eight thoracic somites free; abdomen of eight somites, with furcae anales; thoracic limbs Phyllopod-like. *Nebalia*.

2. *Arthrostraca*: seven, rarely six free thoracic somites; eyes sessile; no cephalothoracic shield.

(a) *Amphipoda*: body laterally compressed; branchiae on thoracic limbs; first three pairs of abdominal feet natatory: e.g. *Caprella*, *Cyamus*, *Talitrus*, *Orchestia*, *Gammarus*, *Hyperia*, *Phronima*.

(β) *Isopoda*: body more or less compressed dorso-ventrally; first pair of abdominal feet form an operculum, covering the other pairs which are branchiate: e.g. *Tanais*, *Anceus*, *Cymothoe*, *Anilocra*, *Serolis*, *Idotea*, *Asellus*, *Bopyrus*, *Entoniscus*, *Ligia*, *Oniscus*, *Armadillo*.

3. *Thoracostraca*: all or some thoracic somites fused to head; a cephalothoracic shield; eyes mostly stalked.

(a) *Cumacea*: 4-5 free thoracic somites; two pairs of maxillipeds; abdomen in ♂ carrying two, three, five pairs of natatory feet; eyes sessile: e.g. *Cuma* (= *Diastylis*), &c.

(β) *Stomatopoda*: short cephalothoracic shield; five pairs of maxillipeds; branchiae on abdominal feet; abdomen large; e.g. *Squilla*.

(γ) *Podophthalmata*: large cephalothoracic shield; two to three pairs of maxillipeds. (i) *Schizopoda*: thoracic feet (eight pairs) biramose (*Mysis*, &c.).

(ii) *Decapoda*: thoracic somites fused to head; five last pairs of thoracic feet uniramous and seven-jointed.

(a) Abdomen long, *Macrura*; e.g. *Lucifer*, *Sergestes*, *Penaeus*, *Palaemon*, *Craugon*, *Astacus*, *Nephrops*, *Scyllarus*, *Palinurus*, *Pagurus*, *Birgus*.

(b) Abdomen short, *Brachyura*; e.g. *Dromia*, *Maja*, *Cancer*.

See lit. pp. 176-7, 181, 186, 189.

A. *Entomostraca*, Gerstaecker, Bronn's Class. und Ordn. des Thierreichs, v. Abth. 1. 1866-79, and except *Cirripedia*, Baird, British Entomostraca, Ray Soc. 1850.

*Phyllopoda*: *Branchiopoda*, Packard, 'North American *Phyllopoda*,' Rep. U. S. Geol. Survey, xii. 1883. *Branchipus and Artemia*, Claus, Arb. Zool. Inst. Wien, vi. 1886. *Limbs of Apus*, Ray Lankester, Q. J. M. xxii. 1882; Packard, 'Homologies,' &c. American Naturalist, xvi. 1882. *Estheria and Limnadia*, Gruber, A. N. 31 (1), 1865. *Limnadidae*, Klunzinger, Z. W. Z. xiv. 1864.

*Cladocera*: *Polyphemidae*, Claus, Dk. Akad. Wien, xxxvii. 1877. *Daphnidae*, Id. Z. W. Z. xxvii. 1876. *New British sp.*, Ray Lankester, A. N. H. (5), ix. 1882. *Lep-todora*, Forrest, Journal Roy. Micr. Soc. ii. 1879; Weismann, Z. W. Z. xxiv. 1874.

*Ostracoda*: *Cytheridae*, Kaufmann, Recueil Zool. Suisse, iii. (2), 1886. *Halocypridae*, Claus, Schriften Zool. Inhalts. Wien, 1874. *Cypridinae*, Id. Z. W. Z. xxiii. 1873; Zenker, Monograph, A. N. xx. (1) 1854. Brady, 'Recent British *Ostracoda*,' Tr. L. Soc. xxvi. 1870; Id. *Ostracoda*, Challenger Reports, i. 1880.

*Copepoda*: Brady, 'Free and semi-parasitic *Copepoda*,' 3 vols. Ray Soc. 1878-1880; Id. *Copepoda*, Challenger Reports, viii. 1883; cf. Baird's British Entomostraca, Ray Soc. 1850. *Cyclops*, Hartog, J. L. S. xviii. 1885. *Development*, Urbanovics, Z. A. vii. 1884; and of *Cetochilus*, Grobben, Arb. Zool. Inst. Wien, iii. 1881. *Generative organs of free Copepoda*, Gruber, Z. W. Z. xxxii. 1879. *Parasitic forms*: *Chondracanthidae*, Vogt, Mém. Inst. Genève. xiii. 1877; *Lernaeidae*, Claus, Marburg

Schriften, Suppl. pt. 2. 1868; *Lernaeopodidae*, Kurz, Z. W. Z. xxix. 1877; *Argulidae*, Claus, Z. W. Z. xxv. 1875; *Lernanthropus*, Heider, Arb. Zool. Inst. Wien, ii. 1879; cf. Z. A. iii.

*Cirripedia*, Hoek, Challenger Reports, viii. 1883; x. 1884; Id. Tijdschrift Nederl. Dierk. Vereen, vi. 1882-85. *Peltogaster, nervous system*, Yves Delage, A. Z. Expt. (2), iv. 1886. *Sacculina*, Id. op. cit. (2), ii. 1884. *Laura Gerardiae*, de Lacaze Duthiers, A. Z. Expt. viii. 1879-80 (Mém. Acad. Sciences, Paris, 42, 1883).

B. *Malacostraca*; see lit. p. 176-77.

*Leptostraca*; *Nebalia*, Packard, American Naturalist, xvi. 1882; Claus, Z. W. Z. xxii. 1872; cf. von Willemoes-Suhm, 'Atlantic Crustacea,' Tr. L. S. (2), i. 1870.

*Arthrostraca*, Gerstaecker, Bronn's Klass. und Ordn. des Thierreichs, v. Abth. ii. 1881-86 (not finished). *Caprellidae (Amphipoda)*, Mayer, Fauna und Flora des Golfes von Neapel, vi. 1882. *Amphipoda of Kiel*, Blanc, Nova Acta, 47, 1885. *Organismus der Phronimiden*, Claus, Arb. Zool. Inst. Wien, ii. 1879. *Platyscelidae*, Id. ibid. *Amphipoda der Adria*, Nebeski, Arb. Zool. Inst. Wien, iii. 1881. *Crustacea Isopoda Terrestria*, Budde-Lunde, Havniae, 1885. *Tanaidae and Apseudes*, Claus, Arb. Zool. Inst. Wien, v. 1884. *Tanais*, Blanc, Recueil Zool. Suisse, i. 1884. *Serolis*, Beddard, Challenger Reports, xi. 1884. *Bopyridae*, Waltz, Arb. Zool. Inst. Wien, iv. 1882; Kossmann, Z. W. Z. xxxv. 1881. *Entoniscus (Cryptoniscidae)*, Kossmann, Mitth. Zool. Stat. Naples, iii. 1882; Id. SB. Akad. Berl. 1884. *Isopod Anatomy*, Huet, Journal de l'Anat. et Physiol. xix. 1883. *Cymothoidae*, Schiödte and Meinert, Nat. Tidsskrift (3), xii, xiii, xiv.

*Thoracostraca. Cumacea: Cuma Rathkii*, Burmester, Inaug. Diss. Kiel, 1883; Egg, &c., Blanc, Recueil Zool. Suisse, ii. 1885; Dohrn, 'Bau,' &c. J. Z. v. 1870; Sars, Nye Bidrag til Kundskaben, &c., ii. Middlehavets Cumaceer, Christiana, 1878 (Arch. Math. og Naturvid.); Norman, A. N. H. (5), iii. 1879; Spence Bate, ibid. (2), xvii. 1856. *Stomatopoda*, Brooks, Challenger Reports, xvi. 1886. *Schizopoda*, Sars, Challenger Reports, xiii. 1885. *Decapoda Macrura: Lucifer*, Brooks, Ph. Tr. 173, Pt. 1. 1883.

*Typical Zoaea*, Birge on *Panopaeus*, Studies Biol. Lab. Johns Hopkins Univ. ii. 1883. *Development of some Fresh-water Decapoda: Palaemon potiuna*, Fr. Müller, Z. A. iii. 1880; *Palaemonetes*, Mayer, Mitth. Zool. Stat. Naples, ii. 1881, p. 197; *Atyephira*, Ishikawa, Q. J. M. xxv. 1885.

*Unicellular cutaneous glands*, cf. Claus, Beiträge, &c., Arb. Zool. Inst. Wien, iii. 1881, p. 6; Nebeski '*Amphipoda of Adriatic*,' ibid. *Antennary glands*, Grobben, ibid.

*Brain of sessile-eyed Crustacea; comparison of eyed and eyeless forms* (with lit.), Packard, Mem. U. S. National Acad. Sciences, iii. *Eye of Penaeus*, &c., Patten, Mitth. Zool. Stat. Naples, vi. 1886, p. 625; *of Branchipus*, Claus, A. N. H. (5), xviii. 1886; *of blind Cambarus*, Leydig 'Untersuchungen zur Anat.' &c., Bonn, 1883, p. 36.

*Lungs of terrestrial Birgus latro*, Semper, Z. W. Z. xxx. 1878. *Anal respiration*, Hartog, Q. J. M. xx. 1880, pp. 244, 485.

*Circulation of Mysis (Schizopoda)*, Yves Delage, A. Z. Expt. (2), i. 1883; *of Arthrostraca*, Id. ibid. ix. 1881; cf. Claus, cited, p. 181, ante. *Heart of Copepoda*, Claus, Beiträge, &c. Arb. Zool. Inst. Wien, iii. 1881, p. 2. *Blood of Callinectes*, Howell, Studies Biol. Lab. Johns Hopkins Univ. iii. 1886.

- Urinary organs in Amphipoda*, Spencer, Q. J. M. xxv. 1885; *in Stomatopoda*, Claus, 'Circulation in Stomatopoda,' Arb. Zool. Inst. Wien, v. 1884, p. 12.
- Sexual organs of ♀ Cladocera*, Weismann, Z. W. Z. xxvii. 1876; xxviii. 1877; ♂, &c., xxxiii. 1880 (cf. 'Rechtfertigung,' xxx. 1878); *of Ostracoda*, F. Müller, Zeitschrift f. Ges. Natw. (Giebel) 53, 1880; *of Cytheridae (Ostracoda)*, W. Müller, A. N. 50. (1), 1884; *of Oniscidae (Isopoda)*, Friedrich, Zeitschrift f. Ges. Natw. (Giebel), 56, 1883; *of ♂ Decapoda*, Brocchi, A. Sc. N. (6), ii. 1875.
- Hermaphroditism in Cymothoidae*, Mayer, Mitth. Zool. Stat. Naples, i. 1879, p. 165; cf. Nebeski, Beiträge, &c. Arb. Zool. Inst. Wien, iii. 1881, p. 24.
- Parthenogenesis in Apus*, &c., von Siebold, 'Beiträge zur Parthenogenesis der Arthropoden,' Leipzig, 1871; *in Cladocera*, Weismann, opp. cit. *supra*; *in Ostracoda*, Weismann, Z. A. iii. 1880, and F. Müller, op. cit. *supra*.
- Changes of colour in adaptation to surroundings*, Matzdorff, on *Idotea tricuspidata*, J. Z. xvi. 1883; Weber, *Isopoda Trichoniscida*, A. M. A. xix. 1881, p. 591; cf. Seidlitz, 'Beiträge zur Descendenz-Theorie,' Leipzig, 1876, pt. 1; *in Nika edulis*, Jourdain, C. R. 87. 1878.
- Sexual colours of Daphnidae*, Weismann, Z. W. Z. xxx. (Suppl.), 1878.
- Parasitism*, cf. Kossmann, Z. A. v. 1882, p. 60.
- Sexual (male) Polymorphism; in Amphipoda* Chilton, (5), xvi. 1885; cf. Norman, on *Eryontidae*, A. N. H. (5), iv. 1879. *Influence of surrounding media on shape*, Schmankewitsch, Z. W. Z. xxix. 1877; cf. Brauer, Z. A. ix. 1886.
- Stridulating Crustacea*, Wood-Mason, Nature, xviii. 1878; *Neptunus vocans*, Milne Edwards, Bull. Soc. Philomath, Paris, 1878; *Palinurus*, T. J. Parker, P. Z. S. 1876.

## PYCNOGONIDAE.

### (Pantopoda.)

Marine Arthropoda with a body composed of a cephalothorax, three free thoracic somites, and a rudimentary abdomen. The cephalothorax consists of a tubular proboscis with a terminal mouth, a prae-oral, two post-oral head somites, and one coalesced thoracic somite. It bears four pairs of appendages, three of which belong to the head, viz. a pair of 2-3 jointed prae-oral mandibles often terminated by a chela, a pair of slender palpi, of ovigerous legs usually ten-jointed, and the first pair of thoracic limbs which, like the other three pairs, are eight-jointed and borne upon processes of the somite. The limbs have a terminal and often two accessory claws. The mandibles may be absent, or the palpi, or both, and the ovigerous limbs may be present only in the male, but there is some variety even among specimens of the same genus. The abdomen is rarely segmented and is connected to the thorax by a joint. It bears the anus terminally. The integument contains numerous glands. The supra-oesophageal ganglion innervates the mandibles and eyes, which are placed dorsally on a tubercle of the cephalothorax. The infra-oesophageal (= 1st thoracic) ganglion innervates the palpi and ovigerous legs,

and is composed of two ganglia fused. There are four well-developed thoracic ganglia, and two others which are either rudimentary or aborted. The species inhabiting shallow water have four eyes, those living below 400 fathoms rudimentary eyes without pigment, or none at all. The eyes appear to be monostichous and monomeniscous. The alimentary canal consists of an oesophagus dilated posteriorly, and containing a masticatory apparatus; of a mesenteron beset with cellular villi (= glands) and giving off caeca which enter the proboscis in many instances, the mandibles and limbs, but not the palpi and ovigerous limbs. Their number is not regular apparently. There is a dorsal heart which is continuous dorsally with the integument, open anteriorly and furnished with two pairs of lateral ostia, and either a third pair or a single posterior aperture. Respiration is cutaneous, and there are respiratory cavities or depressions opening externally by a pore. The testis consists of two dorsal tubes united posteriorly, and sending processes outwards into all the thoracic limbs, or into the three or the two last pairs only. The ducts open externally by a ventral pore on the tibial joints. The ovary either resembles the testis, or the portion within the body becomes atrophied. The branches in the limbs open in the same position as do the branches of the testis, but there are no true ducts. Copulation takes place. The eggs are fecundated externally, and are carried by the male on the ovigerous limbs, by the female also in *Nymphon brevicaudatum*. They are attached by the secretion of special glands placed in the fourth joint of the limbs. The three pairs of cephalic limbs are formed as a rule first, and the young may be hatched in this condition. They remain attached to the ovigerous limbs by a thread secreted by a gland lodged in the basal joint of the mandible. The larvae of *Phoxichilidium* are entoparasitic in various *Hydrozoa*. The affinities of the group are doubtful.

The terms cephalothorax, mandible, palpi, &c. must not be taken as implying a homology with the parts so named in *Arachnida* or *Crustacea*.

Hoek, Challenger Reports, iii. 1880; Dohrn, Fauna und Flora des Golfes von Neapel, iv. 1881.

## PHYLUM ECHINODERMATA.

*Coelomate Metazoa in which the bilateral symmetry of the larva is more or less completely replaced by a radial symmetry. Calcifications of the integument form a mesodermic skeleton generally of great completeness, and a special section of the primitive coelome develops into a water-vascular system, which has a locomotor and often a respiratory function. The five peripheral vessels of this system define five radii and five intervals or interradii, the ambulacra and interambulacra respectively. There is a metamorphosis.*

The typical Echinoderm larva is a bilaterally symmetrical organism with well-marked dorsal and ventral surfaces, the latter the smaller of the two. The mouth is ventral and subterminal at one pole, the anus (= gastrula mouth) ventral and subterminal at the other, and the digestive tract takes an antero-posterior course between the two with a curve convex to the dorsal surface. The right and left peritoneal (= coelomic) sacs unite around it, and the dorsal union between the two walls persists as the mesentery, at the anterior end of which is the water-tube and pore. The *Holothurioidea* retain some to a greater, others to a less extent these characteristics. Their nervous and water-vascular systems with the longitudinal muscle bands are, however, invariably disposed radially. In all other Echinoderms there is a paramount radial and with few exceptions pentamerous symmetry, and the only trace of the primitive bilateral symmetry is to be found in the mesentery supporting the water-tube and plexiform organ; but though this mesentery is more or less antero-posterior it does not lie in the primitive median dorso-ventral plane. A secondary plane of bilateral symmetry however is often established, as in irregular *Echinoidea* and the *Crinoidea*. Furthermore the dorsal or abactinal surface of the adult corresponds to the right side with more or less of the dorsum of the larva, and the ventral or actinal surface to its left side with more or less of the ventral surface. The mouth of the adult is in the centre of the actinal surface, the anus excentric on the abactinal, though in the course of growth it may travel round interradially to the oral surface. It must be carefully noted, therefore, that the point from which nerves and water-vascular vessels radiate in the *Holothurioidea*, lies in the larval antero-posterior axis, and that they are parallel both to this axis and the median dorso-ventral plane. But in other Echinoderms the point from which they radiate lies on the left side in a dorso-ventral axis at right angles approximately both to the primitive antero-posterior axis and median dorso-ventral plane.

The calcareous deposits in the integument take the form of spicules or variously shaped plates. The *Holothurioidea* alone retain a muscular integument. In all other Echinoderms the muscular system is greatly aborted and is only developed in relation with the movements of special parts of their skeleton. In this skeleton there are two important systems of plates, the apical and oral, corresponding respectively to the centres of the dorsal and oral surfaces in the adult. The apical system comprises a dorso-central plate round which are arranged, passing from the centre outwards, at first in a spiral but afterwards in a circle, (1) five basal plates interradially in position; (2) five radial plates radial in position. To these may be added (1) within the circle of basals, a circle of five underbasal plates radially placed, and (2) externally to the radials five primary interradial plates. Underbasals occur only in *Asteroidea*, *Ophiuroidea* and

*Crinoidea*; and when they are present the base of the apical system is said to be dicyclic, when absent monocyclic. Primary interradials occur in *Asteroidea*, *Ophiuroidea* and *Pelmatozoa*. The oral system is completely developed only in certain *Pelmatozoa*. In its typical form, as seen in some *Actinocrinidae* among *Palaeocrinoidea*, there is an oro-central surrounded by five interradial oral plates, and these in their turn by circles of oral radials and interradials, the whole forming a dome, beneath which lies the mouth. Apertures pass to the mouth between the orals. As a rule, however, the oro-central is not formed, and the oral plates alone represent the oral system. The region of the body between these two systems of plates is moulded in a fashion characteristic of the various classes. In *Echinoidea* it is spherical or compressed dorso-ventrally, and the ambulacra and inter-ambulacra extend in parallel lines or meridians from the oral to the apical area. In the Brachiote Echinoderms (*Asteroidea*, *Ophiuroidea*, *Crinoidea* and *Cystoidea*) the radial meridians are prolonged outwards into arms surrounding a central disc, while the interradial remain more or less undeveloped. At the same time the ambulacra are confined to the ventral surfaces of the disc and arms, and there is developed outside the apical system an area of dorsal surface known as the anti-ambulacral. The skeletal plates corresponding to these different regions vary much. It is of importance, however, to note whether the radial water-vascular trunks are supported (i) by a system of external, i. e. super-ambulacral, plates alone (*Echinoidea*), or of internal, i. e. sub-ambulacral, ossicles alone (*Asteroidea*), or of both combined (*Ophiuroidea*). Radial anti-ambulacral ossicles attain great importance, and form the arm skeleton in *Crinoidea* and *Cystoidea*.

The central nervous, the water-vascular and blood-vascular systems form circumoral rings connected with radial prolongations. The nervous elements consist of parallel fibres with interposed ganglion cells. The ring and nerves lie at the base of the ectoderm cells in *Asteroidea* and *Crinoidea*, but in other Echinoderms in the cutis, and then they are surrounded by a cellular sheath. A peripheral sub-ectodermic plexus is well developed in *Asteroidea*, and a more deeply placed plexus in *Echinoidea* and *Holothurioidea*. The *Crinoidea* possess an anti-ambulacral nervous system. Eyes are found in *Echinoidea* and *Asteroidea*. Auditory organs in a few *Holothurioidea*. †The blood-vascular system is apparently mesodermic in origin. Its ring is connected, except in the *Holothurioidea*, with radial vessels lying between the radial nerves to the outer, and the water-vascular vessels to the inner side. It is also connected, except in the class named, with a plexiform organ or gland—the so-called heart—which lies in the primitive mesentery supporting the water-tube. The epithelium of the plexiform vessels appears to form, at least in *Echinoidea* and *Asteroidea*, blood corpuscles, which are coloured and respiratory in

function. In *Thyonella gemmata?* (*Holothurioidea*) and *Ophiactis virens* (*Ophiuroidea*), there are corpuscles tinted with haemoglobin<sup>1</sup>. The organ cannot be considered as excretory. It is connected with an aboral vascular ring in *Asteroidea* and *Ophiuroidea*, groups in which rings as well as vessels are sometimes plexiform. The water-vascular system is a specialised portion of the coelome developed from the archenteron as a vesicle independent of the peritoneal vesicles (*Crinoidea*); or as a common vaso-peritoneal vesicle subsequently divided (*Holothurioidea*); or from the left of two peritoneal vesicles (*Echinoidea*, *Asteroidea*, *Ophiuroidea*). In the last-named group a water-vascular vesicle which aborts is derived also from the right peritoneal vesicle. The embryonic water-vascular vesicle, however formed, always lies on the left side. It surrounds the oesophagus at a later stage, and thus becomes a ring from which arise five caeca. These caeca lengthen out into the five radial water-vascular vessels; each one gives origin to a terminal azygos process, the tentacle of *Echinoidea* and *Asteroidea* as well as to paired lateral processes, the tube feet or pedicels. The processes are hollow, and extend into and raise the integument. The tube feet are variously modified in the different classes, and often become enlarged into organs of respiration or touch. At their inner ends they are often connected to a dilatation or ampulla. The ring itself gives origin to circumoral tentacles in the *Holothurioidea*, and it is frequently provided with one or more dilatations or Polian vesicles depending into the coelome. It is also connected to the exterior by a water-tube and pore. The pore lies in the larva anteriorly in the median dorsal line or interradius, a position retained in *Holothurioidea*: but in *Echinoidea*, *Asteroidea* and *Ophiuroidea*, owing to the remarkable difference between the dorsal and ventral surface of the larva and adult, the pore shifts either actinally (to the left) or abactinally (to the right), and lies in the interradius which originally corresponds to the anterior extremity, i. e. the one in which the circles of apical and oral plates close. It may be supposed that the first formed pore in *Crinoidea* indicates the homologous interradius. In all *Crinoidea*, however, there are formed, during growth at least, five water-tubes and five pores, one in each interradius, but generally more, and the two sets of structures only communicate through the coelome. They are continuously connected in all other Echinoderms. A simple pore is retained by certain *Elasipoda* among *Holothurioidea*, and some *Ophiuroidea*, but in others the aperture is usually closed by a calcareous pore plate or madreporite. The madreporite and water-tube, stone canal or madreporic tube, are rarely multiple. The former may be withdrawn into the coelome (most *Holothurioidea*); retain its independence (some *Asteroidea*); or fuse with a basal (other *Asteroidea*, *Echinoidea*); or with an oral (*Ophiuroidea*). The primary water-pore

<sup>1</sup> Howell, Studies Biol. Lab. Johns Hopkins Univ. iii. (6), 1885; Foettinger, Archives de Biol. i. 1880.



pierces an oral in *Crinoidea* as do others formed later. The epithelium of the water-vascular system is ciliated partially or throughout. The coelome is derived invariably from a right and left peritoneal vesicle, either separate outgrowths of the archenteron or split off from a common outgrowth (*Holothurioidea*). The walls of the two outgrowths fuse round the archenteron, and the dorsal fused portion persists as the mesentery, already mentioned, while the ventral portion is absorbed. The coelome is large, its wall generally ciliated, its cavity filled by a liquid of about the same specific gravity as sea-water, and containing, where it has been examined, but little proteid material and relatively few corpuscles.

The larval mouth and oesophagus are carried on into the adult in *Holothurioidea* and *Ophiuroidea*, but in *Echinoidea* and *Asteroidea* the oesophagus of the adult is a new formation, growing out from the archenteron to the left side, that to which the mouth is said to be transported. The larval anus is a persistent gastrula mouth. It is retained in *Holothurioidea*, closed permanently in *Ophiuroidea*, and a few *Asteroidea*, said to be retained in *Echinoidea* and other *Asteroidea*, but in some instances it certainly closes and a new anus is formed subsequently. The digestive tract is typically a spirally coiled tube. The oesophagus lies in the madreporic interradius, and if the Echinoderm be regarded from the oral surface, the tract passes to the right, and the anus is situated in the fourth interradius in *Holothurioidea* and *Echinoidea*, but in the fifth, i. e. the one adjoining the madreporic, interradius in *Asteroidea* and *Crinoidea*. The tract is saccular in its first section in *Asteroidea*, and wholly saccular in *Ophiuroidea*. It is generally ciliated except in *Holothurioidea*. There are radial glandular caeca in *Asteroidea*, and to the anal end of the intestine there are appended, as also in many *Holothurioidea*, two caeca. Respiration is carried on by external prolongations of the coelome (dermal branchiae of *Asteroidea*, peristomal gills of some *Echinoidea*); by modified tube feet (many *Echinoidea*, tentacles of *Crinoidea*); or by the expanded anal end of the intestine with its two appended caeca or respiratory trees (many *Holothurioidea*). In all cases, however, the tube feet must have a limited respiratory function, and sea-water diffuse through the walls of the stone canal and water-vascular vessels into the coelome. There is no excretory organ.

The sexes are separate. The Ophiuroid, *Amphiura squamata*, is said, however, to be hermaphrodite. The genital glands are more or less branched interradiial caeca, single in *Holothurioidea*, multiple in other Echinoderms. Details vary in the different groups. Impregnation is either external, or the spermatozoa pass from the water into the female ducts. A few forms in all groups except *Crinoidea* are viviparous. Development is then abbreviated and takes place *internally* in the genital bursae (*Ophiuroidea*) or the coelome (a *Chirodota*, *Phyllophorus urna*

among *Holothurioidea*); or else *externally* in depressed ambulacra protected by the spines (certain *Echinoidea*); among the dorsal spines or paxillae (the Asteroid *Leptychaster*); among the dorsal ambulacral processes (the Holothurioid *Cladodactyla crocca*); or in special marsupia formed by stalked plates (the Holothurioid *Psolus ephippiger*), or by a soft skin (the Asteroids *Pteraster* and *Hymenaster*, and Echinoid *Anochanus*). The Asteroids, *Echinaster Sarsii* and *Asterias Mülleri* bend their arms ventrally and so protect the ova. The female in most of these instances is distinguishable from the male. A sexual difference in colour has been noticed in the Asteroid *Oreaster (Pentaceros) turritus* and Ophiuroid *Ophiothrix Petersi*. Otherwise the sexes are alike.

Among the *Holothurioidea* the majority mutilate themselves by discharging their Cuvierian organs. The *Aspidochirotae* also break off the alimentary tract behind the water-vascular ring but repair the injury. If irritated, the *Synaptae* break the body up into sections and certain species of *Stichopus* resolve their skin into a diffuent mucus. *Asterioidea*, *Ophiuroidea* and *Crinoidea* regenerate an injured arm, and the two latter, especially the *Ophiuroidea*, possess the power of throwing the arms off. In the *Asterioidea* and *Ophiuroidea* the organism may be formed anew from an arm with a portion of the disc or perhaps even without it. It is possible indeed that asexual multiplication may thus take place normally in some genera. The *Crinoidea* appear to have the power of regenerating the visceral mass as a whole when removed or lost naturally as it sometimes is.

Segmentation of the ovum is total. The gastrula is formed as a rule by invagination. It is stated to be delaminate in the Ophiuroids *Ophiothrix versicolor* and *Amphiura squamata*. The mesoblast is derived from amoeboid cells which originate from the invaginated cells (i. e. hypoblast), and the epithelium of the coelome and water-vascular vessels from the vaso-peritoneal vesicles, hollow outgrowths of the archenteron, solid only in certain *Ophiuroidea*. The larval oesophagus is a stomodaeum. The larva is at first uniformly ciliated, but the cilia are subsequently restricted to certain bands. *Antedon* has four transverse bands and a posterior tuft. In all other Echinoderms, with the exception of a few with shortened development, the free-swimming larva has a prae-oral and a prae-anal ciliated ridge. These ridges either unite into a single closed longitudinal band (*Holothurioidea*, *Echinoidea*, *Ophiuroidea*) or form two separate but closed bands of which the prae-anal is longitudinal (*Asterioidea*). The Holothurioid larva is known as *Auricularia*. Its ciliated band is somewhat undulated and breaks up into transverse ciliated bands, usually five in number, constituting the so-called *Pupa-stage*. The prae-oral lobe is large. The Asteroid larva closely resembles the Holothurioid. Its ciliated band develops soft arms, and it is then known as *Bipinnaria*; or as *Brachiolaria*, if three

special arms covered with warts are also developed at the anterior dorsal extremity independently of the ciliated band. The Echinoid and Ophiuroid larva is known as *Pluteus*. It is distinguished by the small size of the prae-oral dorsal area, and the large size of the post-anal area, and by the growth in the course of the ciliated band of arms directed anteriorly, and supported by a provisional calcareous skeleton. The arms common to the *Pluteus* of both classes are, a pair of anterior or oral arms, a pair of posterior or prae-anal arms, and a pair of antero-lateral arms. All these processes, &c., are secondary characters, and are absorbed during the metamorphosis of the larva into the adult.

The Echinoderms are marine; a few *Holothurioidea*, however, can live in brackish water. They may be grouped into the classes *Holothurioidea*, *Echinoidea*, *Ophiuroidea*, *Asteroidea*, *Crinoidea* and the wholly extinct *Cystoidea* and *Blastoidea*. The *Holothurioidea* are sometimes termed *Scytodermata*; the *Echinoidea*, *Ophiuroidea* and *Asteroidea* may be grouped together as *Echinozoa*, and the remaining three classes as *Pelmatozoa*.

It has recently been asserted that the water-vascular and blood-vascular systems are closely connected in *Echinoidea* and *Crinoidea*. The work of Ludwig on *Asteroidea* and *Ophiuroidea*, and of Ludwig and P. H. Carpenter on *Crinoidea*, appears to settle the question in the negative, so far as those groups are concerned. It is probable also that the *Echinoidea* will be found to conform to the same type of arrangement; cf. P. H. Carpenter, Q. J. M. xxiii. 1883, and xxv. 1885.

For the interradius of the water-pore, see Ludwig, Z. W. Z. xxxiv. 1880.

In *Asterina gibbosa* the larval mouth and oesophagus are closed, and a new mouth is formed in relation with a new oesophagus, which grows out from the archenteron to the left side of the larva. The larval anus (= gastrula mouth) is also closed, and the anus of the adult is a new formation. Ludwig, Z. W. Z. xxxvii. 1882.

For the formation of the arms, &c., in the Starfish just named, see p. 312, *ante*. *Sexual Dimorphism*, Studer, Z. A. iii. 1880, p. 523.

*Suckers*, Niemiec, Recueil Zool. Suisse, ii. 1885.

*Fossil Echinodermata*, Zittel, Handbuch der Palaeontologie, Abth. 1, Palaeozoologie, i. pp. 308-560.

## CLASS HOLOTHURIOIDEA s. SCYTODERMATA.

*Echinodermata with elongated bodies, and a tough integument with well developed muscular coats, and as a rule a feebly developed calcareous skeleton. There is a circle of circumoral tentacles borne by the water-vascular ring, and the madreporic tubercle is usually placed internally. The mouth is ventral or terminal; the anus ventral, terminal, or dorsal.*

The body is often more or less vermiform, or in cross section pentagonal. In other instances one surface corresponding to three ambulacral

vessels, or the trivium, and to the larval ventral surface, is distinctly flattened as in many *Aspidochirotae*; and the flattening may be carried so far as to form a creeping sole, as in *Psolus* and *Colochirus* among *Dendrochirotae* and all *Elasipoda*. The surface corresponding to the remaining two ambulacral vessels or the bivium—the larval dorsum—is then more or less convex. In *Rhopalodina elegans* the dorsal surface is extremely short so that the mouth and anus are closely approximated, while the ventral surface is large and convex. The body walls are in many *Elasipoda* produced into a distinct rim bordering the ventral surface, and in the family *Psychropotidae* the dorsum is produced, as in the larva, anteriorly to the mouth, which thus lies at some distance from the anterior extremity. The body walls consist of a cuticle, an ectoderm, a connective tissue layer of some thickness imbedding pigment and other cells, calcareous deposits and bundles of nerve fibrils; of a layer of circular or transverse muscles, and five radial bands of longitudinal muscles placed internally to the radial nerves and water-vascular vessels. The circular muscles are sometimes interrupted in the radial lines, in *Elasipoda*, and except in this group, the longitudinal muscles consist in each radius of a right and left band. These bands are attached anteriorly to the radially placed pharyngeal ossicles, and they each give off in *Dendrochirotae* retractor muscles for the pharynx. The apical system of plates is not represented. The five calcareous plates in *Mülleria*, &c., or the ten in *Rhopalodina* which surround the anus have probably nothing to do with it. The oral system is represented by five calcareous valves which close over the mouth and tentacles in *Psolus ephippiger*, or the young *Psolinus brevis*. It is perhaps present also in some larval forms. The calcareous deposits of the body are as a rule represented only by scattered spicules as in most *Elasipoda*, by wheels (=rotulae), e.g. in *Chirodota*, by anchors with plates in *Synapta* or variously shaped plates, all however small in size. Well developed calcareous plates are found in some instances, e.g. in *Ocnus* and *Psolus*; and in *Echinocucumis* and *Echinostoma* they carry spines. Overlapping plates have been observed in a larval *Holothuria* and *Cucumaria*. Spicules are commonly found in the walls of the tube feet, and in *Elasipoda* they occur in various tissues, e.g. mesentery, walls of digestive tract, &c. The body walls are lined by a ciliated epithelium which is continued over the mesentery. The coelome is large, and a special section of it, the oesophageal sinus, surrounds the pharynx. The pharyngeal ossicles are formed in the outer wall of this sinus. They are sometimes absent (*Embolus*) or very rudimentary. Among the *Elasipoda*, the *Elpidiidae* have five radially placed spicules; the *Psychropotidae* five plates (?), and the *Deimatidae* a ring-shaped network. Typically there are five radially placed ossicles, notched or perforated, by the radial nerves and water-vascular vessels, alternating each with a single interradianal ossicle, but the number of the

latter varies and may be increased with an increase in the number of the tentacles in *Apneumona*. The pharynx of some *Dendrochirotae* is protected by a row of calcareous plates.

The circumoral nerve-ring not only gives off the radial nerves but other nerves to the tentacles. There appears to be a plexus with ganglion cells in the integument, and the nerves to the tube-feet and tentacles are in some instances connected with sense-cells in the ectoderm. The dorsal processes of *Elasipoda* are especially rich in nerves, and are probably tactile in function. Auditory vesicles, ten in number, have been found at the origin of the radial nerves from the ring in *Synapta*. Similar structures occur in the *Elpidiidae*, and are either confined to the ring, or spread also along the two lateral nerves of the trivium. They inclose numerous otoliths. The five caeca first developed by the water-vascular ring in the larva appear to correspond with the five primary tentacles, and are inter-radial. A second set of five caeca develop into the radial water-vascular vessels. The tentacles increase in number subsequently, and in the adult vary from ten to thirty, but their interradial origin is not evident, and the ring appears to give off five vessels from which the tentacular branches and radial vessels are alike derived. In *Thyonidium* the ten tentacles are alternately large and small, and in the *Dendrochirota* the ventral pair are constantly of a smaller size than the remainder. They vary much in shape. In *Haplodactyla* they are cylindrical, but they may be peltate (*Aspidochirotae*), arborescent (*Dendrochirotae*), and peltate, digitate or pinnate in others. Tentacular suckers are found in some *Synaptidae*. The tentacles are sometimes retractile, and this is especially the case in *Dendrochirotae*, in which the pharynx has special retractors. There are ampullae to the tentacles in *Aspidochirotae*, *Molpadia*, *Chirodota*, &c., but never in *Elasipoda* or *Dendrochirotae*. There is generally one Polian vesicle which is ventral, and on the left side in *Elasipoda*, but in some forms the number may be greatly increased. The radial water-vascular trunks are absent in *Apneumona*; present but devoid of feet in *Apoda Pneumonophora*; and the same is the case with the two vessels of the bivium in *Psolus*. The tube feet are either partially or completely retractile, and furnished with a terminal disc which is supported by a calcareous plate except in the majority of *Elasipoda*, or they are conical *papillae* without discs. Both kinds may occur in the same animal, e.g. *Stichopus*, or the first kind alone, e.g. *Cucumaria*, or the second alone, e.g. many *Holothuriae*. Among the *Elasipoda* the median ambulacrum of the trivium has rarely any feet, and the lateral ambulacra carry cylindrical feet, as a rule few and paired from side to side of the ventral surface. The *papillae* or conical processes are usually dorsal. They are well developed in most *Elasipoda*, and are paired from side to side. In the same group there is often a long dorsal appendage with a broad base, which extends across the median dorsal inter-

ambulacrum anteriorly, in the middle, or posteriorly, and is penetrated by processes from the two radial vessels of the bivium. The tube-feet may be arranged in rows or scattered over the surface irregularly as in *Dendrochirotae Sporadipoda*, and they are frequently less numerous in the bivium. They possess ampullae which project slightly from between the circular muscles. In *Elasipoda* there are spaces branched or unbranched in the integument connected with the feet and dorsal papillae (=processes, Théel), and true ampullae are rarely found and only in connection with the dorsal processes. The stone-canal is generally single but may be multiple or branched. In many *Elasipoda* it opens on the dorsal surface medianly by usually one or rarely several pores close to the generative pore; and when it is retracted into the coelome, it does not hang freely but is partly imbedded in the integument. It hangs freely in the coelome or is attached to the mesentery in other Holothurioidea. It may or may not be terminated by a calcareous madreporic plate, but whether it is or not, it is covered by coelomic epithelium. Numerous corpuscles occur in the water-vascular system. The blood-vascular system consists of a series of spaces in the connective tissue, not lined by an epithelium, and disposed as a circular peripharyngeal plexus closely connected to the water-vascular ring, but placed posteriorly to it, and a ventral and dorsal intestinal vessel, the latter usually double except in *Elasipoda*. They are united by anastomoses round the intestine. The ventral vessel has been observed to contract from the centre to either end; the dorsal is connected to a plexus in the mesentery by which the left respiratory tree is loosely invested in *Aspidochirotae* and *Apoda Pneumonophora*.

The mouth is placed centrally in a peristome surrounded by the circle of tentacles. It is very frequently turned to the ventral surface; always in *Elasipoda*, and to an especial degree in the family *Psychropotidae*. It is in many instances terminal or even turned dorsally, and opens into a pharynx. The digestive tract is straight in some *Apneumona*, but is generally disposed in a descending, an ascending and a descending section. The first section is supported by a mesentery which is attached to the median dorsal line interradially, and corresponds to the dorsal line of union between the right and left peritoneal vesicles of the larva, the ventral union being absorbed. The ascending section is borne by a mesentery attached to the left dorsal interradius, and the second descending by one attached to the right ventral interradius. The tract is therefore slightly coiled. The pharynx is followed by the short 'stomach,' which has well-developed muscular walls, and is separated by a constriction from the intestine by far the longest part of the tract. The last portion or rectum is dilated, forming the so-called cloaca, which has been observed to contract rhythmically. Its walls are connected to the integument by radial muscles. There are appended to it, except in *Apneumona* and *Elasipoda*,

two (rarely more) branched outgrowths—the respiratory trees—homologous with the two interradial intestinal caeca of Asteroidea. The mesentery in the *Apneumona* bears, especially at its base, a number of ciliated funnel-shaped bodies either scattered or in groups. Processes known as Cuvierian organs are attached to the cloaca. They are invariably absent in *Synaptidae*, and perhaps also in some others. They are discharged when the animal is irritated, and have been variously stated to be solid or to contain an axial cavity.

The generative organs consist of either a single bundle of caeca attached to the left side of the mesentery anteriorly, or of two bundles right and left (*Stichopus* among *Aspidochirotae*, *Dendrochirotae*, and many *Elasipoda*). The duct is single and opens by a single pore placed in the dorsal median line outside the circle of tentacles or within it in *Dendrochirotae*. In some *Elasipoda*, however, it branches and opens by a corresponding number of pores. The sexes are separate with the exception of the *Apoda Apneumona* and *Pneumonophora* (?).

*Psolinus* develops without a metamorphosis, and the embryo is not ciliated. *Cucumaria* passes at once into the pupa stage, while others, so far as observed, pass through an *Auricularia* into a pupa stage; see p. 548. The larval mouth and anus persist in the adult.

Holothurioidea are found in all seas. The *Aspidochirotae* swallow quantities of sands, &c.; others feed on small animals. Fossil wheels (of a *Chirodota*?) have been found in Jurassic strata, and remains of a *Chirodota* and *Synapta* even as early as the Carboniferous strata in Scotland.

The Holothurioidea may be divided into—

1. *Elasipoda*: primitive deep sea forms, with a well-marked bilateral symmetry, tube feet restricted to the flat ventral surface, and papillae on the dorsum. The stone-canal often opens externally by a pore, and there are no respiratory trees, (*Elpidiidae*, *Deimatidae*, *Psychroprotidae*).

2. *Pedata*, with well-developed tube feet and papillae, subdivided into

(a) *Aspidochirotae*, with peltate tentacles provided with ampullae, with five radial and five interradial pharyngeal ossicles, and left respiratory tree loosely connected to the mesentery; e. g. *Holothuria*, *Stichopus*.

(b) *Dendrochirotae*: with arborescent tentacles, retractor muscles to the pharynx, and two sets of generative caeca; e. g. *Cucumaria*, *Psolus*.

3. *Apoda*, devoid of tube feet and papillae, subdivided into

(a) *Pneumonophora* (= *Molpadidae*), with the left respiratory tree connected as in 2. a; ? hermaphrodite.

(b) *Apneumona* (= *Synaptidae*): devoid of radial water-vascular vessels, respiratory trees, and Cuvierian organs; hermaphrodite; e. g. *Synapta*, *Chirodota*.

*Holothurioidea*, Théel, Challenger Reports, xiv. 1886. *Elasipoda*, Id. ibid. iv. 1882. *Variations in Holothurians*, Lampert, Biol. Centralblatt, v. 1885-6.

*Histology*, Hamann, Beiträge, &c., 'Die Holothurien,' Jena, 1884; Id. Z. W. Z. xxxix. 1883; Jourdain, Annales Mus. Nat. Hist. Marseilles, i. 1883.

*Pharynx of unknown Holothurian with calcareous plates*, Moseley, Q. J. M. xxiv. 1884. *Cotton Spinner (Holothuria nigra) ejecting Cuvierian organs*, Bell, P. Z. S. 1884.

*Haemoglobin in Holothurian (Thyonella gemmata)*, Howell, Studies Biol. Lab., Johns Hopkins Univ., iii. (6), 1886.

*Ciliated funnels of Apneumona*, Semper, 'Reisen im Archipel der Philippinen,' i. 1868, p. 32.

## ECHINOZOA.

Echinodermata in which the calcareous skeleton attains great perfection and bears spines fixed or free, whilst the muscular system is much reduced. The apical system, always present in development, may be obscured by the formation of other plates and is always relatively small. Oral system either absent or represented by five oral plates. The oral surface is ventral in locomotion.

### CLASS ECHINOIDEA.

*Echinozoa with spherical, heart-shaped or shield-shaped bodies, sometimes much flattened dorso-ventrally. The plates of the calcareous skeleton are well developed and usually immoveably joined edge to edge, and carry moveable spines. The tube feet have terminal discs supported by calcareous plates, but are often much modified. The mouth lies in a peristome, and is usually central but may be displaced in the anterior radius. The anus lies either within the apical system (endocyclic) or outside it in the posterior interradius (exocyclic).*

The outer surface of the body is covered by a ciliated ectoderm and connective tissue layer which contains amoeboid pigment cells and a nerve-plexus. The apical system is always well developed. It consists typically of the usual plates—a dorso-central, surrounded by five basals and five radials. Under-basals and primary single interradials are never present. Among *Desmosticha* the dorso-central persists as a single plate only in some *Saleniidae*. It is usually replaced by or broken up into a series of irregular plates among which the anus opens. In *Clypeastroidea* and *Petalosticha* it is not traceable in the adult at any rate<sup>1</sup>. The basals are large and are pierced each by one genital pore, or in *Palaeo-echinoidea* by 3-5 pores. One—the posterior—is generally imperforate in *Clypeastroidea* and always in *Petalosticha*, and it appears to be absent (? aborted) in the majority of the latter group. The radials are largest in the old types such as *Cidaridae* and *Saleniidae*, smaller in the *Petalosticha*, and smallest in the *Clypeastroidea*, the most recent group of *Echinoidea*. They

<sup>1</sup> It is figured in *Echinobrissus scutatus*. (Zittel's Palaeontologie, Abth. 1, Palaeozoologie, i. Fig. 388 d. p. 528).



are each perforated by a pore which transmits the azygos tentacle and the nerve to the eye speck. The pore is double in many *Palaeo-echinoidea*. From their relation respectively to the genital apertures and the eye specks the basals and radials are generally termed *genitals* and *oculars*. The plates of the ambulacra abut against the radials, of the interambulacra against the basals, and new plates in both these series are added only at the margin of the apical system, between it and the plates already present. And as new plates are added successively, the older plates recede towards the peristome. Consequently they extend in meridional lines from the apex to the margin of that area. One ambulacrum is anterior; one interambulacrum posterior, and easily recognisable by the presence of the anus in it in exocyclic forms, i. e. *Clypeastroidea* and *Petalosticha*. In these forms a plane of bilateral symmetry is established through the two meridians named. The ambulacra, one on either side the anterior ambulacrum, constitute with it the trivium: the remaining two, one on either side the posterior interambulacrum, make up the bivium. It has been found that the plates in the ambulacra immediately bordering the peristome show certain constant peculiarities in the trivium and bivium, and it is consequently possible to recognise the corresponding tracts in the endocyclic forms, i. e. *Desmosticha*, which are characterised by their regular and radial symmetry<sup>1</sup>. Bearing this plane of bilateral symmetry in mind, and imagining the Echinoid as lying with the peristome downwards, there are two interambulacra on the left and right sides, and the right anterior basal is somewhat enlarged and porous forming the madreporite. In some *Clypeastroidea* the madreporite extends into the centre of the apical system and in the majority all the basals and radials are porous and the sutures between them fused. In this case the genital apertures are frequently displaced outside the apical system in the interambulacra. In many *Spatangidae* the madreporite extends backwards into the posterior interambulacrum, thus dividing the apical system, and in this case the left

<sup>1</sup> If a *Spatangus* be placed mouth upwards—the reverse of the natural position—and the ambulacrum in the bivium to the left of the observer be numbered I and that to the right V, and the remaining ambulacra II, III, IV, from left to right; and if the two plates in each ambulacrum bordering the peristome be lettered *a* and *b*, following the same direction from left to right, then it will be found that the plates I *a*, II *a*, III *b*, IV *a*, V *b* are large and are pierced by a double pore, while the plates I *b*, II *b*, III *a*, IV *b*, V *a* are small and pierced by one pore. The basal plate of the interradius between II and III is the madreporite. Taking this same plate and interradius as a guide, Lovén has shown that if the ambulacra and plates in any other Echinoid be marked in the same manner, the same sequence of large and small plates with more and fewer pores may be noted. Even in the *Cidaridae*, where the pores are alike on all plates, a difference of size, &c. is noticeable. It may be added that the larger plates in the bivium are placed symmetrically with reference to the odd interambulacrum. See Lovén, A. N. 39, 1873, or *Études sur les Échinoïdes*, Kongl. Svenska Vetenskap-Akademiens Handlingar. xi. No. 7. Stockholm, 1874; also Agassiz, Challenger Reports, iii. 1881, for a criticism.

The ambulacra II and III are the two that form the bivium in the Holothurioid, I, IV, V the three that form trivium.

anterior basal may become porous. The genital pore of the right anterior basal is sometimes lost in this family; so also, but more rarely, that of the left anterior if porous. Consequently as the posterior basal and its pore are absent in all *Petalosticha*, certain *Spatangidae* possess only two genital pores (and glands)—viz. those corresponding to the right and left posterior interambulacra. The apical system retains the typical disposition of its plates in *Desmosticha* and *Clypeastroidea*. It is then termed *compact*. But among *Petalosticha*, the plates in most *Ananchytidae* are arranged in two antero-posterior rows touching one another in the middle line; and in the *Collyritidae* (= *Dysasteridae*) the two radials corresponding to the two posterior ambulacra or bivium are separated by a considerable distance from the other plates of the apical system to which they are connected by two irregular rows of supernumerary plates. In the former case the apical system is said to be *elongated*, in the latter *dis-jointed*.

The oral system of plates is represented in *Palaeostoma mirabilis*, one of the *Spatangidae*, by five large interradial plates surrounding the mouth, but it is doubtful if this system exists in other Urchins.

The five ambulacral and interambulacral areae make up the *corona* or *test*. The typical structure of the test is as follows:—Each of the ten areae consists of two rows of pentagonal plates, less numerous but larger in the interambulacra. The pentagon is so disposed that an angle is turned to the central line of union of the two rows in each area and a flat side to the line of union between adjoining areae. The plates are firmly united by their edges and the test is therefore resistant: a suture indicates the line of union. Each plate is perforated by a double pore. Hence the term *pore-plate*. The two pores give exit to two processes from the ampulla within the test which unite and form a tube foot. The important variations from the type structure are the following. Among *Palaeo-echinoidea*, *Bothriocidaris* has but a single row of interambulacral plates, whilst the number is increased in the remaining groups, as is the case also in some genera in the ambulacra. The central rows in each area are in these instances hexagonal. Among living Urchins *Astropyga* (*Diadematiidae*) and some species of *Phormosoma* (*Echinothuridae*) have an increased number of interambulacral plates. There is an overlapping of the plates in *Palaeo-echinidae*, in *Astropyga*, and *Echinothuridae*, a group in which it is well marked, and the test as a rule very flexible. An overlap is slightly indicated also in *Spatangidae*, a group in which the two rows of plates in the posterior interambulacrum not only are somewhat separate, but can be approximated by muscles. In the same family the pore is single on the majority of the plates except those at the apical and oral extremities. The middle region of the expanded plates in the petaloid portion of the ambulacra of *Clypeastroidea* may be marked by rows of fine pores in

addition to the two large pores connected by a furrow (*yoked* pores) at the outer edge. And the remaining plates of the ambulacra may possess similar rows which may extend on to the interambulacral plates forming *pore-areae*. In the family *Scutellidae* these fine pores are arranged on the actinal surface in lines—*pore-fasciae*—sometimes branched. The *pore* plates in *Cidaridae*, *Clypeastroidea*, and *Petalosticha* retain their regular succession. In the two last named the dorsal sections of the ambulacra gradually dilate from the apex and then contract more or less completely near the margin of the test forming *petala*, arranged in a rosette. In *Petalosticha* however the anterior ambulacrum is often unlike the rest, not much expanded, and its pores small or obliterated. The remaining sections of the ambulacra have plates so much expanded laterally in *Clypeastroidea* that the peristomial ends of the interambulacra are often constricted or excluded from the peristomial margin. In the *Cassidulidae* the peristomial ends of the ambulacra dilate into *petala* or *phyllodes*, forming a figure known as *floscella*. In the Ectobranchiate *Desmosticha* on the contrary the pore-plates at a little distance from the apex lose their typical arrangement. Certain plates (*half* plates) remain small in size and fail to reach the central line of the ambulacrum: others increase in size, and there is a fusion of three or more primary plates to form secondary plates. Near the peristome the secondary plates themselves may fuse. As to the interambulacral plates, they become much expanded near the peristome of *Spatangidae*, especially in the posterior meridian, where the single plate ending the series is expanded laterally, forming the *labrum*. It is preceded by two broad elongated plates, the *sterna*, and these by the *episterna*. The whole structure constitutes a raised *plastron*. The interambulacral plates in the typical *Clypeastroidea* and *Petalosticha* are irregular in shape<sup>1</sup>.

The test as a rule retains a regular outline. In the *Scutellidae*, however, notches often correspond to the ambulacra and to the posterior interambulacrum at the margin of the flattened disc. They may be converted into foramina during growth, and are sometimes very numerous in the region of the bivium.

The peristome is membranous. It is covered by plates continuous with the ambulacra and interambulacra respectively, and set free from the corona in the *Cidaridae*. In ectobranchiate *Desmosticha* there are five pairs of perforated radial buccal plates close to the margin of the mouth, and the rest of the membrane is either soft or irregularly plated. The same radial perforated plates are present in *Clypeastroidea* with the addition of a single interradian between each pair. The peristome becomes more or less excentric during growth in *Petalosticha* and in the most typical family, *Spatangidae*, transversely elongate as is the mouth itself. It has imperforate plates. A membranous area or *periproct* covered by irregular plates sur-

<sup>1</sup> For the 'tag,' see Martin Duncan, A. N. H. (5), xvi. 1885.

rounds the anus. It is produced by resolution of the dorso-central plate in the *Desmosticha*. In the exocyclic forms it is placed on the dorsal side either above the margin of the test, or on the margin or below it, and its position shifts during growth.

The test is lined by a layer of connective tissue and the ciliated epithelium of the coelome, which is continued over the surfaces of the contained organs. Its inner surface bears calcareous processes or pillars, except in *Petalosticha*. In the *Scutellidae* the dorsal and ventral surfaces of the test are thus closely united. In the *Clypeastridae* the pillars surround the petala, and one or more pair arise from the interambulacra close to the peristome. Of these the largest are the *auriculae*. The *Desmosticha* also possess a circle of auriculae, rising from the interambulacra in the *Cidaridae*, extending also on to the ambulacra in ectobranchiate forms in which, as a rule, they form a perfect arch under which pass the radial water-vascular vessels and nerves<sup>1</sup>.

To the plates of the corona are attached various structures—spines, clavulae, pedicellariae, and sphaeridia. The spines are generally restricted to the interambulacra in *Palaeo-echinidae*. They are attached to tubercles which vary in size in accordance with the size of the spines themselves, and are perforate or imperforate centrally. The larger tubercles are surrounded by a smooth area—the scrobicula—and this by a ring of smaller scrobicular tubercles which bear correspondingly small spines. The spines vary much in shape and in the structure of the calcareous stem<sup>2</sup>. When first formed they are similar both in shape and structure in all groups alike. The *Petalosticha* retain the primitive condition, as do some *Clypeastroidea* and a few *Desmosticha*. But in the oldest genera and families the spines increase in size and vary much in structure. The attachment takes place by a socket, and a capsular muscle. Clavulae, found only in *Spatangidae*, are minute spines with expanded head and a calcareous pedicle covered by ciliated epithelium, attached to minute tubercles which form regular bands known as *fascioles* or *semitae*. Fascioles surrounding the petaloid ambulacra or making a ring below the anus are historically the earliest to appear. The pedicellariae are modified spines with a calcareous, sometimes jointed, pedicle, bearing three, rarely four valves. The form of the valves is very variable and serves to distinguish different kinds of pedicellariae. They are opened and shut by special muscles. On the inner face of each valve of the pedicellariae globiferae there is a gland, and at its base a touch-organ. The pedicle is also sometimes surrounded by a circle of similar glands<sup>3</sup>. Pedicellariae are absent

<sup>1</sup> See Martin Duncan, 'Perignathic girdle,' &c. J. L. S. xix. 1885.

<sup>2</sup> In the soft Urchins (*Echinothuridae*) the larger spines are swollen at the apex, and inflict a painful and poisoned wound. For the structure of the poison apparatus, see C. B. and P. F. Sarasin, Z. A. ix. 1886, p. 81.

<sup>3</sup> Hamann has described under the name of 'Globiferi' what appears to be pedicellariae

from the peristome of *Cidaridae*, and are not found in *Clypeastroidea* nor in *Petalosticha* with the exception of *Echinoneus* and the *Spatangidae*. Sphaeridia are absent only in *Cidaridae*, and occur on the peristome and ambulacra. They are freely exposed in *Desmosticha* and most *Spatangidae*, lodged in some of the latter in depressions of the test which in others, in *Clypeastroidea* and *Cassidulideae* (?all) are converted into closed cavities. They increase in number with the age of the individual, are renewed like the spines, and like them are moveably connected to the test. As they are at once set in motion by any chemical change in the sea-water they are probably olfactory and gustatory in function. Structurally they are modified spines, spherical or oval in shape, and composed of calcareous laminae perforated by irregular channels. These channels are filled with branched nervous cells connected to nerves which enter the globule at its base. The nervous cells end in club-shaped projections lying between the epithelial cells covering the exterior in a single layer. The epithelial cells are ciliated in patches.

The circumoral nerve ring lies beneath the peristomial membrane and the radial nerves internally to the ambulacral plates which are therefore superambulacral in position. There is a plexus within the test which governs the coordinate movements of the spines. Branches pass out with the tube feet and at their bases, are connected to an external plexus with ganglion cells, from which filaments pass up the stalks of the pedicellariae and innervate the valve-muscles. At the tips of the feet they end in the terminal disc in a plexus connected apparently with sense-cells. The structure of the eyes lodged on the ocular plates does not seem to be accurately known. A *Diadema* has recently been found in which compound cellular eyes are distributed on the genital plates, interambulacra, ambulacra, and round the bases of the spines. The animal is sensitive to changes of light and shade. There is a circumoral blood-vascular and water-vascular ring, which lie at the base of Aristotle's lantern in *Desmosticha*. The structural details of the blood-vascular system are much disputed. The presence of a plexiform organ (= ovoid gland) connected with the oral ring is generally admitted, and there is little doubt that radial trunks exist not only in *Spatangus* but in other Urchins. The plexiform organ extends to the madreporite and has been stated to open

globiferae, in which the valves have become obsolete, leaving only the glands. They are found in many Urchins (A. N. H. (5), xvii. 1886, p. 386). Martin Duncan has discovered in some of the bodies in question atrophied valves (op. cit. (5), xviii. p. 67). Hamann also finds that the inner aspect of the valves in all kinds of pedicellariae is covered, in addition to ciliated cells, with sense-cells bearing setae and connected to nerve-fibrils. In the ped. globiferae the sense-cells are collected into one or more elevations, sometimes also into an apical elevation as well (A. N. H. (5), xvii. p. 469). Cf. Martin Duncan's remarks, op. cit. xviii. p. 68. The muscles of the valves of pedicellariae are transversely striated (Hamann, op. cit. p. 388; Beddard, *ibid.* p. 428). For lit. of pedicellariae, see p. 194.

externally through it (?). There are two intestinal vessels, one—the ventral vessel—coursing along the inner side of the tract, the other—the dorsal—on the outer. They only extend a certain distance along the intestine and are connected by capillaries. The ventral vessel opens into the oral ring. The water-vascular ring is connected to radial trunks which pass on the outer side of the masticatory organs, whilst the corresponding blood-vessels are said to pass on the inner side upon the walls of the pharynx in *Desmosticha*. The ring has five Polian vesicles in *Desmosticha*, each placed in an interradius, and many vesicular appendages in *Clypeastroidea*. The Polian vesicles appear to contain blood-vascular plexuses. The stone-canal is membranous in *Echinus*, calcareous in *Cidaris*, and extends, as usual, to the madreporite. It has been stated recently that it becomes continuous with the plexiform organ in *Spatangus*. The tube-feet are connected to ampullae within the test, and are typically furnished with a sucking disc supported by a calcareous rosette and by pieces in the walls of the feet themselves. The feet belonging to the buccal plates of the peristome end not in a disc but in two or more processes. The dorsally placed feet in *Desmosticha* are often branched and respiratory. The fine pores of *Clypeastroidea* emit minute feet of the ordinary structure, the yoked pores of the petala flat pinnate respiratory feet. Similar pinnate feet proceed from the pores of the petala in *Petalosticha*, a group in which there are locomotive feet both with and without terminal discs. It is a rule that the feet within an area inclosed by a *fasciole* differ from those without it. Brown pigment corpuscles, apparently respiratory in nature and containing iron, are met with in the coelome, water-vascular and blood-vascular vessels, together with corpuscles of different colours. The buccal or tegumentary gills, which are characteristic of the *Ectobranchiate Desmosticha*, are ten arborescent hollow diverticula of the coelome; they pass outwards in the peristome, each through a notch between the peristomial ends of the ambulacra and interambulacra. In the *Cidaridae* or *Entobranchiate Desmosticha* five diverticula with lateral branches project radially from the jaw-chambers between the alveoli into the coelome. Their walls are supported as a rule by calcareous deposits, and their cavities perhaps communicate with the exterior. They have also been found in a *Diadema*<sup>1</sup>.

The digestive tract in the *Desmosticha* and *Clypeastroidea* commences with a pharynx surrounded by a complex masticatory organ, termed in the former 'Aristotle's lantern.' This apparatus consists of an interradiation portion—viz. five sharp-pointed teeth supported by five sockets or *alveoli*, each composed of a right and left half covered above by corresponding *epiphyses*, and of a radial portion—viz. the *rotula* and the *radii*. The *alveoli* are massive and placed horizontally in *Clypeastroidea*, vertically in *Desmo-*

<sup>1</sup> Stewart, Tr. L. S. (2), i. 1879.

*sticha*. The apparatus is moved by special muscles of which some are connected to the auricles. The *Palaeo-echinoidea* possessed similar masticatory organs. There is an oesophagus, followed by an intestine ending in a rectum. The commencement of the intestine is marked by a small dilatation in *Desmosticha*, by a large caecum in *Petalosticha*. The oesophagus lies in the madreporic interradius: the intestine is arranged in two coils, an inferior and a superior. The former passes through radius III to IV, V, I and II (see Lovén's formula, note, p. 555) into the madreporic interradius, where the latter commences and turns back through radius II, to I, V and IV. The rectum commences in the interradius between III and IV, and runs vertically or obliquely to the anus. Mesenteric bands connect the coils to the test, and in *Petalosticha* to one another. In the *Desmosticha* and *Petalosticha* a tube—the *siphon*—arises from the posterior extremity of the oesophagus and lies closely applied to the inner margin of the intestine into which it opens again at or near the end of the inferior coil. It is the 'convoluted organ' so-called of *Spatangus*. A second siphon has been observed in some *Petalosticha* (*Schizaster*, *Brissus*, &c.). There is a special anal muscle. The position of the anus has been already pointed out. The pedicellariae have been observed removing the faeces from the apex of the shell.

The generative glands are arborescent caeca, large when sexually mature in *Desmosticha*, opening by a single duct on the basals or in the interambulacra (viviparous *Cidaridae*; some *Clypeastroidea*). They are typically five, but, as already stated, the number is often reduced. The ripe testes are milk-white, the ovaries yellowish-brown.

The free swimming larva is a *Pluteus*. It differs from the Ophiuroid *Pluteus* in the absence of lateral arms, and the presence of an antero-internal pair to which are added in some *Petalosticha* an antero-external pair and three processes from the post-anal area. Many Echinid *Plutei* have a pair of ciliated 'epaulettes' on each side behind the ciliated band from which they are developed originally. They are not present in the *Pluteus* of *Dorocidaris*.

The deep-sea Urchins are related to forms prevalent in the Chalk. The *Palaeo-echinoidea* appear in the Lower Silurian strata. The oldest exocyclic forms are found in the Lias. Typical *Clypeastroidea* occur in the Upper Chalk, small however in size, and the larger genera develop from the Miocene to the present time. Typical *Spatangidae* appear in the Lower Chalk; the older forms (*Collyrites*, *Clypeus*) in middle Jurassic strata.

The Echinoidea may be classified into—

1. *Palaeo-echinoidea*: with a variable number of meridional rows of interambulacral and sometimes of ambulacral plates. The plates overlap one another,

and the test therefore cannot have been firm. Aristotle's lantern present. Anus exocyclic only in *Cystocidaris*. Basal plates pierced by three to five, radials by two, pores. Spines small as a rule, and restricted to interambulacra.

2. *Desmosticha* (= *Regulares*, *Endocyclica*): of spheroidal or flattened circular form. All ambulacra and interambulacra of equal length. Anus endocyclic. Mouth central. Complex manducatory organs (Aristotle's lantern). Subdivided into

(a) *Entobranchiata* = *Cidaridae*: devoid of external gills. Auricular arch not complete and interradiar. Ambulacral and interambulacral plates continued on to peristome; pores in straight rows; pore plates primary and subequal.

(b) *Ectobranchiata*: external gills present. Auriculae extend over the radii. Interambulacral plates not continued on to peristome. (*Saleniidae*, *Echinothuridae*, *Arbaciadae*, *Diademataidae*, *Echinidae*.)

3. *Clypeastroidea* (= *Exocyclica* in part): shield shaped, often flattened. Mouth central, with manducatory organs. Dorsal portion of five ambulacra petaloid. Ambulacra of great breadth. Anus exocyclic. (*Clypeastridae*, *Scutellidae*.)

4. *Petalosticha* (= *Exocyclica* in part, *Spatangoidea*): more or less heart-shaped. Mouth more or less excentric; no manducatory organs. Anus exocyclic. Ambulacra petaloid, and anterior one often unlike the other four. Subdivided into

(a) *Cassidulideae*: oval, with mouth central or subcentral; no petaloid ambulacra or all petaloid. (*Echinoneidae*, *Cassidulidae*.)

(b) *Spatangidae*: mouth excentric and transversely elongate; a labrum; four ambulacra, petaloid as a rule; fascioles often present. (*Collyritidae*, *Ananchytidae*, *Spatangidae*.)

*General anatomical account*, Köhler, *Annales Mus. Nat. Hist. Marseilles*, i. 1883. See also A. Agassiz, 'Revision of Echini,' *Harvard Mus. Catalogue*, No. vii. pt. iv. or iii, 1872-74; Id. *Challenger Reports*, iii. 1881.

*Test*, Zittel's *Palaeontologie*, Abth. 1, *Palaeozoologie*, i. 1876-80.

*Classification of Desmosticha*, Bell, *P. Z. S.* 1881.

*Cyanosoma urens*, an *Echinothurid*, and its poison apparatus, Sarasin (C. F. and P. B.), 'Ueber einen Lederigel,' &c., *Z. A.* ix. 1886. *Pourtalesia*, Lovén, *Kongl. Sv. Ak. Handl.* xix. No. 7, 1883.

*Pedicellariae*, cf. lit, p. 194, and note, p. 558, *ante*. *Sphaeridia*, Ayres, *Q. J. M.* xxvi. 1886.

*Structure of teeth*, Giesbrecht, *M. J.* vi. 1880.

*Nervous system*, Prouho, C. R., 102, 1886; Romanes, 'Jellyfish, Starfish, and Sea-urchins,' *Internat. series*, 1885, cap. x.; Id. and Ewart, *Ph. Tr.* 172, 1881, p. 835.

*Compound eyes in an Urchin* (*Diadema*?), Sarasin (C. F. and P. B.), *Z. A.* viii. 1884.

*Vascular system, points in dispute*, Carpenter, *Q. J. M.* xxiv. 1884; xxv. 1885.

*Echinochrome or blood-colouring matter*, MacMunn, *Q. J. M.* xxv. 1885.

*Pluteus of Dorocidaris*, Prouho, C. R. 101, 1885.



## CLASS ASTEROIDEA.

*Echinozoa with bodies flattened dorso-ventrally, pentagonal in outline or prolonged into arm-like extensions, usually five in number. Arms with a ventral ambulacral furrow lodging the tube-feet which end in discs. The madreporite lies dorsally in an interradius. Caecal extensions of the digestive tract extend into the arms. The anus is dorsal. The genital glands are at the base of the arms and extend more or less into them. Pedicellariae present universally.*

The ectoderm cells develop a cuticle and are ciliated. There are among them, in some instances at least, gland and sense cells, and a sub-ectodermic plexus of nerve fibres and ganglion cells. A system of connected spaces ramifies through the connective tissue of the integument and appears to communicate with the peri-haemal spaces. The apical system of plates is well defined in the young Asteroid and includes a dorso-central, five basal and radial plates. The radials appear late, and are preceded in point of time by the *terminal* plate at the apex of the growing arm. This plate is large, and, as in Ophiuroidea, moves outwards with the growth of the arm. It supports the ocular tentacle or first azygos tube-foot, and is connected to the primary radial by a linear series of plates, of which the last formed is, as in Ophiuroidea, next to it. The basals<sup>1</sup> appear early, and the water-pore (madreporite) is frequently but by no means invariably connected to one of the circle. Under-basals are present in the young *Asterina gibbosa*, and persist in some adult forms, e.g. *Zoroaster fulgens*, many *Goniasteridae*, &c. The apical system is generally not traceable in the adult, but it persists in *Zoroaster fulgens*, many *Goniasteridae*, &c. The oral system is represented by five plates which constitute the odontophores of the adult. They are inconspicuous, and, as a rule, hidden by the mouth plates, but in some deep-water species appear in part on the surface. The calcareous structures of the body wall or perisome occur as (1) granular ossicles; (2) a network of ossicles, some of which bear spines; (3) plates variable in size, and mutual closeness; and (4) paxillae or plates bearing spines which spread out at their summits into a number of radiating processes (*Astropectinidae*). There is often a special series of dorsal and ventral *marginal* plates bordering the edges of the arms. Spines, when present, are relatively short: they are fixed or free, the latter being especially the case with those at the sides of the ambulacral grooves over which they can be closed. The pedicellariae are either sessile or stalked (*Asteriadae*), but the stalk never contains calcareous supports. The valves or blades are two in number except in *Luidia*,

<sup>1</sup> The basals are commonly termed genitals, but they do not appear to have any connection with the genital apertures as they have in the majority of Echinoids.

where there are three. They are either hinged at their base or the bases of the valves cross one another like the blades of a pair of scissors, and they are opened and closed by special muscles. The length of the valve is greater than its breadth, except in the form known as valvulate pedicellariae.

A series of paired *vertebral* or *ambulacral* ossicles, really *sub-ambulacral* by position, underlies the ambulacral grooves in their whole extent. The ossicles are narrow rods with flattened sides which are closely fitted to one another, and correspond one to the other on opposite sides of the grooves except in the Palaeozoic *Encrinasteriae*, in which they alternate. A single series of pores is formed by the juxtaposition of grooves on the flat sides of the rods. These pores are arranged in a straight line in the majority. Sometimes after the first three they are disposed in a zigzag line, i. e. are alternately near and remote from the outer ends of the rods. These ends lie just below the ectoderm at the edges of the ambulacral groove. The inner ends of each member of a pair which are moveably articulated together, meet dorsally to the radial water-vascular vessel, perihæmal spaces, bloodvessel, and nerve. A muscle runs ventrally from each right to each left ossicle, and the contraction of these transverse muscles deepens the groove. A single series of *adambulacral* ossicles lies at the outer ends of the (sub)-ambulacrals, each ossicle corresponding to the interval between two of the latter. And externally to the adambulacrals is a variable number of series of *intermediate ambulacral* ossicles, intervening between the adambulacrals and the ventral marginal ossicles when present. The members of the first pair of ambulacral and adambulacral ossicles form the *mouth plates* or *oral angle pieces*. These parts are modified in one of two ways. Either the ambulacral ossicles are the more prominent while the adambulacral remain small, e. g. in *Asterias*; or *vice versâ*, as in the majority of Asteroidea. In the first instance the oral angle piece projects across the mouth radially, in the second interradially; and the two types may be distinguished as ambulacral and adambulacral respectively. The arms are usually five in number, rarely more, as in *Solaster*, *Archaster*, *Brisinga*. They can be bent ventrally as well as sideways by special muscles, and their tips where the eyes are situated are normally curved slightly upwards. They are extensions of the disc, broad at the base; and the relative proportions of disc to arms is variable. The interradial portion of the disc is consequently much extended or much reduced, and in the latter case there are sharp interradiial angles to which correspond internal folds. *Brisinga* alone has a small disc and long arms sharply marked off from it, and therefore wears an Ophiuroid aspect.

The dorsal perisoma, except in *Brisinga*, develops numerous minute and delicate processes. These are tubular and contractile. They contain an extension of the coelome, and are known as *dermal branchiae*. The

oral nerve ring with its radial trunks lies at the base of the ectoderm cells, which are large and columnar in these tracts, and contain numerous sense cells. They are merely an exaggerated development of the plexus of fibres and ganglion cells present between the ectoderm of the perisoma. The fibres, however, are more numerous and run all in the same direction. There is an eye speck present on the ventral side of the base of the terminal arm-tentacle except in *Brisinga*. It consists of an aggregation of minute invaginations of ectoderm cells, many of which develop pigment. The blood-vascular system consists of an oral ring with five radial vessels: of an aboral ring which is circum-anal and gives off ten genital vessels in pairs and two intestinal vessels, one on either side of the dorsal extremity of the plexiform organ. These rings and vessels may themselves be plexiform. The plexiform organ or heart so-called connects the two rings and lies to the inner, i. e. adcentral side of the stone-canal. It is attached dorsally on the central side of the madreporite. A right and left perihæmal space surround the radial vessels; an outer and inner circular space the oral ring, of which the latter is connected to a perihæmal space inclosing the plexiform organ and stone-canal. Other spaces surround the aboral ring and its vessels. None of these spaces are separated *inter se* by complete partitions, and it is stated that the inner oral space and the spaces of the genital vessels are connected to the lacunar canals in the perisoma. Feeble contractions have been observed in the intestinal vessels and plexiform organ. The latter contains numerous amoeboid brown cells which also occur in the vascular system generally; in the water-vascular system, especially in Tiedemann's vesicles, and sparingly in the coelome. They are probably respiratory like the similar cells of Echinoidea. The water-vascular ring bears four pairs of Tiedemann's vesicles on its inner aspect interradially. The fifth interradius contains one vesicle and the origin of the stone-canal. This canal has calcareous plates in its walls, is lined with ciliated epithelium, and its cavity is sometimes simple, sometimes broken up into many tubes by internal septa. There is an ampulla at its dorsal end close to the madreporite. This structure is interradially placed, and is sometimes multiple. It is sometimes in connection with one of the basals of the apical system, but is not so at first, nor in some adults, e.g. *Zoroaster fulgens*, &c. The radial water-vascular vessels are placed in the axis of the ambulacral groove, immediately ventral to the inner ends of the (sub)-ambulacral ossicles. The tube-feet are arranged in a single row on either side of the vessels. Each foot sends off at its base a canal which, passing through the corresponding pore inclosed by two adjacent (sub)-ambulacrals, expands on the dorsal side into an ampulla. These ampullae are absent in *Brisinga*. The feet are terminated by sucking discs, except in the *Astropectinidae*, where they are pointed. They are richly supplied by nerves, and gland cells have been detected on their discs. The terminal

tube-foot is azygos and the first of the series developed. It forms the so-called tentacle, and has no disc.

The ciliated digestive tract consists of an oesophageal (cardiac) division with short radial pouches, which are eversible and are retracted by special muscles; of a stomach (pyloric division), from which caeca radiate into the arms, and a tubular intestine which opens by an anus placed dorsally and a little excentrically. The anus is absent, however, in all the *Astropectinidae* (*Astropecten*, *Ctenodiscus*, *Luidia*, *Leptychaster*) the genus *Archaster* excepted. The stomachal caeca commence as five narrow tubes, each of which divides once, and the ten branches thus formed bear numerous lateral branches with ampullae. They are suspended to the dorsal perisoma of the arms by double mesenteries. The intestine has close to the anus two interradial ampullae—sometimes five, each of which may divide once (*Culcita*). The anus in *Zoroaster* is placed interradially within the circle of under-basals. The digestive tract is attached by a dorsal mesentery to the body walls. The coelome is ciliated and extends into the arms. These extensions are narrow in *Brisinga*, in all others large. The generative glands are generally ten in number, and are placed interradially. They consist of branched caeca with a common duct, which, as a rule, opens dorsally by one or, more rarely, by many pores on a calcareous plate placed at the base of the arm interradially, and called in the latter case a *sieve-plate*. When mature the glands extend into the cavities of the arms. There is sometimes a greater or less number of genital glands extending up each side of the arms and opening by separate ducts, a condition most perfectly developed in *Brisinga*. A blood space surrounds the glands, and it is possible that an infertile rhachis may extend to the aboral blood-ring, as in Ophiuroidea.

The free swimming larva is known as *Bipinnaria* or *Brachiolaria*.

Most Asteroidea live in shallow water, but there are a number of deep-water genera which possess primitive or peculiar characters (*Zoroaster*, *Brisinga*, &c.). The group appears in the lower Silurian.

The Palaeozoic Asteroidea are classified as *Encrinasteriae*, characterised by the alternate arrangement of the ambulacral ossicles. In all living Asteroidea they are opposite. Viguier proposes (A. Z. Expt. vii. 1878) to group the latter as

1. *Asteriae ambulacrariae*, with the mouth plates ambulacral, the pedicellariae pedunculate, straight or crossed, and the ambulacral pores as a rule arranged in zigzag, so that there are apparently two rows of feet. *Asteriadae*, *Heliasteridae*, *Brisingidae*.

2. *Asteriae adambulacrariae*, with mouth-plates adambulacral, sessile pedicellariae, and the ambulacral pores as a rule in a straight line. Other Asteroidea.

See lit. pp. 194, 196.

*Brisingidae* of the 'Talisman,' Perrier, C. R. 101, 1885.

*Haematoporphyrin in integument*, MacMunn, Journal of Physiology, vii. (3), 1886.

## CLASS OPHIUROIDEA.

*Echinozoa with a disc-like body and slender arms sharply marked off from it; arms plated; no ambulacral groove; madreporite on actinal surface, usually fused to an oral plate; tube-feet pointed, lateral in position; no anus; genital bursae at base and sides of arms, interradial.*

The character of the integument, the number and arrangement of the plates on the body are subject to much variation. The extent to which the apical system retains the typical arrangement, or is obliterated by subsequently formed plates, differs much even within the limits of the same genus. When it is traceable, there is a dorso-central plate surrounded either (1) by a ring of five radials which typically appear before the remaining apical plates; or (2) by a ring of five basals (*Ophiomitra exigua*); or (3) by basals and radials with or without (4) superadded underbasals. There is often a circle of five primary interradials (inter-brachials), each plate touching a basal and thus separating the radials from one another. Second, third, &c. interradials carry on the line and abut on the actinal surface against the five large orals known as *buccal shields*. These shields are as a rule very distinct, and are absent only in the sub-class *Euryalida* with the exception of *Trichaster*. The integument of the disc is soft in the *Ophiomyxidae*. Calcareous granules and spines may cover the outer surface of the plates. In the *Euryalida* plates are absent, and granulations cover the surface and frequently bear attached spines. It is the only group of Ophiuroidea in which structures resembling pedicellariae have been found. They occur singly on the ventral side of certain pores for the tube-feet, and take the form of a pedicle bearing two hook-like valves which are however not apposed but placed side by side. The arms are distinct at their base; they are branched in the *Astrophytidae*, and in this family as well as in other *Euryalida* their extremities, owing to the absence of calcareous shields, can be rolled up towards the mouth. They are covered in the *Ophiurida* by a single series of dorsal shields, of right and left lateral or *adambulacral* shields, and of ventral, *super-ambulacral* or *ambulacral* shields. A pair of large shields, termed 'radials,' but not to be confused with the apical radials, overlie the bases of the arms dorsally. The *adambulacral* shields are large, their distal margin projecting and generally provided with spines. An aperture between the edge of one shield and of its successor, and the corresponding *super-ambulacral* gives exit to the tube-feet. It is often surrounded by a ring of small plates. The lateral shields appear about the same time as the vertebral ossicle: and, in *Amphiura*, the ventral a little before the dorsal shield. The *terminal* plate becomes tubular and grows round the tentacle (azygos tube-foot) at the tip of the arm. Within the arms is a linear series of large more or less disc-like *vertebral*, *ambulacral*, or *sub-ambulacral* ossicles, placed dorsally to the radial water-vascular trunk.

These ossicles take up the greater part of the cavity of each arm. Each one is composed of a right and left half immoveably united by suture. In certain deep-sea *Ophiurida*, however, each half retains the embryonic character of a curved bar united to its fellow at either end. The ossicles are connected by well-developed articulations, and there is a series of intervertebral, dorsal and ventral, muscles longitudinally disposed by means of which the arms are actively moved, principally in a horizontal plane. The halves of the two first pairs of ossicles are separated. The right half of the first ossicle in one arm approaches the left half of the corresponding ossicle in the adjoining arm to form a paired interradial peristomial plate which is internal, and placed dorsally to the triangular *oral angle pieces*. Each angle piece projects interradially, and the mouth has consequently a stellate figure. The piece consists of a right and left half united moveably by a joint. And each half has its apex formed by the first adambulacral which is borne upon a support, the second ambulacral of its own side. This second ambulacral is covered externally by the second adambulacral or *lateral buccal shield* which lies at the side of the *buccal shield* or *oral plate*. The ventral margin of each angle piece supports spines, the *buccal papillae* at the sides, the *dental papillae* at the apex of the triangle. The vertical oral edges of the conjoined first adambulacrals support a row of spines, the *palae angulares* with basal pieces. The latter generally fuse to form a bar, the *torus angularis*. The second ambulacral is pierced by the two first tube-feet or *buccal feet* which protrude into the cavity of the mouth. An aperture limited by the first and second adambulacrals and the first superambulacral shield gives exit to the third tube-foot.

The nerve ring lies on the inner or oral surface of the peristomial plates. The five radial nerves immediately underlie the superambulacral shields. Branches pass outwards on the tube-feet in which there is a sub-ectodermic nerve layer; and such a layer may perhaps exist beneath the ectoderm of the body-surface. Two genital nerves arise distally to the branches for the buccal feet. The blood-vascular ring and radial vessels lie beneath the corresponding nerve structures. There is an aboral ring or plexus which alternately ascends dorsally on the arms, and descends ventrally in the interradial spaces; a perihæmal space also incloses the stone-canal, and the plexiform organ which connects the two rings in the madreporic interradius. The water-vascular ring has a ciliated stone-canal ending with an ampulla on one of the buccal shields which is pierced by a pore. Some species of *Astrophyton* have five madreporites (pore plates), one in each interradius. *Trichaster elegans* is remarkable for possessing five simple pores instead of pore-plates. The stone-canal in these cases is similarly multiplied. The ring sometimes possesses four Polian vesicles, one in each inter-

radius except that which contains the madreporite. The vesicles may be replaced by ramified caecal tubules (*vasa ambulacralia cavi*). The radial vessels lie in a groove on the ventral surface of the ambulacral ossicles. The branches to the tube-feet perforate the aboral end of the ambulacral ossicles. The feet are simple and conical, and there are no ampullae. The two first pair, or *buccal feet*, are derived from a branch of the ring itself which bifurcates. Delicate calcareous plates are found in the walls of the ring and feet. Globular cells tinged with haemoglobin occur in the water-vascular system of *Ophiactis virens*.

The mouth is hidden by the interradial oral structures. The digestive tract is globular with radial expansions, which do not, however, extend up the arms. It is lined by ciliated epithelium, and is fixed to the body walls by connective tissue threads which cross the coelome. This cavity is not large, and extends outwards above and below the ambulacral ossicles. The genital organs consist of an infertile rhachis contained within the aboral blood plexus, and connected to a numerous set of fertile genital caeca, which are disposed in a vertical series, and open on either side of a genital bursa close to its aperture. These bursae have delicate walls of invaginated perisoma, which sometimes contain calcareous plates. They extend inwards dorsally to the digestive sac, and open by slit-like ventral apertures, one on either side the base of an arm. There are therefore two bursae in each interradius. The bursal aperture is divided in *Ophioderma* into an adoral and an aboral part; the bursa itself is single, but the genital caeca are confined to the dorsal portion, and to the interradial wall. Currents of water flow in and out of the apertures, and the bursae have probably a respiratory function. The adradial wall of each bursa is supported by a genital plate. The genital caeca are surrounded by a blood plexus derived on the interradial side from the aboral ring, on the adradial from a special genital vessel.

The free swimming larva is a *Pluteus*, and differs from the Echinoid *Pluteus* in possessing a pair of lateral arms developed from the sides of the anal portion of the ciliated ring.

Some *Ophiurida* develop a phosphorescent light from the dorsal aspect of the arms. Both sub-groups of the Class appear in the Silurian strata.

There are two sub-groups—

1. *Euryalida*: devoid of plates in the integument; with simple or branched arms, which can be rolled up towards the ventral aspect at their tips; pedicellariae present. *Astrophyton*, *Trichaster*, and *Astronyx* are the principal genera.

2. *Ophiurida*: with simple arms, superambulacral shields, and five buccal shields; the disc has either a soft integument or is covered by granules or plates. There are several families.

See lit., pp. 194, 196.

*Formation of arm skeleton*, Ludwig, Z. W. Z. xxxvi. 1882. *Pedicellariae in Euryalida*, Id. Z. W. Z. xxxi. 1878.

*Apical system*, P. H. Carpenter, Q. J. M. xxiv. 1884.

*General anatomy*, Id. Q. J. M. xxi. 1881.

### PELMATOZOA.

Echinodermata which are fixed permanently or temporarily by an aboral stem, generally jointed and containing a neuro-vascular apparatus. The apical system incloses or supports the visceral mass. The oral system may form a tegmen calycis or be resorbed partially or completely. The water-vascular ring does not open direct to the exterior. Mouth and anus on the actinal surface.

### CLASS CRINOIDEA.

*Pelmatozoa with arms more or less branched, borne upon the radials and in most instances furnished with pinnules. There is an ambulacral and anti-ambulacral nervous system. The lateral extensions of the radial water-vascular vessels form tentacles (=tube feet) which are disposed in groups. Water-tubes and water-pores lead into the coelome; no stone-canal.*

The oral or actinal surface forms a disc, the aboral or abactinal a supporting calyx. The latter consists either solely of the plates of the apical system or may include also the basal joints of the arms, i. e. second and third radials, &c., and the lowest pinnules. The dorso-central plate retains its normal position in the few genera, all extinct, in which no stem is developed, e. g. *Marsupites*. But in the stalked Crinoid it forms the base of attachment, and is separated from the other plates of the apical system by the joints of the stem<sup>1</sup>. These joints may be few, or exceedingly numerous, e. g. in fossil species with stems seventy feet long, and are usually provided with well-formed surfaces of union. The *Comatulidae* break away from the stem at a certain stage of growth. The topmost joint of that structure then constitutes the central element of the calyx, and is termed the *centro-dorsal* plate. Under-basals are found in some fossil *Palaeocrinoidea* and *Neocrinoidea*. The basals vary from five to three in number, but all living species possess five except *Hyocrinus* which has three. In living *Comatulidae* except *Thaumatocrinus* and *Atelecrinus* they unite into a small *rosette* plate which is concealed from without by the centro-dorsal and radials. The first radials are five in number in all *Neocrinoidea*; other numbers, however, occur abnormally. They are concealed from view by the centro-dorsal and second radials in living *Comatulidae* except *Thaumatocrinus* and *Atelecrinus*. In many extinct forms

<sup>1</sup> *Holopus* is attached by an 'irregular encrusting calcareous expansion.'



especially Palaeozoic, the adjoining edges of the first radial plates are partially separated by the circle of first interradians, and in the living *Thaumatocrinus*, and the extinct Palaeozoic family *Rhodocrinidae*, an interradian alternates with a radial and touches the basals. Higher orders of interradians are found in many Palaeozoic and some Mesozoic species, but in the latter, as well as the living forms, the interradians, when present, are as a rule numerous and irregular.

The oral system is represented by a circle of five orals surrounding the mouth in *Thaumatocrinus*, *Holopus*, *Hyocrinus* and *Rhizocrinus*. Present in the pentacrinoid, i. e. stalked *Antedon*, they are resorbed during growth. They are large, and their circle is broken by the anal tube in many Palaeozoic genera, in many of which an oro-central is present, and together with the circle of orals forms a *vault*, *dome*, or *tegmen calycis* arching over the mouth. The extinct *Actinocrinus* has in addition circles of dome radials and interradians, but as a rule such plates are small and irregular. In all these forms the ambulacral grooves ascend the *dome*, and enter the oral vestibule between the bases of the orals.

The surface of the disc between the ambulacra and their divisions, as well as its continuation upon the arms, is sometimes naked, though calcareous spicules are present at the edges of the ambulacra. It is, however, as a rule protected by irregular *anambulacral* plates, continuous at the edges of the disc with the interradians. The edges of the ambulacra themselves are generally guarded on the disc, arms and pinnules by a series of *covering* plates (*adambulacrals*) which in some *Comatulidae* are represented by soft lobes. Whether plates or lobes, they alternate *inter se* on opposite sides of the grooves over which they can close. They are often borne upon the edges of a single series of *side* plates.

The plates of the calyx, disc and ambulacra develop as cribriform calcareous films, and are thickened by addition of new films.

To the radials are attached the arms, and to certain joints of the stem, the cirri. The arms generally branch dichotomously, and the joint known as *axillary*, which bears the branches, has two equal oblique and terminal facets, one for each branch. The growing point of the arm or its branches forks at short intervals, and one division of the fork, alternately the right and left, remains relatively short and small constituting a pinnule<sup>1</sup>. In the living *Hyocrinus*, however, and some fossil forms, the pinnule is about as long as the part of the arm distal to its point of origin. Such pinnules resemble the branches of an arm, but the

<sup>1</sup> Pinnules are absent from every axillary joint, and from the proximal of two joints united by ligament or by syzygy. The lowest brachials of *Atelectrinus* (*Comatulidae*) and of *Bathycrinus* and *Rhizocrinus* are also devoid of them, and in *Antedon* it has been observed that the pinnules of the lowest brachials (3-7) are developed at a late period. Hence it appears that pinnules may be formed independently of the growth of the tip of the arm.

facets upon the joints by which they are borne are somewhat laterally placed, whilst those for the continuation of the arm are sub-terminal. The cirri are borne in whorls upon certain joints of the stem, hence termed *nodal*, which are separated one from the other by a series of *internodal* joints. The centro-dorsal of the *Comatulidae* bears several whorls of cirri, but in development it has a first whorl of five cirri placed radially. In *Rhizocrinus* the upper part of the stem is bare, the lower part bears branching cirri, and may itself be resolved into branches. The pentacrinoid *Antedon* and *Holopus* have no cirri, nor have some fossil forms in which the stem tapers to its apex, and was probably coiled round some foreign object when the animal fixed itself. The stem is normally attached by the terminal joint or dorso-central plate. In some individuals growing in muddy bottoms, this attachment is either lost or not developed, and the stem ends by a rounded nodal joint. The animal in this case anchors itself by its terminal cirri as do the *Comatulidae*, and it is probably free to move about as they do by alternate flexions and extensions of the arms. Or else the tips of the cirri are permanently attached to stones or rocks as they are in *Rhizocrinus*.

In *Thaumatoocrinus* the arms like the radials are five in number, but in other *Comatulidae* and stalked living Crinoids they are ten or more, owing to the branching of the five rays. The arms themselves, their branches and pinnules, like the stem with its cirri, are made up of a single series of calcareous joints. The series is rarely double (certain sp. of *Encrinus*, some *Palaeocrinoidea*). The calcareous matter is deposited in the form of fasciculated bundles. The joints of the arms are termed *brachials*. The first two joints, or the first four or six joints in *Metaocrinus*, are the second, third, &c. radials. The third radial is as a rule an axillary. If the arms branch twice the joints between the first and second places of division are known as *distichals*; if thrice, the joints between the second and third places of division are designated *palmars*.

The mode in which the calcareous parts of the skeleton unite varies. Union occurs (1) by suture of the edges of the plates in the apical system; (2) by striated muscle bundles in addition to ligaments between the radials (first radials so-called) of the apical system and the second radials; between a pinnule-bearing brachial, its successor and the pinnule; and in many instances between every two pinnule joints; (3) by bundles of ligamentous fibres solely between the joints of the stem and cirri; between brachials and the joints of pinnules not united by muscles. The lines of union between plates of the calyx may be obliterated by ankylosis, e.g. basals of *Bathycrinus*. The ligamentous connections may become very close, and the external line of union may disappear. Two joints thus connected are termed a *syzygy*, e.g. internodal joints of the stem in some instances, second and third radials very commonly, and brachials not connected

by muscles. The bundles of ligaments uniting the joints of the cirri and the dorsal inter-articular ligaments between brachials not united by syzygy appear to be contractile. The cirri can lay hold of neighbouring objects, and may be tetanically curved by stimulation of their axial nerve cord. Slow bending movements of the stem have been observed.

The mouth is central, the anus excentric and interradiial on the disc save in *Actinometra* (*Comatulidae*), in which the mouth is excentric or marginal and the anus subcentral. *Thaumatocrinus* and Palaeozoic forms have the anal interradius large and the symmetry of the disc thereby destroyed. Four interradiial plates stretch from a first interradiial towards the anus in the former. In the extinct *Cyathocrinidae* there is a heavily plated anal sac. If the anal interradius be considered as posterior when the disc is turned upwards, the gut passes from the mouth to the left, then anteriorly and round the right side of the calyx to the posterior interradius, where it turns upwards and forwards to the anus. The mouth is thus in the centre of a spiral coil (endocyclic). In *Actinometra* there are three additional coils concentric with the anus; the mouth is exocyclic. The digestive tube is ciliated, and divisible into oesophageal, median, and anal sections. The coelome is more or less filled with connective tissue supporting the gut, blood-vessels, and nerves. Calcareous spicules and plates are developed in this connective tissue. In some species of *Antedon* there is a well-marked axial and perivisceral cavity in the disc<sup>1</sup>. The prolongations of the coelome in the arms and pinnules form two canals—one, the *subtentacular*, occasionally divided into a right and left canal underlying the radial water-vascular vessel, the other, the *coeliac*, lodged in the ventral (oral) groove of the calcareous brachials and pinnule joints. The two canals communicate at the apices of the arms and pinnules, and a current caused by ciliated cups lodged in the pinnule joints sets up the subtentacular and down the coeliac canal. A smooth peristome surrounds the mouth, and from it radiate the five ambulacral or food grooves which divide and ascend the arms, their branches and the pinnules, with minute extensions on the tentacles. The groove with underlying blood-vessel and tentacles is absent from the adoral pair of pinnules in *Antedon*, and from a variable number of posterior, i.e. adanal, arms in *Actinometra*. The grooves with their extensions are, unlike the rest of the peristome (body-surface), covered by a columnar ciliated epithelium, among which are probably sensory cells. The cilia waft any particles of food (*Radiolaria*, *Foraminifera*, *Diatoms*, &c.) to the mouth. Below this epithelium, and rarely separated from it by a connective tissue lamella, is the ambulacral nerve. These nerves are connected by a circumoral ring, or more probably by a

<sup>1</sup> In consequence of this fact the visceral mass of the disc is easily detached. *Hyponeme Sarsii* (Lovén), a supposed Cystoidean from Torres Straits, is the visceral mass of an *Antedon* common at Cape York.

plexus beneath the oesophagus. Irritation of the nerve causes only movements in adjoining pinnules. There is an anti-ambulacral nervous system composed of fibrils and ganglion cells, and both sensory and motor in function, governing the flexion and extension of the arms in swimming. It consists of a central mass lodged within or below (*Comatulidae*) the circle of basals from which an extension passes down the stem with an axial branch to every cirrus. Five axial branches enter the basals, and each of them divides into two. Two adjoining branches enter each radial and pass on, dividing as the arm divides and entering the pinnules. A commissure connects all the ten secondary branches in the first radials, and another commissure the two main branches in the axillary radials. But there is some difference of detail in various Crinoids. The axial nerves are at first lodged in a ventral groove throughout their course, a condition permanent in some *Palaeocrinoidea*. But in all living Crinoidea the calcareous matter finally surrounds them. The cords give off branches in each joint, one pair to the thin aboral integument, two other pairs to the lateral and oral surfaces. Bipolar cells have, in some instances, been seen in the course of these branches. Their ultimate twigs appear to be connected with the muscles (brachial) through stellate cells and through other similar cells with the integument and with the tactile papillae furnished with sensory hairs on the tentacles. A set of branches or a plexus at the side of the ambulacral grooves in the disc and arms forms a parambulacral system with a longitudinal connecting nerve in *Actinometra nigra*. And in *Antedon Eschrichtii* there is a circumoral labial plexus.

The blood-vascular system consists of a circumoral ring with an ambulacral vessel underlying the nerve; of a dense circumoesophageal labial plexus connected to the oral ring and sending out branches to the genital plexus as well as intervisceral vessels; of a plexiform organ lying interradially in the disc anteriorly to the mouth and connected to the labial plexus, genital and intervisceral vessels, and extending into the 'chambered organ' of the calyx. This organ lies between or below (*Comatulidae*) the basals, and within the central portion of the aboral nervous system. It consists of five peripheral and radial chambers and a central plexus or 1-2 vessels. Five vessels pass, one from each chamber, to the corresponding cirrus and are continued down the stem dilating in each nodal joint and sending off a branch to each cirrus. The plexus supplies the remaining whorls of centro-dorsal cirri in *Comatulidae*, and is continued down the stem in stalked forms. It has recently been shown that two vessels separated by a septum lie in the centre of the axial nerves of the arms.

The water-vascular system consists of a circumoral ring and radial vessels, all of which are beneath the corresponding blood-vessels. Calcareous subambulacral plates sometimes occur in the connective tissue

under the radial water-vascular vessels. In some *Palaeocrinoidea* they were regularly arranged in two series. Ciliated branched *water-tubes* depend from the ring and origins of the radial vessels and open into the coelome. *Water-pores*, or short tubular canals with a median ciliated dilatation, open into the coelome from the exterior. Water-tubes and pores, taken together, correspond to the madreporic system of other Echinoderms. In a young larval *Antedon* one tube and one pore are found—the latter in an oral plate—in the interradius to the left of the anus, the one which contains the madreporite in Asteroidea. In an older larva there is a tube and pore in each of the five interradii, a condition persistent in *Rhizocrinus lofotensis*. The water-tubes are numerous in other adult Crinoids, e.g. thirty in each interradius in *Antedon rosacea*. The water-pores are few and pierce the orals in *Hyocrinus*. In *Antedon rosacea* there are 1500 on the disc. They are relatively few in the anal interradius and in *Actinometra* are found on the arms and pinnules. Here they open into the genital canal or coelomic space surrounding the genital rhachis. When the disc is covered with plates the pores may be scattered singly or grouped up to the number of twenty in a plate. The radial water-vascular vessels give off alternately to the right and left, in groups of three each, delicate tubular branches, respiratory in function, which form the tentacles homologous with tube-feet. The vessel is slightly dilated on the side opposite to the origins of the tentacles.

The genital gland appears to consist of a central portion, not always traceable, within the labial blood-vascular plexus from which a branch extends along the arms and pinnules, surrounded by a plexus of blood-vessels, and contained in the genital canal a special offset of the coelome. These structures lie between the subtentacular and coeliac canals. The gland is essentially a tube lined by an epithelium, from which are derived spermatozoa and ova, according to sex. The greater portion is not fertile, and constitutes the rhachis. Fertile portions occur rarely in the disc and arms. In *Holopus* alone they are always in the arms; otherwise they are confined to the pinnules, where they form round or elongated masses. The duct in the female is a wide canal, in the male one or two fine canals to each mass. The mode in which the ducts are formed is unknown.

Sacculi or aggregations of colourless vesicles of unknown function are found in variable numbers at the side of the radial water-vascular vessels, and in *Antedon* in the walls of the digestive tube. They are absent in *Actinometra*, where, however, isolated vesicles may occur in the perisome. Two colouring matters giving special absorption bands are found in Crinoids, Pentacrinin from *Holopus*, *Pentacrinus* and *Metacrinus*, and Antedonin from three species of *Actinometra*. The yellow or rose-red pigment in *Antedon* gives no bands. The arms of *Comatula* and some other Crinoidea may become locally deformed by the attacks of the *Myzostomidae*, a

parasitic order of Chaetopoda; see p. 609. Extinct species seem to have been similarly attacked (von Graff).

*Holopus* and *Hyocrinus* are abyssal forms (1200–2500 fathoms); an *Antedon* has been dredged at 2900 fathoms, but the majority of Crinoidea occur in shallower waters. They are generally met with in masses, as is the case with Crinoids in the Silurian, Carboniferous, and Oolitic rocks. *Antedon* is a cosmopolitan genus; *Holopus* is confined to the Caribbaean sea. Stalked Crinoids are found between the parallels of 68 N. and 46 S. latitude; *Comatulidae* between 81 N. and 52 S. The *Holopodidae* originate in the Upper Silurian, *Pentacrinus* in the Trias, *Antedon* in the lower Oolite. Many fossil *Comatulidae* are large in size.

The gastrula mouth in *Antedon* closes early, and is not terminal and posterior, as in other Echinodermata, but behind the larval third ring of cilia, on a flat ventral surface (cf. p. 548, *ante*). The water-vascular vesicle is formed after the left and right coelomic vesicles, which become placed terminally, the left orally, the right aborally at the base of the stem into which it extends. The water-vascular vesicle grows round the oral end of the archenteron, and subsequently divides the left peritoneal vesicle into an anterior and posterior portion. The former forms the oral vestibule, enclosed within the oral plates. The mouth is formed in its floor, and the ambulacral grooves grow out from it radially. Hence their epithelium is hypoblastic in origin. The posterior section sends out the subtentacular canals, as the right vesicle does the coeliac. The water-vascular ring develops ten pairs of tentacles within the vestibule. Five pairs are simple and short, and are interradial like the oral plates. The other five are radial, and consist each of three tentacles, the central one of which is carried outwards in the growth of the arm. The five orals are at first large, and one is pierced by the primary water-pore; they are eventually resorbed as is the anal interradial plate, which at first touches a basal, and is afterwards raised on to the disc.

The Crinoidea are divisible into—

1. *Palaeocrinoidea* (= *Tesselata*): calyx not invariably pentamerous; a tegmen calycis generally present; anal interradius large, with an anal interradial touching a basal. Palaeozoic.

2. *Neocrinoidea* (= *Articulata* + *Holopus* + *Marsupites*): calyx pentamerous; interradials rarely intervene between the radials; orocentral always absent; orals, when present, surround the mouth. Mesozoic and recent. *Comatulidae* and other living Crinoidea.

*General anatomy*, P. H. Carpenter, Challenger Reports, xi. 1884. *New sp. of Metacrinus*, Id. Tr. L. S. (2), ii. (14), 1885. *Variations in structure of arms*, Id. *ibid.* ii. (17), 1886.

*Fossil forms*. See in addition to Zittel's work, cited p. 549, *ante*, de Loriol, 'Palaeontologie Française,' Paris, x., pt. 1, 1882–84; Wachsmuth and Springer, 'Revision of *Palaeocrinoidea*,' Proc. Acad. Nat. Sc. Philadelphia, 1879, 1881, 1885; cf. P. H. Carpenter, *supra*, and in A. N. H. (5), xvii. 1886, p. 276.

*Deformities in fossil Crinoids due to Myzostomidae*, von Graff, Palaeontographica, xxxi.

*Antiambulacral nervous system*, Milnes Marshall, Q. J. M. xxiv. 1884.

*Process resembling copulation in Comatula*, Jickeli, Z. A. vii. 1884 (A. N. H. (5), xiv.).

### CLASS CYSTOIDEA.

Extinct Pelmatozoa, either sessile, or furnished with a short stalk. The body is ovate or globular, and covered with polygonal plates rarely arranged with regularity. The stem-joints are round and ring-like, the median canal being large. It is pointed below, and the joints are sometimes telescoped one into the other. The mouth is elevated and central, and five ambulacral grooves may be traced radiating from it in many instances. A tube covered by plates probably represents the anal tube, and a third aperture, sometimes present, a genital or ovarian opening. Arms, two to five in number, are generally present, but are feeble and unbranched. They may carry pinnulae, and the ambulacral grooves may be protected by *covering plates*. Elevations pierced by double pores (= water-pores?) are developed on more or fewer plates in many species. In others there are grooves pierced by pores which form a rhombic figure, one part of the figure being on one plate, the other on an adjoining plate. These *pectinated rhombs* are sometimes few in number, isolated, and devoid of pores; and the two halves of the rhomb are occasionally separate and distinct.

The Cystoidea appear in the Lower Silurian, reach a maximum of development in the Upper Silurian, and die out in the Carboniferous strata in which they occur sparingly.

### CLASS BLASTOIDEA.

Extinct Pelmatozoa with a short stem, an ovate body, and five-rayed ambulacral area. The calyx consists of three basals, five radials and five (interradial) orals. Each radial is *forked*, enclosing a sinus, in which is lodged an ambulacral area. The orals, or '*deltoid pieces*,' are attached to the ends of two adjoining prongs belonging to two different radials or '*fork pieces*.' The mouth is central. The ambulacral area is formed by five *lancet* plates with median longitudinal grooves. *Side* plates rest upon each lancet plate laterally, and in some forms there is also a row of *outer side* plates. Jointed pinnules in a single or double row are attached to the outer edge of each ambulacral groove. The inner side plates are marked by grooves leading outwards, each one to a marginal pore. The pores lead to a cleft (*hydrospire cleft*) at the outer edge of the lancet plate, and the cleft in its turn to an underlying *hydrospire* canal, into which open a system of interradian lamellar tubes, the *hydrospires*, supposed to be

respiratory in function. A single or double aperture lies at the apex of each oral or deltoid piece. These are the *spiracles* or efferent external apertures of the hydrospires. The anus is confluent with one of them. The genital ducts probably opened into some portion of the hydrospires, and the spiracles in that case discharged the genital products. A circum-oral ring with five radiating tubes, one under each lancet piece, represents the water-vascular ring and ambulacral tubes.

In some American forms a vault of minute plates, without definite arrangement arches over the mouth and spiracles, except in *Elecrinus*, where there is an oro-central and five orals. A series of *covering plates* may be continued down the ambulacral area concealing the groove. This arrangement is identical with what obtains in many *Palaeo-crinoides*.

The Blastoidea appear later than the Crinoidea and Cystoidea in the Upper Silurian, and reach their greatest development in the Devonian and Carboniferous strata in which they die out.

Carpenter (P. H.) and Etheredge, A. N. H. (5), ix. 1882; Carpenter, op. cit. (5), xv. 1885.

## VERMES.

The classes and minor groups collectively termed Vermes do not constitute a phylum in any way comparable for example to the phyla Mollusca or Echinodermata. It is easy to show that the various Molluscan and Echinoderm classes are derived by a modification of a set of well-defined and peculiar characters. There is consequently amid much diversity a common thread running through the series. On the contrary the types of structure seen in most Vermian classes are very distinct from one another; they are specialised and therefore genetically remote. Attention nevertheless may be directed to certain general features.

The antero-posterior axis is usually of considerable length, the transverse and dorso-ventral short; but in the *Myzostomidae* and a few Polyclad *Turbellaria* the antero-posterior and transverse axes tend to an equality, and hence the body is disc-like. A ventral aspect is always distinguishable from a dorsal except in *Acanthocephala*; it is usually characterised by being flattened for locomotor purposes: sometimes also by the presence of various apertures, e.g. mouth, anus, &c., or of the main nervous cords. Bilateral symmetry is well marked, but a more or less apparent radial symmetry is observable in some Polyclad *Turbellaria*<sup>1</sup>. A division of the body into

<sup>1</sup> Much stress has lately been laid on the Ctenophoran characters of certain Polyclad *Turbellaria*. The presence of a free dorsally placed mass of otoliths in two genera, and of Ctenophore-like ciliary plates in one of the two, are striking features. But the existence in *Turbellaria* of a well-developed excretory system, the confinement of the principal nerve-cords to a ventral plane even when their radial symmetry is most marked, are features decisive against any close alliance with *Ctenophora*.



somites is distinct in *Chaetopoda* and *Archi-Annelida*; present but obscured by a secondary annulation of the somites in *Hirudinea*; probably aborted in *Gephyrea*. It is indicated by the presence at regular intervals of bundles of dorso-ventral muscle-fibres, &c., in *Nemertea* and Triclad *Turbellaria*. The *Enteropneusta* retain a division of the body into two regions, a collar and trunk, in correspondence with the mode of development of the coelome. The segmentation of the strobila in *Cestoda* is seemingly correlated solely with reproductive necessities. Other Vermes are certainly unsegmental. A large prae-oral lobe or prostomium is present in *Enteropneusta* and *Gephyrea chaetifera*. The corresponding region in *Chaetopoda*, *Archi-Annelida*, and *Hirudinea* is much reduced, and may in some cases be an outgrowth of the peristomial segment.

The coelome may be large, and is sometimes divided into compartments in segmented Vermes; it may be represented by irregular passages between the mesoderm cells, or even absent (?) altogether as in Acoelous *Turbellaria*. In the *Hirudinea* it undergoes obliteration (diacoelosis) to a very great extent during growth, and may be partially replaced by spaces secondarily formed (metacoelosis) in the mesoderm. It opens externally by special pores in many oligochaete *Chaetopoda*. In the *Enteropneusta* and *Chaetognatha* it is an enterocoel developed from the archenteron; in the segmented Vermes, and probably in *Nematoda*, it is a schizocoel; and in *Rotifera* it appears to be a permanent archicoel. The coelomic channels of *Trematoda*, &c., are apparently intercellular spaces<sup>1</sup>.

The characters of the integument and disposition of the muscles of the body-wall are subject to much variation. It may be noted that the ectoderm, hypodermis or epidermis cells are transformed into the cuticle of *Trematoda*. It is uncertain whether or not the same is the case in *Cestoda* and *Acanthocephala*, but in the first-named the hypodermis is perhaps represented by sub-cuticular cells.

The nervous system may retain a position in the hypodermis (= ectoderm) as in *Enteropneusta*, some *Chaetopoda*, *Archi-Annelida*, Gephyrean *Priapulidae*, some *Nemertea*, *Chaetognatha*, and to a certain extent in *Nematoda*. In the *Turbellaria* the central ganglia do not always bear any direct relation to the mouth or pharynx; and in *Nemertea* the commissures of the cephalic ganglia surround the proboscis and not the oesophagus. A peripharyngeal union of the cephalic ganglia is exceptionable in *Trematoda*. The ventral nerve-cords are segmented more or less distinctly in those Vermes in which the segmentation of the body is pronounced. Numerous longitudinal nerve-trunks of almost equal importance are found in *Trema-*

<sup>1</sup> Fraipont's view as to the existence of *intercellular* coelomic spaces or channels in *Cestoda* and *Trematoda* is opposed by Pintner, who holds that, in some *Cestoda* at least, there is a system of *intracellular* canals with which the basal processes of the flame-cells are connected. The former view seems more likely to prove correct.

*toda*, some Polyclad *Turbellaria* and *Nematoda*. An almost radial symmetry in the *Turbellaria* in question is noticeable, but the ventral position of the trunks destroys an otherwise apparent resemblance to *Ctenophora*. Complete circular nerve-rings connecting the longitudinal trunks from place to place are present in some *Gephyrea*, *Trematoda*, and *Nematoda*. The predominance of the dorsal nerve-cord and the great development of a diffuse sub-epidermic nerve-layer in *Enteropneusta*, the varying positions of the two lateral cords in *Nemertea*, i.e. lateral, more ventral or more dorsal, and their occasional supra-anal union, are points bearing on the supposed relationship of these groups to Chordata. Organs of special sense occur in the shape of sense-cells with sense-hairs, aggregated into remarkable lateral sense-organs in the Chaetopod family *Capitellidae*; of sensory papillae, of eyes and otocysts. But the last-named are far from common.

A digestive tract is not even indicated in development in *Cestoda* and *Acanthocephala*, probably in consequence of a long continued ancestral endo-parasitic life dependent on a supply of ready digested food. It is rudimentary in most male *Rotifera*, and in the sporocyst of *Trematoda*. It is replaced by the central parenchyma of the body, into which food passes through the mouth in the *Acoela* among *Turbellaria*. The form of the tract varies. Sacculation more or less distinct occurs in segmented Vermes. There is no anus in *Trematoda* or *Turbellaria*, and, what is more, there is no evidence to show that it has become aborted. When present it is terminal, ventral and sometimes dorsal (some *Chaetopoda*, Sipunculid *Gephyrea*, *Hirudinea*). It is primitively dorsal in the larval *Balanoglossus Kowalewskii* (*Enteropneusta*), but becomes terminal by the abortion of the sub-anal portion of the body. The existence of laterally placed respiratory apertures opening from without into the anterior part of the digestive tract may, among other features, indicate a connection between the *Enteropneusta* and the ancestral forms of the Chordata.

A vascular system is developed in *Enteropneusta*, most *Chaetopoda*, the *Polygordiidae* among *Archi-Annelida* and the *Gephyrea*, with the exception of *Priapulidae*<sup>1</sup>. It consists of a system of tubes, some portion of which is contractile, completely closed off from the coelome. In *Hirudinea* the vessels appear to communicate with the remnants of the coelome as well as with the secondarily formed metacoelome. Haemoglobin occurs in the vascular plasma of many *Chaetopoda*, of *Gnathobdellidae* among *Hirudinea*, in the blood corpuscles of some *Nemertea*. Another respiratory pigment, chlorocruorin, is found in some *Chaetopoda*. Specialised haemoglobin-tinted corpuscles are found in the coelome of a few *Chaetopoda*, and the

<sup>1</sup> The *Nemertea* also possess a vascular system. The cephalic vessels are spoken of by Oudemans as lacunar, and Hubrecht regards the whole system as well as the cavity of the proboscis-sheath as remnants of an archicoele. The communication in some Nemerteans between the nephridia and the vascular lacunae is in favour of this view.

Gephyrean *Thalassema Neptuni*: haemerythrin replaces the haemoglobin in some members of the Gephyrean family *Sipunculidae*. Colourless corpuscles of fixed outline occur in the vascular system of many *Chaetopoda*, some Gephyreans, as well as in the coelome of some of the latter (*Priapulidae*).

No excretory or nephridial system has been discovered in *Chaetognatha* and *Acanthocephala*, and, if present in *Enteropneusta*, it has a peculiar form, unless the canals communicating with the coelomic cavities of the collar and proboscis may be deemed to be metamorphosed nephridia. It is peculiar also in *Nemertea* and *Nematoda*. But in other Vermes it falls under one of two types, according as to whether it commences (1) by flame-cells, or (2) by ciliated funnels. A flame-cell is a cell bearing a long flattened but pointed cilium, which projects freely into a funnel-shaped space with proper walls. The cell may or may not have basal processes connecting it to the surrounding tissues. The funnel-shaped space is continuous at its apex with a tubular canalicule, by which it is connected to the system of excretory vessels. It is said by Fraipont to have, in certain instances at least, e.g. in *Cestoda*, a lateral opening into the coelomic spaces of the mesoderm; but the existence of this opening is denied by Pintner and others. Such flame-cells are found in *Trematoda*, *Cestoda*, *Turbellaria*, and *Rotifera*. The system of excretory vessels with which they are connected varies in disposition to a certain extent. It may have, as in some *Cestoda* and *Turbellaria*, numerous external apertures, which show a more or less perfect segmental arrangement in certain of the latter (some Triclads); but as a rule there are only one or two apertures variously situated and terminal to the main canals. The vessels themselves seem to be intracellular, i.e. to consist of a series of perforated cells, and cilia may occur in their course. They may form a network, but in most cases there are two or more main longitudinal canals, the terminations of which may be contractile. The second type of excretory system occurs in *Chaetopoda*, *Archi-Annelida*, *Hirudinea*, and in *Gephyrea* in a modified form. It begins with a series of intercellular funnel-shaped apertures, composed each of a variable number of cells bearing cilia. The funnels have primitively a segmental arrangement, a pair to each somite of at least the middle region of the body, but this arrangement may be lost or masked. They lead in *Chaetopoda* and *Archi-Annelida* into tubes which may be in part intracellular, are sometimes convoluted, and have segmentally disposed external apertures. In the *Hirudinea* the excretory tubes are also intracellular, but though their external apertures are segmentally disposed, they form a network which is either continuous or has become much restricted and discontinuous<sup>1</sup>. Two sets of nephridia are distinguishable in *Gephyrea* except *Priapulidae*, where

<sup>1</sup> The presence of nephridial lobes in the medicinal Leech and its allies is perhaps best explained on the hypothesis that the lobes represent a restricted or disconnected network of vessels.

no excretory apparatus has been detected: (1) sacs, each with a single funnel leading into the coelome, typically paired but restricted at the outside to four pairs in all, and opening externally on the ventral aspect; (2) sacs, with numerous funnels leading into the coelome, and opening externally with the rectum; but there is reason to believe that this communication with the rectum is secondarily acquired<sup>1</sup>. The second kind of nephridia (2 *supra*) is present only in *Gephyrea Chaetifera*, side by side however with the first kind. The type of renal organ with ciliated funnels is limited to groups in which a coelome is present, and is probably an adaptation to it (Lang); and it is a noteworthy fact that the funnels so far as is known are developed independently of their excretory tubes. The *Rotifera* are said to be an exception to the statement, in so far that a coelome is present, yet their nephridia belong to the first type. The same is true of some *Turbellaria*. Their coelome however is probably an archicoele. Larval or provisional nephridia, commencing with flame-cells, occur in many Polychaetan Trochospheres; with the flame-cells aborted in *Polygordius* among *Archi-Annelida*, and in *Echiurus* among *Gephyrea*, and in a very rudimentary condition in *Hirudinea*. A pair of these organs is found in the head, and may be branched as in *Polygordius* and *Echiurus*. A second pair of organs in *Polygordius* has a structure similar to the first pair. A right and left longitudinal canal grows backwards from the first pair or cephalic nephridia in *Polygordius*, and gives origin to the permanent nephridia, afterwards disappearing. Similar but persistent canals connecting the permanent nephridia have been discovered in *Polymnia nebulosa* (= *Terebella Meckelii*). In the Polychaetan Trochospheres a pair of these larval nephridia is found in the head, and one or more pairs in the body. Provisional cephalic nephridia have also been observed in larval *Oligochaeta*. It is possible that the excretory system of the *Turbellaria*, especially the *Triclada*, with its more or less segmentally arranged apertures as well as longitudinal canals, represents a primitive condition which becomes modified in other cases (1) by the suppression of the longitudinal canals, and (2) by the formation of intercellular funnels coupled with a well-marked segmental arrangement of the parts persisting and of the external apertures<sup>2</sup>. The relation which the nephridia acquire, either temporarily or permanently, to the sexual organs is entirely secondary.

<sup>1</sup> The male *Bonellia viridis* has two simple nephridial tubes, each with a single internal funnel, which open externally and independently, but near the posterior attachment of the intestine. The corresponding organs in the larval *Echiurus* open similarly at first; their subsequent connection to the rectum is therefore secondary. It is doubtful how far the Gephyrean nephridia retain a renal function.

<sup>2</sup> A very interesting discussion on these points will be found in Lang's 'Polycladen,' Fauna, &c. des Golfes von Neapel, xi. 1884, pp. 674-79. The occasional presence of a longitudinal canal in connection with segmental nephridia is especially noteworthy. The primitive segmental duct of *Vertebrata* is perhaps to be derived from it.

Hermaphroditism is characteristic of *Chaetopoda Oligochaeta*, *Hirudinea*, *Trematoda*, *Cestoda*, *Turbellaria*, and *Chaetognatha*. It generally takes the form of successive hermaphroditism, i.e. one of the two genital products, nearly always the male, ripens at an earlier period than the other. Self-impregnation takes place sometimes, and probably often, in *Trematoda*, and, so far as is known, it is the rule in *Cestoda*. Reciprocal impregnation is the rule in other instances. The Nematode genus *Angiostomum* is a unique example of an organism which, though anatomically speaking a female, is a self-impregnating hermaphrodite. Both genital products are formed from coelomic epithelium in *Chaetopoda*, *Archi-Annelida*, the Gephyrean *Sipunculidae* and *Echiuridae*. They are conveyed away by nephridia, except perhaps in the *Chaetopoda Oligochaeta* (see pp. 207-8). In *Hirudinea* as in *Chaetognatha*, the genital glands are derived from special cells set apart at a very early period<sup>1</sup>. The ducts of the ovaries and testes are developed independently of the glands in the first-named; and Nusbaum holds that they are two pairs of modified nephridia. In *Chaetognatha*, whilst the ovaries acquire ducts, but how is unknown, the testicular products are thrown into the coelome and carried away by open canals. In other classes of Vermes, and in *Priapulidae* among *Gephyrea*, there are genital organs either continuous or becoming continuous with ducts, or else simply bursting externally as in *Enteropneusta* and *Nemertea*. Accessory organs to the genitalia are present in the hermaphrodite groups, and are in some instances extremely complicated.

Peculiarities of development are noted under each class. There is, however, a larva, the Trochosphere or *Trochophora*, which occurs in *Polygordius* in a simple and characteristic form: in *Chaetopoda Polychaeta*, and in *Echiurus* among *Gephyrea*. The general characters of this larva are (1) the presence of a prae-oral lobe with apical nerve ganglion, the future supra-oesophageal ganglion or thickening, from which a nerve, the future oesophageal commissure, runs backwards towards the anus (? in all); (2) of a prae-oral ring of cilia to which are often added a post-oral ring and an adoral band between the two rings; (3) of an archicoele; (4) of a ventral mouth leading into an oesophagus (=stomodaeum), a stomach, and intestine (=archenteron), and a short rectum (=proctodaeum), which is terminal, and sometimes surrounded by a patch or ring of cilia. There are optic organs on the ganglionic thickening, and contractile cords connecting it to the oesophagus, as well as provisional cephalic renal organs (*supra*)<sup>2</sup>.

<sup>1</sup> The early origin of genital organs as special cells has also been observed in *Insecta*, in *Moina*, among *Cladocera* (*Crustacea*), in *Nematoda*, and entoproctous *Polyzoa*. How far it may be significant it is difficult to say. The ducts in *Insecta* are in most instances partly derived from the genital cells, partly from invaginations of hypodermis, the latter sometimes wanting. The same is true as to *Nematoda*.

<sup>2</sup> A circular nerve corresponds to the prae-oral ring in the Trochosphere of *Polygordius*, and the Serpolid *Eupomatus*; and a second, corresponding to the post-oral ring, has been detected in the

The body of the adult is formed by a lengthening and segmentation of the region between the post-oral ciliated ring and anus. The Trochosphere is probably derived from an organism (*Trochozoon*) resembling the early stage of a Turbellarian larva (Müller's larva), from which the Nemertean *Pilidium* is also undoubtedly derived<sup>1</sup>. The prostomium of the Trochosphere must be taken to correspond with the aboral apex of the primarily ovate body of the Turbellarian larva, which undergoes a tilt in one direction, while the mouth, which is at first situate at the opposite end of the same vertical axis, comes to lie behind the apex; at the same time that side of the originally symmetrical body which is now opposed to the apex in its altered position commences to lengthen and grow into the body of the worm. The characteristic prae-oral ring of the Trochosphere is derived from the equatorial band of the simple larva. The body of the Vermian, like the Molluscan Trochosphere, grows in such a way that its posterior apex lies on the oral aspect of the equatorial ring, and the anus, which is never present in the Turbellarian is consequently, when formed, below, i.e. on the oral side of the ring. On the contrary, in the Enteropneustan *Tornaria* and the larval form of all Echinoderms (except *Crinoidea*?), it is on the apical or aboral side of the equatorial ring, which in these instances takes a longitudinal direction.

The development of the Nemertean from the *Pilidium*, or from the larva of *Desor*, and of the *Hirudinea*, is remarkable for the new formation of the permanent ectoderm and the discarding of the larval ectoderm, provisional nervous system, and musculature. The *Hirudinea*, like the *Oligochaeta Chaetopoda*, have no special larval form, a want probably due to an abbreviation of development. The *Tornaria* of some species of *Balanoglossus* has a resemblance to the *Bipinnaria* of *Asteroidea*. It differs from it as from the Holothurian and Echinoid larvae, and agrees with the Trochosphere in the possession of optic organs and a ganglionic rudiment at the apex of the

first-named. See Hatschek on the head of *Polygordius* and the Trochosphere of *Eupomatus*, in Arb. Zool. Inst. Wien, vi. (1), 1885. Attention was first drawn to the prae-oral circular nerve by Kleinenberg. Its resemblance to the nerve following the edges of the ciliated lateral lobes in the *Pilidium*, as described by Salensky, is very striking, especially from the point of view of the possible origin of the Trochosphere from some *Pilidium*-like ancestor. See Salensky, Z. W. Z. xliii. 1886. It is generally held that the ventral nerve-cord originates independently of the supra-oesophageal ganglion. Hatschek, whose observations on *Polygordius* and *Echiurus* are followed in the text, doubts this fact. At any rate such an origin is not primitive. The division of the digestive tract into stomodaeum, archenteron and proctodaeum, e.g. in *Eupomatus*, is probably typical. In the larval *Serpula*, however, as described by Conn (Z. A. vii. 1884), the blastopore lengthens out antero-posteriorly, closes, and at its two opposite ends appear the mouth and arms; the middle region corresponding to the median ventral line joining the two. It is possible, however, that an epiblastic stomo- and procto-daeum may be formed subsequently. Compare Hatschek's account of the formation of the stomodaeum in *Eupomatus* (loc. cit. *supra*). The Trochosphere of the last-named possesses a pair of otocysts, and, like all Serpulid larvae, an adanal vesicle formed by a vacuolated ectoderm cell according to Hatschek, by an endoderm cell according to Conn.

<sup>1</sup> The Chaetopod larva (of a Clymenid?), known as *Mitraria*, has a remarkable resemblance to a *Pilidium*. See Metschnikoff, Z. W. Z. xxi. 1871, p. 233.

prae-oral lobe, as well as of the contractile cords to the oesophagus. The fact that a species of *Balanoglossus* has a larva differing very much from *Tornaria* and belonging to a simpler type, but that both larvae agree in the mode of origin of the coelome as five archenteric pouches, makes it probable that the Echinoderm characters of the *Tornaria* are not primary. The mode of origin of the coelomic spaces is however a point in which the Enteropneustan larvae contrast also with the Trochosphere. The permanent coelome of the segmented Vermes is a schizocoel, which develops as a series of splits in the mesoblast of each of the somites, into which the two mesoblastic bands divide on either side of the body. There is some doubt however whether the schizocoel in these instances is or is not to be looked on as an abbreviated form of development of an enterocoel as it is in *Vertebrata*. The nature of the two head cavities is a point still unsettled. They may be (1) archicoelic, and appear to be so in *Archi-Annelida*, or (2) schizocoelic, as described by Kleinenberg in *Lumbricus trapezoides*<sup>1</sup>.

Asexual reproduction occurs in some *Chaetopoda* either by the formation of new intercalated somites, the growth of one of them into a head, followed, sooner or later, by fission; or by regeneration of the organism from a few detached somites. Some *Nemertea* may be similarly regenerated from fragments of the body. Simple fission occurs in a few *Turbellaria* with the formation of either chains of individuals, or of two individuals which separate at once. The formation of proglottides in *Cestoda* is probably not to be regarded as an instance of gemmation. The asexual origin of certain generations of digenetic *Trematoda* from a single cell belongs to a different class of phenomena; see General Introduction. Alternation of Generations is observable in a few *Chaetopoda*, in all digenetic *Trematoda*, and some *Nematoda*. Most *Hirudinea*, all *Trematoda*, and *Cestoda*, a very large portion of *Nematoda*, and all *Acanthocephala* are parasitic, and with the exception of *Hirudinea* and Monogenetic *Trematoda*, endo-parasitic. Isolated instances of either commensalism or parasitism occur in *Chaetopoda*, *Nemertea*, *Turbellaria*, and *Rotifera*.

Thirteen classes are distinguishable among Vermes. Of these (1) the *Enteropneusta* are completely isolated, but in the organisation of the adult certain resemblances may be traced to the Chordata. The *Chaetopoda* (2) constitute a well-defined class<sup>2</sup>, to which (3) the *Archi-Annelida* are closely allied. The *Gephyrea* (4) are most probably to be regarded as

<sup>1</sup> The difficulty as to the coelomic spaces of the head hinges on the following points: (1) that there is primitively a forward growth into the head of mesoblast from the trunk; (2) that this growth becomes more and more pronounced in the higher forms, and (3) takes place at, relatively speaking, an earlier period of larval or embryonic existence. Hence the coelomic spaces in question may have, and rightly have, different values assigned to them in different instances.

<sup>2</sup> The *Oligochaeta* among *Chaetopoda* ought perhaps to be separated entirely from the *Polychaeta* on account of the peculiarities of their generative ducts.

highly modified *Chaetopoda*, but it is by no means certain that the three families of *Gephyrea* should be retained within the limits of a single class. The affinities of (5) the *Hirudinea* are doubtful: they possess in development mesoblastic somites similar to those of *Chaetopoda*, as well as provisional renal organs. Their vascular and reproductive systems are peculiar. The nephridial rete found in certain genera is perhaps a primitive feature. Classes 2-5 are sometimes grouped together as *Annelida*. The Rotifera (6) are an isolated class; they represent in all probability a highly specialised form of Trochosphere, and retain a primitive type of nephridia. The *Nemertea*, *Trematoda*, *Cestoda*, and *Turbellaria* are sometimes grouped together as *Platyhelminthes*. The *Nemertea* (7) are a very distinct class. The possession of an anus, of a system of vessel-like coelomic spaces, the characters of their nervous, nephridial, and reproductive systems, distinguish them from the other three classes named. The *Trematoda* (8) and *Cestoda* (9) are modified by parasitism, but in many respects, e.g. in the character of the nervous, nephridial, and reproductive organs, resemble (10) the *Turbellaria*. It is uncertain how far the last named class is to be regarded as degenerate, or the reverse. The larva of some *Polyclads* is beyond doubt primitive. The *Chaetognatha* (11), *Nematoda* (12), and *Acanthocephala* (13), have sometimes been grouped together as *Nematemnthes*. They are, however, perfectly distinct, not only one from the other, but as far as can be judged from all other classes of Vermes, and the last mentioned of the three is most profoundly modified by parasitism.

For a discussion on larval forms, see Balfour, *Comp. Embryology*, ii. p. 297 et seqq.; for the development of a typical Trochosphere larva, Hatschek 'On *Eupomatus uncinatus*,' *Arb. Zool. Inst. Wien*, vi. (1), 1885; and for points of interest (origin of oesophageal commissure, mesoblast of head, circular nerves of ciliated rings), *Id. ibid.* 'On head of *Polygordius*.'

There are several interesting Vermian genera or groups, which do not fall under any of the thirteen above-mentioned classes, and which can only be briefly touched upon here. They are as follows:

1. The genus *Dinophilus*, with several species, all minute in size, and marine with the exception of *D. sphaerocephalus* from brackish water. There is a head (= prostomium), body, and short ventral tail. The head carries two eye-specks and sensory hairs. It is ciliated either uniformly or in two bands. The body is uniformly ciliated (*D. vorticoides*, *D. metameroïdes*), or the cilia are disposed in rings corresponding to the division of the body into six or seven segments, except on the ventral surface, which is uniformly ciliated. The segmentation of the body is superficial. A nervous system is represented by a ganglion in the prostomium, giving off two anterior and two posterior nerves (*D. apatris*), or two lateral cords situated in the hypodermis, which disappear in the last segment (*D. gigas*). The mouth is ventral, and in the first segment of the body (*D. gigas*); it leads into a pharynx, oesophagus, stomach, and intestine, all ciliated. The anus is dorsal to the tail. Opening just behind and into the mouth is a cavity, which contains



a protrusible muscular proboscis, as in *Archiannelida*. There is a coelome, traversed by strands of connective tissue. An excretory system is present. In *D. gyrotiliatus* it consists 'of five pairs of intracellular segmental canals, each with its own external aperture, and terminating internally in a flame-cell' (Lang, quoting Meyer, 'Polycladen,' Fauna, &c., des Golfes von Neapel, xi. p. 678). Flame-cells have been detected in *D. gigas* and *D. apatris*. In the latter a network of fine canals is said to exist beneath the integument, as well as larger ciliated canals. The larger canals, however, are not present in the head. Korschelt observed one of them to open on the ventral surface near the ovary. The sexes are separate. Males and females are alike in *D. gigas* and *D. vorticoides*, dissimilar in *D. apatris*. The male of the latter is much smaller than the female; its head has a single ring of cilia, and the ventral surface of its body is uniformly ciliated; it has no eyes, no digestive tract; a conical perforated copulatory organ lies within a cavity at the posterior extremity of the non-segmented body. The ovary is single in *D. apatris*, and is attached to the digestive tract where the stomach passes into the intestine; the ova are set free into the coelome as large female, and small male, ova, surrounded by a substance which swells up when they are laid; the birth opening is ventral, and in front of the anus. Segmentation in *D. apatris* is unequal; the gastrula epibolic; and the first stages of the development of the male resemble those of the female. In *D. gigas* the testis and ovary are Y-shaped masses of cells, situated as in *D. apatris*. The genital products collect in the coelome, and probably destroy the parents by rupture. Two or four ovaries are stated to exist in other species.

*Dinophilus* is an interesting genus. It is probably to be regarded as a modified Trochosphere, differing very markedly from the modification which gave origin to the *Rotifera*.

*D. apatris* (with lit.), Korschelt, Z. W. Z. xxxvii. 1882. *D. gigas*, Weldon, Q. J. M. xxvii. (1), 1886.

2. *Gasterotricha*. This group of minute organisms is defined by Ludwig as follows: 'Small vermiform animals, with a well-defined ventral surface. Digestive tract straight, divisible into an anterior muscular, and a posterior cellular, region. Mouth and anus ventral. Body clothed with a cuticula, which bears processes differing in character. Cilia, as a rule, confined to the ventral aspect, rarely covering the region of the head. Posterior end of the body, as a rule, forked. No nervous system recognisable. Hermaphrodite? Reproduction by means of summer and winter ova; no metamorphosis.' Eyes may be present. The female aperture lies dorsally in front of the forked end of the body; the ova are set free into the coelome. The distinction between summer and winter ova appears to be known only in *Ichthydium* (*Chaetonotus*) *larus*. The freshwater genera are *Ichthydium* (which, according to Ludwig, includes *Chaetonotus*), *Chaetura*, *Cephalidium*, *Dasydites*, and the marine genera *Turbanella* and *Hemidasys*.

Ludwig, 'Gasterotricha,' Z. W. Z. xxvi. 1876. *Chaetonotus*, Bütschli, *ibid.* *Hemidasys*, Claparède, A. Sc. N. (5), viii. 1867.

3. *Echinoderidae*. Marine. Minute, with a cylindrical body and flattened ventral aspect. The body is segmented into eleven to twelve chitinous rings, of which the first or head is invaginable, and is armed at its anterior margin with four rows of recurved hooks; the second is provided with twelve longitudinal chitinous ribs, and closes over the first when invaginated; the third and fourth are entire,

and the remainder are divided on the ventral aspect, by a median and two lateral fissures, into a large dorsal and two smaller ventral plates. The terminal or anal ring is usually forked. Most of the rings carry spines,—the last usually two of great length, more seldom one. A nervous system is represented by a right and left band, which unite anteriorly (Greeff); and two to eight red eye-specks lie upon the bands. Reinhardt, however, states that he could not find the nervous bands, but found instead four glandular caeca opening into the proboscis. The mouth is anterior and terminal, and leads into an eversible proboscis, armed at its apex with six to eight two-jointed spines; there is a muscular oesophagus, with a circlet of small spines at its commencement, an intestine, and terminal anus. Excretory organs are represented by a pair of sacs in the ninth segment; they end in ciliated ducts, which open separately on the latero-dorsal aspect of the tenth segment. The sexes are separate. The testes and ovaries are paired and saccular; they open terminally. Greeff considered the animal to be viviparous, but Reinhardt states that he mistook the testes with their contents for ovaries. There is a single genus, *Echinoderes*, with several species.

Reinhardt, Z. A. iv. 1881; Greeff, A. N. 35 (1), 1869; Panceri, Atti Accad. delle Scienze, vii. 1878, No. 10, p. 4.

4. *Desmoscolecidae*. Minute, marine, vermiform, with the body contracting both in front and behind. The head is somewhat globular; the body is girt by a series of rings, varying in number in the different species. There are four setae on the head, and a pair on more or fewer of the body-rings, some dorsal and some ventral; they are capable of independent motion. There are two eye-specks, but no nervous system is known. The mouth is anterior and terminal; there is a muscular oesophagus, a straight intestine, and an anus on the dorsal aspect, according to Greeff. The sexes are separate; the testis and ovary are single and saccular; the former opens into the anus, and has two chitinous copulatory spiculae; the latter opens anteriorly to the anus on the same aspect (Greeff). There is a single genus *Desmoscolex*, with several species. The genus *Trichoderma* (Greeff), which has no setae, but is covered with long hair-like processes, is perhaps related to *Desmoscolex*. The male has two spiculae. Both genera are in some respects like the *Nematoda*.

Greeff, op. cit. *supra*, and Panceri, op. cit. p. 2 and p. 7; Reinhardt, Z. A. iv. 1881, p. 591.

5. *Chaetosomidae*. Minute; partly marine, partly freshwater. There are three genera, *Chaetosoma*, *Tristicochaeta*, and *Rhabdogaster*. The first-named has an oval head, and a body pointed posteriorly. The head has a double row of moveable hooks, arranged in a semi-circle; and it is covered, as also the body, with a number of fine hairs. Locomotion is effected by a double row of knobbed rods anterior to the anus. The mouth is anterior and terminal; there is a muscular oesophagus, an intestine, and a rectum, with a ventral anus. The sexes are separate. The testis is a single sac; the vas deferens opens with the anus, and has two chitinous copulatory spicules. There are two ovaries, with a single vagina opening ventrally about the middle of the body. *Tristicochaeta* (Panceri) resemble *Chaetosoma* very closely, but has three rows of locomotor rods. *Rhabdogaster* has the head not marked off from the body, but it is somewhat dilated, like the genital region. The

hairs are restricted to the dorsum. The locomotor rods are very slender and hooked, situated so far anteriorly that the vagina opens among them.

*Chaetosoma* and *Rhabdogaster*, Metschnikoff, Z. W. Z. xvii. 1867. *Tristicochaeta*, Panzeri, op. cit. *supra*, p. 7.

### CLASS ENTEROPNEUSTA.

*Marine Vermes with a ciliated epidermis, and a body divided into three regions, viz. a prae-oral contractile proboscis, a 'collar' surrounding the narrow base of the proboscis, and a long worm-like trunk. The first portion of this trunk is pierced by a double series of dorsally placed respiratory pores: the middle portion bears dorsal lobes formed either by prominent sexual glands, or sexual glands mingled with liver caeca; and the hind portion is distinctly ringed. The mouth is ventral at the base of the proboscis in front of the collar; the anus terminal and widely open, being devoid of a sphincter. There is but one genus, Balanoglossus, with several species from different parts of the world. The animals exhale peculiar and characteristic odours; are brightly coloured, the males differing in tint from the females; and live immersed in mud and sand, which they saturate with mucus. This mucus sometimes sets firmly, as in B. Robinii. Some species are phosphorescent.*

The epidermis consists of a single (?) layer of cells, some with a delicate cuticle and cilia, others unicellular mucous glands<sup>1</sup>. The body-cavity is divided into five sections, an anterior within the proboscis, two paired (right and left) in the collar, and two similarly paired in the trunk, derived respectively from as many outgrowths of the archenteron. The outer cellular walls of these outgrowths form the body-walls, composed of connective and non-striated muscular tissues. The latter is arranged as a well-developed longitudinal coat. In *B. minutus* there is also a delicate external circular coat, wanting in other species. The longitudinal coat consists of several concentric layers in the proboscis. The original cavity of the proboscis is filled by a network of stellate cells in the adult; their interspaces communicate with the exterior by a ciliated (epiblastic) canal opening at the base of the proboscis in the middle dorsal line, or on the left side (*B. Kowalewskii*), or by two such canals (*B. Kupfferi*). The inner walls of the archenteric outgrowths in the collar and trunk form the dorsal and ventral mesenteries, and the lateral transverse muscles of the digestive canal which are interrupted in the line of the mesenteries. The dorsal mesentery is in some species absorbed from place to place in the adult. The cavity or cavities (right and left) in the collar may be much obliterated by growths of connective tissue, but communicate with the exterior by a right and left ciliated (epiblastic) canal opening into the first gill-slits,

<sup>1</sup> Bateson thinks that the second layer of epidermic cells, often supposed to exist, is due to the breaking off in teased preparations of the lower ends of the long cells, Q. J. M. xxvi. p. 513.

or pouches. The cavities in the trunk are completely closed, but large. They contain a fluid, in which, when coagulated by reagents, Spengel observed stellate (? amoeboid) cells.

The nervous system consists of a dorsal and ventral cord, extending to the anus, and connected by a pair of ring-like thickenings in the collar, and of a delicate network of fibrils beneath the epidermis. The cords are sub-epidermic except in the region of the collar, where the dorsal cord is completely independent of the epidermis. The deep part of the cord is fibrous, the superficial part cellular. The dorsal cord in the collar contains a central lumen produced by invagination in *B. Kowalewskii* (Bateson), or either globular or long irregular cavities, lined by a cuticula (Spengel), found also in the middle and posterior regions of adults (Bateson). The dorsal cord is continuous at its anterior end, with a thick circular fibrous layer at the base of the proboscis, which thins away anteriorly. Ganglion cells occur at rare intervals in the cords, except in the dorsal cord of the collar, where they are numerous. Hence this part may be regarded as the central nerve-ganglion (Spengel). Organs of special sense are absent.

The digestive tract is straight. At its anterior end it sends forwards into the proboscis a diverticulum. The cavity of this process is obliterated anteriorly by cells which are vacuolated with nodal nuclei, thus resembling notochordal tissue (Bateson). On its ventral surface is formed a chitinous bar, prolonged behind into two rods, which lie in the walls of the digestive canal in the collar, and give attachment to longitudinal retractor muscles. The first section of the digestive tract is incompletely divided into a dorsal respiratory, and a ventral alimentary part, by two lateral longitudinal folds. The respiratory portion gives origin to paired gill-pouches. These pouches open externally on each side by small pores situated in a longitudinal dorso-lateral furrow: internally, by long U-shaped slits. New gill-pouches appear to be constantly added throughout life at the hind end of the series. They are at first circular, like the gill-pouches of the embryo; but attain the characteristic U-shape by the downgrowth of a dorsal process or valve. The sides of the pouches, and the partitions between them, are supported by chitinous lamellae. Their margins are ciliated, and water passes through them from within outwards. They receive their blood from the median dorsal vessel. The section of the digestive tract behind the branchial region is traversed by a longitudinal dorsal and ventral furrow richly ciliated. In some species (*B. minutus*, *B. claviger*, &c.), the middle section of the tract possesses paired dorsal liver-caeca, the cells of which contain a brown or green pigment. These caeca pass outwards into lobes of the body-wall, and possess an external aperture in *B. Salmoneus*. For the dorsal and ventral mesentery see *supra*. The latter is lost in the collar; as also is the dorsal mesentery, except in *B. Kowalewskii* and *B. Salmoneus*.

The vascular system consists of a dorsal and a ventral vessel lying in the mesenteries, and connected in the collar by an oblique vessel on each side. The dorsal vessel enters the proboscis and ends in a sac, with muscular walls lying immediately *above* the outgrowth from the digestive canal. This sac is pulsatile, at least in the larva, and may be termed 'heart.' There is a system of blood sinuses beneath the epidermis and in the walls of the digestive tract. The blood contains no corpuscles. It is said that the current runs forwards in the dorsal, backwards in the ventral vessel. A peculiar structure lies above, in front of, and at the sides of the heart in the proboscis. It forms the proboscis gland of Bateson, the internal gill of Spengel. Its posterior part is saccular, while its anterior and lateral parts consist of a network of blood-vessels covered with cells. As these cells contain brownish granules, found also outside them in the proboscis cavity, the organ is probably excretory (Bateson).

The sexes are separate, and the sexual glands consist of simple or branched sacs derived from the epidermis (?), opening by external pores, and placed in lobes of the body-walls, which are arranged in a single series to the outer side of the branchial pores, and extend behind the branchial region to a variable distance. The larva of *B. Kowalewskii* is a cylindrical organism with an anterior tuft and a posterior ring of long cilia. The body is covered with short cilia, and the collar is early separated off from the proboscis and trunk by two constrictions (Bateson). In other species (? all) the larva is known as *Tornaria*. It has cilia arranged in a prae-oral, and a longitudinal post-oral or oblique dorso-ventral band, and in one or two, posterior rings. Two eye spots lie at the anterior extremity. It resembles very closely the *Bipinnaria* larva of Asteroidea.

The various species of *Balanoglossus* differ from one another in minor details. The development of *B. Kowalewskii* has been accurately investigated by Bateson. It may be noted that the proboscis gland originates, like the mesoblast, from the wall of an archenteric outgrowth, and that there is neither stomo- nor procto-daeum.

Bateson has proposed to class the *Enteropneusta* under the name *Hemi-Chordata* with the Chordata. Of the points to which he draws attention, the gill-slits formed as outgrowths from the digestive tract, together with their skeleton and blood-supply, the origin of the mesoblast from enterocoelic pouches, the presence of an anterior pouch, which is cut off from the archenteron and opens externally, are undeniable resemblances to *Amphioxus*; and it is possible that the backward growth of the collar over the gill-slits, slight as it is, may be comparable to the epi-pleural folds of that animal. But it must be borne in mind that the anterior enterocoelic pouch is divided in *Amphioxus* into a left and right half, the former of which is converted into a sensory organ, opening into the oral cavity. In *Balanoglossus Küpferi*, instead of one pore there are two, which lead into the interspaces of the cells filling the proboscis cavity, and this may be an original feature. The resemblance, therefore, between the structures is possibly only a general one. As

to the other points Bateson mentions, it may be noted, relative to the notochord of *Balanoglossus*, (1) that it is below, i.e. ventral, to the main dorsal blood-vessel, whereas in all Chordata it is above, i.e. dorsal, to it; (2) that the histological changes undergone by its cells may be simply correlated with its function as a supporting structure, and indeed Spengel states that in the species examined by him, the cells retain their cylindrical form and cilia, and that the organ is regenerated with the proboscis after amputation. In the nervous system the presence of the diffused sub-epidermic network of nerve fibres, of a peripharyngeal band and ventral cord, are points of unlikeness to which attention should be paid; and, it may be added, the canals occurring in the dorsal cord, can scarcely be paralleled with the neural canal of typical Chordata<sup>1</sup>. Nor can much weight be laid on the absence of organs of special sense, or of specialised excretory organs. They are features which are as likely as not due to the mode of life of the animal.

*Tornaria* requires a fresh examination. The anterior enterocoelic pouch is represented in it by a diverticulum, which opens on the dorsal surface, and is eventually shut off from the archenteron, and its cavity is said to become the cavity of the proboscis. The latter represents an overgrown praeoral or prostomial lobe, and it has at its apex two eye-spots, resting on an epiblastic thickening, which should by rights be the supra-oesophageal thickening (Balfour), but it seems to disappear without leaving a trace. Balfour regarded *Tornaria* as intermediate in structure between the Echinoderm larva and the Trochosphere, resembling the former in shape, in the longitudinal band of cilia, the origin and structure of the water-vascular vesicle (= anterior enterocoelic pouch), and in the formation of the body-walls from archenteric diverticula; whilst Trochospherical characters are seen in the prostomial eye-spots, the contractile band from the eye-spots to the oesophagus, the two posterior ciliated rings, and terminal anus. It may be questioned which is the more primitive form, *Tornaria* or Bateson's larva. In one feature the latter appears to differ very markedly from *Tornaria*, viz. in the dorsal anus, which becomes terminal by the atrophy of the post-anal portion of the tail.

Bateson, Q. J. M. xxiv. 1884; *ibid.* xxv. Suppl. 1885; *ibid.* xxvi. 1886. Spengel, Mitth. Zool. Stat. Naples, v. 1884.

*Tornaria*, Spengel, Tagebl. d. Natf. Versaml., München, 1877; Agassiz, Mem. American Acad. of Arts and Sciences, ix. 1873 (or analysis by Perrier, A. Z. Expt. ii. 1873).

Spengel is stated to be preparing a monograph of the genus in the 'Fauna and Flora of the Gulf of Naples.' New species have been recently described by Marion, C. R. 101, 1885, and by Köehler, C. R. 102, 1886.

For relations to *Chordata*, see Bateson, *op. cit. supra*, and Id. 'The Ancestry of the Chordata,' Q. J. M. xxvi. 1886; cf. Köehler, Z. A. ix. 1886.

<sup>1</sup> An invagination in the development of the ventral cord possibly takes place in some *Chaetopoda*, and it is difficult to assign any other origin to the canal which traverses the cord in the *Gephyrea chaetifera*. It is doubtful whether such an invagination *per se* can be held to have a phylogenetic significance. The point can only be determined by future investigation.



## CLASS CHAETOPODA.

*Multisegmental Vermes, with a more or less prominent prostomial lobe; with locomotor organs in the shape of chitinoïd setae, implanted either in the body-wall or in special elevations, the parapodia; with a body divided into somites by external furrows and typically by internal fibro-muscular septa. Cilia are restricted to special regions or certain organs. The nervous system consists of a pair of cerebral or prostomial ganglia, and a paired ventral cord with distinct or indistinct ganglia. The nephridia are typically repeated in each body-somite; the genital organs may be similarly repeated or be restricted to certain somites, usually the anterior. Development is direct or with a metamorphosis.*

Of the two orders, *Polychaeta* and *Oligochaeta*, into which the class is divisible, the former is usually distinguished by the presence of parapodia and by appendages to the head and somites, viz. antennae, cirri, and branchiae.

The division of the body into somites is not well-marked in some *Polychaeta Tubicola*. The number of somites present varies much, and may attain to several hundreds, as in some *Polychaeta Errantia* and terrestrial *Oligochaeta*. Annulation of the somites, as in *Hirudinea*, is very rare. The head is generally distinct, and consists of a prostomium and peristomium. The former varies in size, and in some *Tubicola* and terrestrial *Oligochaeta* becomes obsolete<sup>1</sup>. It usually bears in *Polychaeta* a certain number of appendages, the antennae or tentacles. Two which originate from its inferior aspect, and differ structurally as well as by their innervation from the other appendages, are often termed palpi. The numerous extensile tentacles of the *Terebellidae*, which contain a prolongation of the coelome, and the gill-processes so-called of the *Serpulidae*, appear to belong to the prostomium, as they originate in front of the ring of cilia which limits posteriorly the prae-oral lobe of the larva. The peristomium or buccal somite is sometimes very similar to the following somites, sometimes markedly different, and it may coalesce with 1-3 of them<sup>2</sup>. The body

<sup>1</sup> The prostomium of the adult Chaetopod is certainly a rudiment of the larval prae-oral lobe, when it contains the supra-oesophageal ganglion. It is, however, in some cases, e.g. some *Oligochaeta*, an outgrowth of the following somite, if Vejdovsky's statements are right. Cp. p. 197.

<sup>2</sup> The number of prostomial antennae varies from two to five. When there are five there is a median azygos antenna, a pair of antero- or supero-lateral antennae, and a pair of postero- or infero-lateral; all alike innervated from the cerebral ganglia. The latter are divisible, according to Pruvot (A. Z. Expt. (2), iii. 1885), into an antennary and a stomato-gastric portion. The former supplies the antennae, and where there are five of these structures, as in *Eunice*, it is subdivisible into a part supplying the median and antero-lateral antennae, and a second part supplying the postero-lateral pair. The stomato-gastric portion innervates the palpi, and gives origin to the stomato-gastric nerves as well. The homology of the Serpulidan branchiae with palpi is proved by their innervation from the stomato-gastric portion of the cerebral ganglia. Pruvot's theory that the subdivisions of the

either consists of a uniform series of somites, as in *Oligochaeta* and *Polychaeta Errantia*, or it may be divided into an anterior region, the thorax, and a posterior, the abdomen, with differing somites as in *Polychaeta Tubicola*. The number of divisions may be greater, as in *Chaetopteridae*. The terminal, anal, or pygidial somite is often much reduced. A post-anal cirriform part of the body appears to be present in *Nephtys* (Pruvot), and in the Oligochaete *Criodrilus* there are seven abbreviated post-anal somites (Vejdovsky).

The locomotor setae are implanted in *Polychaeta* in parapodia (*infra*). They are grouped, as a rule in large numbers, into bundles which are either single or double according as the parapodium is uni- or bi-ramose. The number of setae in a bundle, their size and shape is often characteristic. A stout seta or aciculum very commonly forms the centre of the bundle. *Aphrodite* among *Polychaeta* is remarkable for having large numbers of hair-like setae growing from the notopodium. Some of these are iridescent, others form a felt-work over the dorsum. A similar but more sparingly developed felt-work is occasionally present in the allied genus *Hermione*. The setae of *Oligochaeta* are grouped in aquatic and some terrestrial forms in a dorsal and a ventral set. In other terrestrial forms there may be four setae, implanted singly on each side of a somite or a complete or incomplete ring of single setae girthing it. The number of setae in a bundle is always small, and in some terrestrial *Oligochaeta* (*Lumbricus*, *Anteus*, &c.) is reduced to two. The dorsal setae of the aquatic *Oligochaeta* are often remarkably long. The setae are chitinous, their shape and size vary remarkably and are adapted frequently to the necessities of the worm, e. g. the hooked ventral setae of many *Tubicola*, by means of which they creep along their tube. They are moved by special muscles, protrusor as well as retractor, and originate from cellular sacs or trichophores, invaginations of the hypodermis. Each seta in a bundle is the product of a single cell, and either springs from a separate sac or together with others from a common sac. They are rarely entirely absent, as e. g. from the parapodia of *Tomopteris*. In the Oligochaete *Anachaeta* the sacs persist, but do not develop setae.

The parapodia of *Polychaeta* are hollow lateral elevations of the body-wall, either simple (uniramose)<sup>1</sup> or divided (biramose) into a dorsal notocerebral ganglia indicate the presence of somites is perhaps scarcely tenable; at least, it is quite as likely that its division into lobes is the consequence of an increase in the number of cephalic appendages.

The first ventral or sub-oesophageal ganglion is contained in the peristomial somite. It may give off one, or two (*Eunice*), or three (*Phyllodoce*) pairs of nerves indicating a fusion of somites. Actual fusion of a setigerous somite in the young animal with the true peristome has been observed, e. g. in Nereids; cf. Langerhans, Z. W. Z. xxxii. 1879, p. 517. The appendages of the peristome may be parapodia with setae, or cirri usually much lengthened, and then termed by Claparède tentacular cirri.

<sup>1</sup> A few setae are found at the base of the dorsal cirrus in *Eunicidae*. Tufts of fine setae



podium and a ventral neuropodium, which are separated by a greater or less interval and differ in size and form not only in different *Polychaeta* but in different regions of the same individual. They may be absent in certain regions in some *Tubicola*, e.g. from the posterior part of the body in *Arenicola*, &c. The cirri are in intimate relation with the parapodia, and there is usually a dorsal or notopodial cirrus and a ventral or neuropodial. The latter is as a rule insignificant in size. The cirri of the peristome, and following somites, and of the pygidial somite, are frequently much lengthened and enlarged. The organs in question are solid processes of the body-wall, probably tactile in function, with muscular walls, and containing a nerve. They vary in form, and may be conical, filamentous, lamellate, and are sometimes jointed. The *Aphroditidae* are distinguished among *Polychaeta* by the presence of lamellate plates or elytra attached dorsally to the notopodium. They contain a rich supply of nerves and have been regarded as modified cirri, but the two structures sometimes co-exist on the same somite<sup>1</sup>. The branchiae, like the cirri, are processes of the body-wall, but they differ from them either by containing an extension of the coelome, or a single contractile vessel, or an afferent and an efferent vessel which are connected by capillary loops or networks. They are either filamentous, lamellate, pectinate, or branched in shape, and are present either on the majority of the somites, or on certain somites only in *Tubicola*, e.g. the anterior in *Terebella* or the median in *Arenicola*. They are often entirely absent. The prostomial tentacles of *Terebellidae* must possess a respiratory function, inasmuch as they contain a cavity which is an extension of the coelome. The cephalic gills of the *Serpulidae* consist of a more or less distinct basal ridge, the two ridges right and left being connected dorsally, from which spring a number of filaments, varying from 4-50. These filaments usually support each two lateral rows of ciliated processes. They may contain only an extension of the coelome, with the exception of the two median dorsal filaments, which are traversed by a single vessel, e.g. *Haplobranchus*, *Manayunkia*; or all alike are traversed by a similar single vessel which gives off a branch into each lateral process. These vessels contract and dilate alternately. In the tribe *Sabellinae* both ridges and filaments are supported by a cellular cartilage and the filaments are connected by a membrane. In the *Serpulinae*, with few exceptions, e.g. *Protula*, one, rarely both, of the median dorsal filaments is modified into a stopper-like operculum, which closes the tube when the animal

appear in the same position in the sexually mature *Syllidae* and *Hesionidae*. Pruvot concludes therefore that the simple or uniramous character of the pseudopodia in these worms is due to the atrophy of the notopodium.

It is a remarkable fact that the only setae found in *Tomopteris* are the single setae lodged in the extremities of the cephalic appendages. See Greeff, Z. W. Z. xxxii. 1879, Taf. xv. Figs. 40, 41, 47. The large pair of appendages are innervated from the cerebral ganglia (Pruvot).

<sup>1</sup> For the structure of the elytra in *Polynoe*, see Jourdan, Z. A. viii. 1885.

withdraws into it. The operculum retains both a vascular and nervous supply and is probably in part respiratory<sup>1</sup>.

The body-walls consist of a chitinoid cuticle, a hypodermis and muscular layers, a circular and a longitudinal. The cuticle is thin in *Tubicola*. The hypodermis consists of a single layer of cells, the outlines of which are sometimes lost (?). The cells are partly supporting cells, partly sensory, partly glandular. Gland-cells, the secretion of which contains rod-like bodies, as in Nemertea, are very common, especially in tubicolous families, e.g. *Chaetopteridae*, but are by no means restricted to them. The rod-like bodies have been found in the walls of the tube of *Sabella*. Protective tubes are manufactured by some *Errantia* and all *Tubicola*. In the *Errantia* and some *Tubicola*, e.g. *Pectinaria*, the tube is carried about by the animal; in other *Tubicola* it is formed in sand or mud or is attached to stones. It may be soft in consistency, e.g. *Siphonostoma*; tough and parchment-like, e.g. *Chaetopterus*; or stony, as in *Serpulidae*. It is often strengthened by particles of mud, sand, or shell, e.g. *Sabella*, *Hermella*, *Terebella*. The material for the tube is probably secreted by the glands of the body-surface<sup>2</sup>. Cilia are found on the prostomium of the Oligochaete *Aeolosoma* and in *Polychaeta* chiefly on the sides of the prostomium or somites, round the anus, or on the branchiae. *Ophyotrocha puerilis* (*Eunicidae*) retains the polytrochal rings of cilia (*infra*, p. 606). The *Sabellinae* possess a ventral ciliated furrow in the abdominal region, which either ends at the thorax, or passing round its right side, extends along its dorsal median line. The ventral surface, rarely the dorsal, of *Serpulinae* is ciliated but not furrowed. The cilia in both instances convey faecal particles forwards and out of the tube. The circular layer of muscles may be absent, e.g. in *Nephtys*, or be sparingly developed. The longitudinal layer is commonly disposed in *Polychaeta* in four bands, two latero-dorsal, two latero-ventral. The internal ends of the setiparous sacs penetrate and therefore divide the corresponding layer in *Oligochaeta*. The setiparous sacs have special protrusor muscles, derived in *Oligochaeta* from the circular layer. Muscular bands pass from the median ventral line in *Polychaeta*, in an oblique dorso-ventral direction and are inserted into the dorsum, the parapodia, and the setiparous sacs. They consequently divide the coelome

<sup>1</sup> In *Filograna* and *Apomatus* the peduncle of the operculum bears lateral processes, and the stopper is represented by a terminal sphere. For the metamorphosis of the filament, cf. F. Müller, *Facts for Darwin*, 1869, p. 112.

<sup>2</sup> Claparède thought that the material for the tube was secreted entirely by the most anterior pair of nephridia, the only pair, as he supposed, present in *Serpulidae*. Pruvot observed the posterior part of a *Myxicola*, accidentally divided, envelope itself in a tube of mucus, undoubtedly derived in this instance from the hypodermic glands. The presence of the characteristic rods alike in the gland cells and in the substance of the tube of *Sabella* points to the same conclusion. It is also the natural conclusion judging from the analogy of Nemertea. Aggregations of unicellular glands open on the ventral surface of certain segments in *Polydora*, and, according to Jacobi, secrete material for the tube.

into three longitudinal chambers, a median containing the digestive tract, and two latero-inferior<sup>1</sup>. It is also divided by transverse fibro-muscular septa into a series of more or less complete chambers, one behind the other. The septa are well-developed in *Oligochaeta* (except *Aeolosoma*), *Errantia*, and many *Tubicola*, whilst in other *Tubicola* only one or two may be present in the anterior region of the body. The chambers thus made communicate either round the intestine, round the ventral vessel, or by pores variously placed. They are provided with dorsal pores opening outwards in many *Oligochaeta*<sup>2</sup>. The muscular tissue is composed of cells with a superficial fibrillar striated layer, and usually but a slight remnant of protoplasm surrounding the nucleus. A nucleated connective tissue intervenes between the muscle-cells. It is largely developed in the anterior region of the body in many *Serpulidae* and reduces the coelome to two narrow passages. The coelomic surface of the body-walls as well as of all the internal organs appears to be covered by an epithelium, which varies in character not only in different regions of the body but in different Chaetopods<sup>3</sup>. This coelomic epithelium is ciliated in the *Aphroditidae*, polycirrine *Terebellidae*, and the Anangian *Glyceridae*.

The nervous system consists of a pair of cerebral or supra-oesophageal ganglia and a ventral nerve cord, the oesophageal commissures connecting them and a variously developed stomato-gastric system in connection with the pharynx. The dorsal surface of the cerebral ganglia, the ventral surfaces of the ventral ganglia are in contact with the hypodermis in many *Polychaeta*. The posterior termination of the nerve-cord in *Telepsavus costarum*, the whole nervous system of a *Terebella* sp. ?, from Heligoland (Semper), and of *Aeolosoma* (which is reduced to the cerebral ganglia), are included in it as in certain remarkable and primitive worms<sup>4</sup>. The cerebral ganglia are simple in *Oligochaeta*, complex in many *Polychaeta* in which they consist of antennary and stomato-gastric centres, the former supplying the antennae, the latter the palpi or their branchial homologues in some *Tubicola* (cf. note, p. 593). The first two or three ventral ganglia may be united<sup>5</sup>, the remainder are usually distinct. The ventral cord of some *Tubicola* (*Polydora*, *Serpulidae*) is ladder-like, the right and left half of

<sup>1</sup> Bands of muscles are stated to pass across the coelome beneath the intestine, and from one parapodium to another in *Glyceridae*.

<sup>2</sup> See on these pores p. 199, *ante*. Add to what is there stated that the position of the first pore appears to constitute a specific character, and that in one instance at least the worm possesses, when irritated, the power of expelling through them a jet of coelomic fluid to the height of two feet. See Vorderman, Tijdschr. für Nederl. Indie (8), ii. 1882 (Naples Zool. Jahresbericht, 1882, 'Vermes,' p. 273). Our English Earthworm suffers coelomic fluid to escape sometimes if pressed by the fingers.

<sup>3</sup> See on *Arenicola* and *Lumbricus*, Viallanes, A. Sc. N. (6), xx. 1886.

<sup>4</sup> I.e. the *Archi-Chaetopoda*, p. 609, and *Archi-Annelida*, p. 613.

<sup>5</sup> In *Ophelia* (*Tubicola*) a ganglion is situated on each oesophageal commissure, and supplies the first pair of feet (Pruvot).

each ganglion being widely separate and united by transverse commissures. The longitudinal commissures between successive pairs of ganglia are separated in *Phyllodocidae*, but as a rule they are contained within a common sheath. The nerves given off laterally from the ganglia to the parapodia sometimes possess a small ganglion where they branch. The ganglion cells may be spread over the whole extent of the cords, as in *Lumbriculidae* and *Lumbricidae* among *Oligochaeta*, and in the anterior part of the cords in some *Polychaeta*, e. g. *Nephtys*, but they are usually aggregated in the ganglia. The stomato-gastric system is present in all *Oligochaeta* (p. 211) and most *Polychaeta*. In the latter it originates from the cerebral ganglia (e. g. *Eunicidae*, *Serpulidae*), from the same ganglia and the oesophageal commissures as well (e. g. *Nephtys*, *Phyllodoce*), or from the commissures alone (e. g. *Ophelia*). This last mode of origin obtains in all *Oligochaeta*. It is best developed in those *Polychaeta* which possess a muscular pharynx<sup>1</sup>. Supporting or skeletal structures, the so-called 'giant-fibres' or 'neurochord,' are found in nearly all *Oligochaeta* and many *Polychaeta* on the dorsal aspect of the ventral cords (p. 211). For the lateral ganglionic cords of *Oligochaeta*, see p. just cited.

Organs of special sense are found in the form of ciliated grooves, tactile cells or bodies, eyes, and otocysts. Ciliated grooves occur on the prostomium of the *Oligochaetae* *Aelosoma*, and many *Polychaeta*, and are supplied by nerves from the cerebral ganglia. Their function is unknown; it is possibly olfactory<sup>2</sup>. Tactile hypodermic cells furnished with external setae, long or short, and connected basally with a nerve filament, derived either from a nerve or a ganglion cell are probably widely distributed. For their occurrence in *Oligochaeta*, see p. 211. In *Polychaeta* they occur aggregated on papillae of the antennae and the cirri, and of the elytra of *Aphroditidae*, and as special organs in the 'goblet' organs of the *Capitellidae* where they are scattered over the proboscis, prostomium, and thorax; or in *Polyophthalmus* as a single pair in connection with the ciliated grooves; and as 'lateral' organs, one between each noto- and neuro-podium in the *Capitellidae*, or the corresponding bundles of setae of *Polyophthalmus*. The nerves to the goblet and lateral organs end in ganglia. Eyes are absent in all *Oligochaeta* except some *Naidomorpha*. They consist in *Nais proboscidea* of a few large cells covered on one side by small pigmented cells. They may be absent also in some *Polychaeta* and rudimentary in others, and lodged either within, or in close apposition with, the cerebral ganglia. As a rule they are confined to the prostomium, but among *Tubicola*

<sup>1</sup> It forms in *Eunicidae* a sub-pharyngeal ganglionated cord and an oesophageal ring. It has in *Nephtyidae* and *Phyllodocidae* long roots, which end in a ring of minute ganglia. Full details are given by Pruvot.

<sup>2</sup> Ganglion cells are found in connection with the grooves in *Polyophthalmus*. A pair of grooves is found on each segment of the body in *Aricia*.

*Polyophthalmus* possesses in addition to cephalic eyes a number of lateral eyes (twelve pairs in *P. pictus*), one pair to a somite, situated ventrally to the insertion of the oblique dorso-ventral muscles (*supra*): *Leptochone aesthetica* (*Eriographidae* among *Serpulidae*) has a pair on each somite; *Fabricia* (*Sabellinae*) a pair on the anal somite; and many species of *Sabella* (sometimes distinguished under the generic name *Branchiomma*) and the genus *Dasychone* have them on the branchial filaments.

Each eye of *Nereis cultrifera* consists of a hollow sphere filled with a coagulable fluid. Its walls are composed of a single layer of cells: the cells of the anterior or outer aspect are flattened and clear, those of the posterior or inner aspect or retinal cells, to which the nerve is distributed, elongate, and of two kinds commingled, one pigmented, the other not pigmented. The hypodermis cells immediately above the eye are flattened; around it, of great length, whilst the cuticle is unchanged. There is a special optic ganglion for the anterior of the two pairs. The structure of the two eyes of *Alciopé* is similar but differs in the following points. The inner ends of the retinal cells are capped by a rod (or two semi-cylinders) and pigment (? in special cells) is massed at the spot where the rods commence; a spherical lens lies to the outer side of the cavity of the sphere from which it is separated by a membrane. The cephalic eyes of *Polyophthalmus*, which are imbedded in the cerebral ganglia, consist of three clear bodies contained in a pigmented cup; its lateral eyes possess a hyaline lens, a layer of prismatic cells and nervous fibres inclosed in a pigmented capsule, and both cuticle and hypodermis are thinner where they pass over them. The eye of *Hyalinoecia tubicola* is said to consist of a lens-like thickening of the cuticle with two layers of cells applied to it (Pruvot). Otocysts are comparatively rare. A pair is found in the prostomium of some *Tubicola*, e.g. *Arenicola*, *Fabricia*, some *Sabellinae*, and young *Terebellidae*; two or three pairs in the first setigerous somite of *Leptochone*. Three lie near the eyes in the cerebral ganglia of *Polyophthalmus*; and the genus *Aricia* has a pair dorsally placed in a variable number of the body-somites. The otocyst appears to consist of a capsule composed of ciliated cells and containing one or more calcareous otoliths suspended in a fluid.

The mouth is sometimes terminal, more often ventral. It is a transverse or longitudinal slit guarded by two lateral, or by upper and lower, lips, and leads into a stomodaeum, which forms a buccal cavity, and in most *Polychaeta Errantia*, some *Tubicola*, as well as in *Oligochaeta*, a muscular pharynx. The latter is frequently more or less protrusible. Its epithelium is sometimes ciliated and is generally covered by a cuticle: its inner surface is sometimes papillate (e.g. in *Syllidae*), and may be armed with chitinoid teeth, either flattened toothed plates (*Eunicidae*) or pointed cones (*Aphroditidae*, *Nereidae*). Some *Syllidae* possess a pharyngeal tooth

traversed by the duct of a paired poison gland (Langerhans). Glands may be imbedded in the walls of the pharynx or appended to it externally. The archenteric region is divisible into an oesophagus and a stomach-intestine. The length and structure of the oesophagus vary much. In the terrestrial *Oligochaeta* it is sometimes provided with a muscular gizzard, a crop, and lime-secreting glands of Morren (p. 202). The glandular stomach so-called of *Syllidae* immediately following the oesophagus is really a muscular gizzard with radial columns of striated muscles in its walls (Haswell). In some Syllidians and in *Hesionidae* it is furnished with a pair of outgrowths which contain air, probably secreted from the blood and derived in the first instance by the blood from swallowed air<sup>1</sup>. The stomach-intestine is larger in calibre than the oesophagus, and is usually more or less constricted by the attachment of the septa or of muscular bands representing them. It is also usually pigmented. The pigment is contained in the enlarged peritoneal cells ('chloragogen' cells) which form its outer coat, and very rarely in the lining epithelium. A pair of glands may open into its commencement (e.g. *Arenicola*), or a variable number into its dorsal aspect (some terrestrial *Oligochaeta*, p. 202); and in *Aphrodite* each of its segments has appended a right and left glandular caecum branched at its distal extremity. The *Capitellidae* possess a 'siphon' or accessory intestine ventral to the main intestine and opening into it anteriorly and posteriorly. A median longitudinal invagination of all its coats forms the typhlosole of some terrestrial *Oligochaeta* (p. 203). The coats of the oesophagus and intestine are an outer peritoneal cellular coat; an outer longitudinal and inner circular muscle-layer, sometimes, but very rarely, reversed in position; and the epithelium. The latter is usually ciliated and often contains glandular cells. In the intestine its cells may grow in size, be thrown off, and replaced by fresh cells as in some *Oligochaeta* (p. 203)<sup>2</sup>. There is a short rectum, probably always derived from a proctodaeum. The anus is usually terminal, sometimes dorsal. The alimentary canal is as a rule straight, and rarely disposed in coils, e.g. in *Pectinaria* and *Siphonostomum* among *Tubicola*. It is nearly always supported by a dorsal mesentery which incloses the dorsal blood-vessel. The ventral mesentery sometimes disappears completely, sometimes persists so far as to support the supra-nervian vessel.

The vascular or so-called pseud-haemal system is absent in some *Polychaeta*, i. e. *Glyceridae*, *Capitellidae*, *Polycirrus*, *Tomopteris*, which may

<sup>1</sup> The two outgrowths of the oesophagus in *Nereidae* are possibly also air-bladders. The intestine of *Phyllococe lamelligera* has been found to contain air. The four families, *Hesionidae*, *Syllidae*, *Nereidae*, *Phyllodocidae* possess no branchiae. See Eisig, Mitth. Zool. Stat. Naples, ii. 1881, pp. 293-4.

<sup>2</sup> The epithelial cells of the hinder part of the intestine in some Syllidians contain refractile spherules in large numbers. Claparède, supposing them to be of excretory character, termed this portion of the intestine 'région urinaire.'

hence be termed An-angian<sup>1</sup>. It constitutes in all others a closed system of tubes containing a fluid apparently respiratory in function. The system of tubes is divisible into main longitudinal trunks, branches connecting them *inter se*, and capillary networks distributed to the various organs. The principal longitudinal vessels are two, a dorsal or supra-intestinal, and a ventral or supra-nervian, to which may be added a sub-intestinal apposed to the ventral aspect of the intestine. A pair of lateral vessels may extend along the body-walls for a greater or less distance; another pair may accompany the nerve cord, one vessel on either side; and in some terrestrial *Oligochaeta* there is a sub-nervian vessel. The dorsal vessel is double in development and occasionally retains its double character for a greater or less extent, e.g. in *Eunicidae*, in *Staurocephalus*, *Pectinaria*, *Acanthodrilus* sp.? The ventral vessel is said to be double in *Nephtys*, *Myxicola*, *Sabella*: both vessels in *Hermella*. The dorsal vessel is usually connected to a capillary network in the walls of the intestine which is replaced in some *Tubicola* (*Serpulinae*, *Sabellinae*, *Ariciidae*, *Ammonocharidae*, *Chaetopteridae*) by a contractile blood-sinus, the dorsal vessel being itself suppressed in this region. It is connected to the supra-nervian vessel by direct vascular loops in the anterior region of the body, and sometimes for the greater part of its length by the intestinal capillaries, by integumental capillaries in most *Polychaeta* and terrestrial *Oligochaeta*. The pseudo-haemal fluid usually flows forwards in the dorsal, backwards in the ventral vessel, but the direction may be temporarily reversed, or even permanently, as in *Pectinaria neapolitana* (Claparède). The flow is maintained by contractions of the dorsal, more rarely of the ventral vessel, or by specially enlarged vessels, either a portion of the dorsal vessel, e.g. in the oesophageal region of *Terebellidae*, or one or more pair of lateral loops connecting the dorsal and ventral vessels, e.g. in many *Oligochaeta*, in *Ariciidae* and *Chaetopteridae*, &c. Many *Serpulidae* have a voluminous contractile plexus in the oesophageal region to which the intestinal sinus and ventral vessel are severally connected, and from which the branchial vessels take origin. The presence of a protrusible pharynx causes modifications in the anterior ends of the longitudinal trunks.

The vessels are composed in some, probably in all, instances of an epithelial coat, to which may be added, in the larger vessels, a muscular coat. The contained fluid is nearly colourless in *Aphrodite*, feebly yellow in *Chaetopterus*, red in most *Oligochaeta* and some *Polychaeta*, e.g. *Eunice*, *Nereis*, *Arenicola*, *Cirrhatulus*, *Terebella*, the colour being due to haemoglobin dissolved in the plasma<sup>2</sup>, or green\* as in the *Chlorhaemidae*

<sup>1</sup> It is often said to be absent in *Aphroditidae*, but has been detected in *Aphrodite* itself and some other members of the family. The almost colourless character of the contained fluid is the cause of its invisibility here.

<sup>2</sup> Haemoglobin is said by Lankester to occur in large quantities in the nervous system of *Aphrodite aculeata*, in less quantities in the muscular tissue of its pharynx (P. R. S. xxi. 1879, p. 75).

(= *Pherusidae*), e.g. *Siphonostoma*, in *Spirographis Spallanzanii* (= *Sabella ventibrum*), and in many *Serpulinae*, owing to the presence of a respiratory pigment, chlorocruorin, capable of oxygenation and de-oxygenation. Colourless corpuscles of fixed outline are found in the fluid (most *Oligochaeta*, several *Polychaeta*, i.e. *Eunice*, *Staurocephalus*, *Nereis*, *Syllidae*, *Ophelia*, *Cirrhatululus*), pinkish corpuscles in *Magelona* (McIntosh). Special corpuscles tinted with haemoglobin are met with in the coelomic fluid of the anangian *Glycera* and *Capitella*, and red-coloured corpuscles occur similarly in *Heteroterebella sanguinea* which possesses a pseud-haemal system (Claparède). Amoeboid corpuscles are always present in the coelome.

Respiration is carried on partly by integumental capillaries, when present, and in many *Polychaeta* by branchiae (p. 595).

The excretory organs or nephridia occur as a rule one pair in each somite, but they are generally aborted in the anterior region of the body, especially when there is a muscular pharynx. Their number is much reduced in some *Tubicola*, e.g. to eight pairs in *Terebella gigantea*, six pairs in *Arenicola*, and they are therefore present in certain somites only which may be anterior as in the two genera just named, or median and posterior as in *Chaetopterus*, *Sabella*, *Myxicola*. Each organ consists essentially of a ciliated tube terminating internally in a ciliated and generally funnel-shaped orifice, and opening externally by a nephridiopore. This pore varies in position. It is in most *Oligochaeta* near the ventral bundle of setae (see p. 205); near the parapodium in *Polychaeta*, either ventral to it, e.g. in *Polynoe*, or dorsal, e.g. *Sthenelais*, *Notomastus*, or in front of it. The section of the tube contiguous to the pore may be wider in calibre as in *Lumbricus* and its allies, or vesicular as in aquatic *Oligochaeta* and some *Tubicola*, and in both cases is provided with a muscular coat<sup>1</sup>. The vesicle may have a glandular epithelium. It may be the only persistent part of

<sup>1</sup> Cosmovici's account of the nephridia in *Polychaeta* is followed in the text. He applies the term 'organ of Bojanus' to the vesicle, and that of 'segmental organ' to the ciliated tube. The vesicle is probably formed by invagination of the hypodermis, as Vejdowsky has found it to be in aquatic *Oligochaeta*. The presence of the vesicle in some somites, its absence in others, in one and the same animal, e.g. *Ophelia*, is a remarkable fact. A pair of vesicles, very large in size, opening on the head in *Serpulidae*, was supposed by Claparède to secrete the material for the tube. That author figures a stream of mucus passing out of the branchial funnel of *Myxicola*. See Supplément aux Annélides Chétopodes du Golfe de Naples in Mém. de la Soc. de physique et d'histoire Nat. de Genève, xx. 1869, p. 512, Pl. xiv. Fig. 2. The position of the apertures (double, according to Cosmovici, single, according to Claparède) in this animal and in other *Serpulidae* is noteworthy. See note, p. 596, ante.

Cosmovici points out that the nephridial funnel opens into the median chamber of the coelome containing the digestive tract in all *Errantia* and in those *Tubicola* which are distinctly segmented. It opens in other *Tubicola*, e.g. *Arenicola*, into the lateral coelomic chambers (p. 597). The nephridium itself is usually applied in the *Errantia* to the posterior face of a septum; sometimes to the anterior face as in *Cirrhatululus*. For a good figure of the nephridium and its papillate external pore in *Polynoe clava*. see A. G. Bourne, Tr. L. S. ii. Pl. xxxvi. Fig. 22. The pores are papillate also in *Notomastus* (*Capitellidae*).



the organ, e. g. in the anterior somites of the tubicolous *Ophelia*, or it may be entirely wanting as in the posterior somites of the same animal. So far as is known it is not represented in the *Errantia*, nor in some *Tubicola*, e. g. *Hermella*. The remaining part of the nephridium is usually short in *Polychaeta*, but long in *Oligochaeta*, and disposed in loops (p. 204). The whole organ is either contained in a single somite, as in most *Polychaeta*, or the funnel opens into a somite anterior to that in which lie the ciliated tube and external aperture as in *Oligochaeta*, the *Alciopidae* among *Errantia* (Claparède), and the larval nephridia of *Capitella* (Eisig). The nephridia sometimes enlarge at the reproductive season, as in *Spio Mecznikowianus* and the female somites of the hermaphrodite *Microphthalmus*. Certain important variations have been observed. The nephridial funnel is absent in the Oligochaete family *Chaetogastridae*. The number of nephridia in a somite is increased in the terrestrial Oligochaete *Acanthodrilus multiporus* (p. 204) and in the *Capitellidae*. *Notomastus* in this family has occasionally more than one pair in a somite; *Capitella capitata* on the contrary has always 3-4 pairs in the anterior somites in which they occur, 4-5 in the median, 5-6 in the posterior. Moreover the nephridia themselves in this instance have remarkable peculiarities. There may be 2-4 funnels to a nephridium; two adjacent nephridia may be connected by a tube; and the duct of each nephridium divides into two main branches, and each branch into 4-5 minute tubules which probably open externally by separate pores. The nephridia of the aquatic *Oligochaeta* situated in the genital segments atrophy before the sexual ducts develop; they persist in the terrestrial *Oligochaeta* side by side with the genital ducts.

The *Oligochaeta* are hermaphrodite, the *Polychaeta* of separate sexes with a few exceptions, such as certain *Hesionidae* and *Nereis massiliensis* among *Errantia*, and among *Tubicola* certain *Serpulidae* (*Amphiglena*, *Laonome*, *Salmacina*, *Protula*, *Spirorbis Pagenstecheri*, *Sp. communis*). The sexual organs in *Oligochaeta* are contained in the anterior somites, and there is either a single pair, or in terrestrial forms two pairs, of testes and a single pair of ovaries placed in different somites, the ovaries behind the testes, except in *Plutellus*. The organs are attached either to the posterior face of a septum or to the nerve-cord (*Naidomorpha*). The corresponding organs of *Polychaeta* are closely attached to a blood-vessel<sup>1</sup>,

<sup>1</sup> Cosmovici is followed in this account. He found the sexual organs developed in *Tubicola* on a vessel in relation with the nephridial funnel and tube (? *Arenicola*); on branches of a median ventral vessel (*Terebella gigantea*); or of an infero-lateral vessel (*Spirorbis*); on the intestinal walls (*Chaetopterus*); or on the anterior aspect of a septum *vis à vis* to the nephridium (*Hermella*). As to the *Errantia*, he found the glands attached, in *Nereis*, to the supra-nervian vessel; in *Marphysa (Eunicidae)* to the branchial vessels proceeding from the supra-nervian, on the section intervening between that vessel and the nephridial funnels; in *Hermione* and *Sthenelais (Aphroditidae)* to a vessel on the posterior aspect of the septa; in *Cirrhatus* to a vessel on the anterior aspect of the septa. The organs are present in a large number of segments in *Errantia*.

The number of organs present appears to correspond with the number of nephridia in many *Tubicola*. The testes and ovaries are usually very similar, and probably always originate from peritoneal or sub-peritoneal cells. They are scarcely visible save at the period of sexual activity, and consist in *Oligochaeta* of a single mass; in *Polychaeta* of a number of grape-like masses in which the developing ova and spermatozoa are contained within a membrane. Cell-limits are not always traceable in the young organ<sup>1</sup>. The genital products appear to be set free into the coelome, and to ripen there in *Polychaeta* and the Oligochaete *Chaetogastridae*. The testicular cells of other *Oligochaeta* ripen in special pouches developed from the septa—the so-called vesiculae seminales—paired in the terrestrial, unpaired in the aquatic, forms. The ovarian cells ripen in a similar way in some of the aquatic *Oligochaeta*, but in the terrestrial are detached from the ovary only when mature. Special efferent ducts—vasa deferentia and oviducts—are present in all *Oligochaeta*, and in *Eudrilus* the oviducts are continuous with the ovaries, a feature not observed in any other Chaetopod (Beddard). Accessory organs are also present; special copulatory setae which replace the ordinary setae; a clitellum at once a copulatory organ, and an organ for secreting the cocoon, produced at the sexual season by the hypertrophy and increase in number of the cutaneous glands in certain somites; (one only or several) receptacula seminis which closely resemble nephridial vesicles (p. 602, and note), and the vesiculae seminales above mentioned. Much variety exists in the disposition of these parts (pp. 205–8). Though strong structural resemblances exist between the genital ducts and nephridia in *Oligochaeta*, it is by no means certain that the ducts are modified nephridia. As to *Polychaeta*, the escape of the genital products by the nephridia has been observed in *Hermella*, *Arenicola*, *Terebella*, and it probably occurs in other instances as well. It may take place also by rupture of the body-walls<sup>2</sup>. Accessory organs of generation are rare in this order, so far as is known, and are (perhaps) to be regarded as modifications of nephridia or parts of nephridia<sup>3</sup>.

<sup>1</sup> The anterior somites of the hermaphrodite *Microphthalmus* (*Hesionidae*) are male, the posterior female (Bobretzky, Z. A. iii. 1880, p. 139). So *Protula*. In *Spirorbis communis* it is the reverse. *Hesione sicula* and *Tyrrhena*, on the contrary, have hermaphrodite organs, which take the form of longish cylindrical processes, with a blood-vessel in the centre. The surrounding peritoneal cells change into ova and spermatozoa commingled (Eisig, Mitth. Zool. Stat. Naples, ii. 1881, p. 298).

<sup>2</sup> Cosmovici found ova in the nephridial vesicles of *Arenicola*, and witnessed their escape by the nephridiopores in *Terebella* and *Hermella*. A. G. Bourne states that the slightest irritation of the body-walls of *Polynoe clava*, when tense with accumulated genital products, causes rupture and discharge. But the products were never found in the nephridia. Kallenbach, however, states that they escape by the nephridia in *Polynoe cirrata*.

<sup>3</sup> A pyriform vesicle is attached to the nephridia of the sixteenth and following somites in *Alciopoe*, and is filled with sperm in male and female alike. It represents possibly a nephridial vesicle. In the hermaphrodite *Microphthalmus* there is a pair of penial papillae between the second and third setigerous somites. The male ducts open on the apices of these papillae. The ducts are long, coiled, and furnished with ciliated funnels, and may be modified nephridia. The nephridia in the

The spermatozoa of *Oligochaeta* are contained in spermatophores, as is the case also in *Spio Mecznicowianus*, the sole instance among *Polychaeta*<sup>1</sup>. The ova are invested by a vitelline membrane, and are generally coloured. They are impregnated externally to the body, or in transit (?), except probably in a few viviparous forms (*Marphysa sanguinea*, *Syllis vivipara*, a *Cirrhatus*); and in *Oligochaeta* are laid in a cocoon secreted by the clitellum. They are carried under the elytra in *Polynoe cirrata*; attached to a dorsal or ventral cirrus in the *Exogoneae* (of Langerhans) among *Syllidae*, and in the female *Autolytus cornutus* (= *Sacconereis*) they are carried and develop in a ventral sac. In *Spirorbis Pagenstecheri* (= *Sp. spirillum* of Pagenstecher), and some other Sabellids<sup>2</sup> the ova develop in a cavity of the operculum; in *Spirorbis spirillum* (of Gould), and *Manayunkia* they are contained within the tube; in *Terebella*, *Dasychone*, &c. they are attached externally to the tube; and in *Phyllodoce*, *Aricia*, *Ophelia*, they are laid in a mass of jelly-like mucus.

Segmentation is with few exceptions, e.g. *Serpula*, unequal. The *Oligochaeta* have a direct development. A ventral ciliated furrow appears to be common, and in *Lumbricus trapezoides* its cilia extend round the mouth also. The young embryo of the same worm divides into two, and each half proceeds to develop normally. The *Polychaeta* have a more or less pronounced metamorphosis with the exception of the Syllidian *Exogoneae*. The larva is a Trochosphere with a prae-oral lobe of variable size, a small body somewhat pointed posteriorly. The body of the adult is formed by the growth and segmentation of this pointed region. The Trochosphere is ciliated, and the differing modes of arrangement of the cilia have given rise to various descriptive terms, to which a classificatory value has sometimes been given. One and the same larva may have at different times differing arrangements, and the larvae of allied species may be completely unlike<sup>3</sup>. The terms alluded to are as follows: *Atrochae* with the cilia scattered uniformly at first, though disappearing in places subsequently, but never so as to form bands; *Mono-* or *Cephalo-trochae* with a prae-oral band; *Telotrochae* with both prae-oral and peri-anal bands;

female somites develop at the sexual period a sacculæ contiguous to the external aperture, which becomes filled with sperm. The male and female *Capitella capitata* possess a pair of ciliated sacculæ between the seventh and eighth somites, opening both externally and internally. They are filled in both sexes by sperm; ova appear to issue by them in the female, and there are special setae close to their external apertures in the male. The homology of these sacculæ is doubtful. Their external aperture is close to the intersegmental furrow, and they appear relatively late (Eisig, Mitth. Zool. Stat. Naples, i. 1879, p. 114). The structures termed 'elliptical or seminal pouches,' occurring in the sexual somites of *Syllidae*, are perhaps nephridial vesicles (cf. Viguier, A. Z. Expt. (2), ii. 1884, p. 86), unless they are, as Robin appears to have found them to be in *Pionosyllis*, a collection of glands (Bull. Soc. Philomath. Paris (7), vii).

<sup>1</sup> Claparède and Mecznicow, Z. W. Z. xix. 1869, p. 171.

<sup>2</sup> *Sp. laevis*, *Salmacina aedificatrix*, *Psymbranchus caecus*, and *Pileolaria* sp.?

<sup>3</sup> E.g. *Terebella nebulosa* is telotrochous, *T. chouchilega* nototrochous.

*Polytrochae* with bands appearing on the somites between the two telotrochous bands and subdivisible into (1) *Polytrochae* proper with complete bands; (2) *Nototrochae* with only dorsal half-bands; (3) *Gasterotrochae* with only ventral half-bands; and (4) *Amphitrochae* with both dorsal and ventral half-bands which do not correspond; *Mesotrochae* with one or two median bands but devoid of the two telotrochous bands (the *Chaetopteridae* alone). A flagellum or a bunch of cilia are often situated at the apex of the prae-oral lobe, and there may be an anal patch of cilia. The prae-oral band is frequently double, and the mouth is then situated ventrally between the two. A stomodaeal and proctodaeal invagination probably always occur, at least during growth. The blastopore is said to persist as the primitive oral opening in some *Oligochaeta*. It closes in *Serpula* in what corresponds to the median ventral line, and the mouth and anus are formed in positions coinciding severally to its two extremities. The archenteron is more or less saccular, and the anus posterior. The larval digestive tract makes a curve concave ventrally. The ventral nerve-cord is usually said to be derived from two epiblastic thickenings which unite at a later period with the cerebral ganglia, epiblastic thickenings of the prae-oral lobe; cf. note, p. 584. Two provisional renal organs open externally in front of the anterior end of the nerve-cord in some Trochospherical larvae and larval *Oligochaeta*. They appear in the individual produced by fission of *Aeolosoma* (Vejdovsky). Their inner extremities end blindly<sup>1</sup>. Others may be present; see p. 582. The mesoblast forms two 'primitive' bands, at first continuous, afterwards segmented, of epiblastic or hypoblastic origin. The setae may appear before the parapodia; the noto- and neuropodium may arise by the division of a simple parapodium, or the former appears before the latter. Some larvae possess bundles of long slender but provisional setae, comparable to the setae of some fossil forms (Agassiz)<sup>2</sup>.

Asexual reproduction by fission with or without gemmation occurs in some *Oligochaeta* (*Aeolosoma*, *Chaetogastridae*, *Naidomorpha*) and some *Polychaeta* (certain *Serpulidae*, and *Syllidae*). In *Aeolosoma* the worm increases in length (i. e. in number of somites); a somite near the centre of the body enlarges, forms a prostomium, and then separation takes place<sup>3</sup>.

<sup>1</sup> See Harmer, Q. J. M. xxv. 1885, p. 279; Vejdovsky, *Oligochaeta*, Prague, 1885, p. 162.

<sup>2</sup> Claparède divided the larvae into *Metachaetae* with, and *Perennichaetae* without, these provisional setae.

<sup>3</sup> The *Oligochaete* *Lumbriculus variegatus* appears to multiply simply by breaking in two, or, when alarmed or irritated, into several fragments (=Schizogony). The parts or fragments develop new heads and new tails as may be necessary. See von Bülow, A. N. 49, pt. i. 1882; and for the histology of the regenerating tail, Id. Z. W. Z. xxxix. 1883. The *Ctenodrilus monostylos* of Zeppelin (Z. W. Z. xxxix. 1883) undergoes simple fission, and divides in the same way into fragments containing a few—in this case two or more—somites, which develop into a new worm. The *Ct. pardalis* of von Kennel (Arb. Zool. Zoot. Inst. Wurzburg, v. 1882), which is, according to Vejdovsky, a *Parthenope*, multiplies by fission accompanied by gemmation. Both worms last named are marine; their hypodermis contains coloured gland cells similar to those of *Aeolosoma*; their nervous

The process is more complicated in *Chaetogastridae* and *Naidomorpha*. A 'zone of fission' is formed between two somites as soon as the somites increase beyond a certain (? fixed) number. The 'zone' divides into an anterior and posterior portion, the latter forming a head for the posterior set of somites, the former giving rise to a series of new somites. Chains of zooids are thus produced, but the order of the zooids in a chain and the number that constitute a chain, appear to be inconstant (Semper). Under certain conditions, such as unfavourable climatic changes, the zooids become free, lengthen and develop sexual organs. In the Serpulids *Protula* and *Filograna*, the posterior somites are set free from the anterior with previous formation of a head. As to the *Syllidae*, the posterior somites in the genera, *Syllis*, *Trypanosyllis*, and *Opisthosyllis* develop sexual organs and bundles of long slender notopodial setae (= Pubertätsborsten); a head is formed, and then the sexual somites, which are *not constant* in number, are set free as a separate worm<sup>1</sup>. The phenomena are more complicated in the Syllidian tribe *Autolyteae*. Chains of individuals are produced of which the last is the oldest. The derived zooids develop, one by one, their sexual products and long notopodial setae, and are then detached. An anal somite is always formed by the zooid in front of the one upon the point of being detached. As the parent-form in these Syllidians remains non-sexual, an alternation of generations is set up. *Syllis ramosa*, which has been found inhabiting Hexactinellid sponges from the eastern seas is a more remarkable form still. It occurs in branched colonies. Small branches become sexual, develop a head with large eyes and long notopodial sexual setae, and are set free as males and females.

The fissiparous individual among the *Oligochaeta* above mentioned differs like an immature worm from the sexual individual by the absence of clitellum, genital setae, &c. as well as of sexual organs, and by a difference in the number of somites making up the body. The asexual Syllidian differs from the sexual by the absence of the long notopodial setae, and, where fission occurs, also in the shape of the head and size of the eyes. The sexual *Heteronereis*-form of certain species of *Nereis* differs from the immature individual by the shape and size of the parapodia of the genital somites which become adapted for swimming, by the presence of long slender setae, the conformation of the dorsal cirri especially, and the anal somite, and an increase in the size of the eyes. These changes are more marked in certain respects in the male, leading to a slight degree of sexual dimorphism. Such dimorphism, however, is con-

system lies entirely in the hypodermis, and the sole pair of nephridia present appear to belong to the peristomium. They are primitive forms, and are perhaps *Oligochaeta*. See the authors named; and for a discussion on the questions of affinity and generic names, Vejdovsky, System der Oligochaeten, 1885, pp. 164-66.

<sup>1</sup> The non-sexual parent in *Trypanosyllis Krohnii* develops previously to separation a new peri-anal somite. Cf. Marion and Bobretzky, A. Sc. N. (6), ii. 1875, p. 36.

spicuous in *Autolytus prolifer* (*Syllidae*), where the male has been described under the generic names, *Polybostrichus*, *Diploceraea*, and *Crithida*, and the female as *Sacconereis*. Polymorphic generations are found in *Nereis Dumerilii* (Claparède). Certain individuals become sexually mature but are of separate sexes; others appear to become hermaphrodite (= *Nereis massiliensis*); others again are metamorphosed into a *Heteronereis*, of which two forms are known, one large and tubicolous, the other small and pelagic.

The Chaetopoda appear to have considerable powers of reparation after injury, and the formation of a new head with anterior somites, and of new posterior somites has been observed. Phosphorescence occurs in some terrestrial *Oligochaeta* and some *Polychaeta*. The light is sapphirine, violet or green; it appears either over the surface of the body in general, or in certain limited spots, e.g. on the elytra of *Polynoe*, and is due in some cases to the secretion of unicellular hypodermic glands<sup>1</sup>.

The *Oligochaeta* are either freshwater or terrestrial. The *Polychaeta* are marine<sup>2</sup>, but a freshwater *Lumbriconereis* and a Nereid have been found in Trinidad (von Kennel), and a freshwater tubicolous genus, *Manayunkia*, occurs in N. America (Leidy). The Chaetopoda are free except some *Tubicola* which fix their tubes to stones, shells, or to living animals, e.g. *Serpula* and *Spirorbis* to Crabs; *Branchiomma vigilans* to *Aphrodite*; and various others to Starfish (*Astropecten*), or on Sea Urchins (*Cidaris*). A few *Polychaeta* are pelagic (*Alciopidae*, some *Phyllodocidae*; *Tomopteris*; *Typhloscolex*): others only at the reproductive season (*Heteronereis*, *Syllidae*). Certain *Tubicola* bore into rocks or shells (*Heterocirrus* = *Dodecaceria*, *Polydora ciliata*, *Sabella saxicava*). Most *Errantia* are carnivorous; the *Tubicola* and *Oligochaeta* are vegetable feeders. The only instances of parasitism are the Eunicid *Oligognathus Bonelliae* in the coelome of the Gephyrean *Bonellia*, *Alciopina parasitica* (? a larval *Alciopae*) in a *Pleurobrachia* (*Ctenophora*), an Amphinomidan in the branchial cavity of *Lepas anatifera* (*Cirripidia*)<sup>3</sup>, and the family *Myzostomidae* (*infra*, p. 609). Commensalism also occurs; e.g. *Polynoe Scolopendrina* and *Harmothoe Marphysae* inhabit the tunnels of *Marphysa sanguinea*.

The fixed *Tubicola* with calcareous tubes are found from the Silurian upwards. Undoubted remains of *Errantia* occur in the Solenhofen slates, and probably in the Silurian (*Nereites*, *Crossopodia*). Structures from the

<sup>1</sup> For the rosette organs of *Tomopteridae*, which consist of an assemblage of yellow coloured sacs with a nerve supply, and are apparently phosphorescent organs, see Greeff, Z. W. Z. xlii. p. 440; and on the elytra of *Polynoe* which are phosphorescent, Jourdan, Z. A. viii. 1885.

<sup>2</sup> The *Polychaeta* live at all depths in the ocean. 'No definite law as to the presence or absence of genera at particular depths can be enunciated,' but 'the majority of abyssal forms are tube-dwellers' (McIntosh). A Terebellid *Leaena abyssorum* and a Serpulid *Placostegus benthalianus* were dredged by the Challenger in 3212 fathoms. Cf. Challenger Reports, xii. 1885.

<sup>3</sup> Fritz Müller, Facts for Darwin, 1869, p. 44.

Silurian, Devonian and Carboniferous have been identified as Eunicidan jaws.

The class Chaetopoda contains, in addition to the two orders *Polychaeta* and *Oligochaeta*, two others, the *Chaetopoda ectoparasitica* and the *Archi-Chaetopoda*, described separately here, because of their interesting peculiarities. The first-named order contains highly modified worms, but its position among *Chaetopoda* must be regarded as settled by the discovery of the larval form. The *Archi-Chaetopoda* resemble the *Archi-Annelida* (*infra*, p. 613) in the large size of the peristomial somite, the similarity *inter se* of the remaining somites, and in the position of the nervous system within the hypodermis, as well as in the connection of the intra-muscular nervous plexus with cells of the hypodermis.

*Chaetopoda ectoparasitica* = *Myzostomidae*. There are two genera included in this group—*Myzostoma*, parasitic on various *Comatulidae* and a few Pentacrinoids, and *Stelechopus*, parasitic on *Hyocrinus* sp.? The body of *Myzostoma* is symmetrical and non-segmented, usually disc-shaped, occasionally elongate. It is provided with five pairs of short ventral and radially arranged parapodia, each armed with a chitinous hook and a supporting rod; five pairs of suckers commonly alternate in position with the parapodia. The margin of the body has ten pairs of cirri at least, or a larger number, which are furnished with terminal bundles of stiff sensory (?) setae and a ventral furrow lined by adhesive cells. There is a chitinous cuticle, and cilia occur in isolated patches on the dorsal and ventral surfaces. The nervous system consists of a large ventral ganglion, with five pairs of lateral nerves. A supra-oesophageal ganglion appears to be absent. The alimentary canal consists of a protrusible muscular proboscis, an oesophagus, a stomach, which gives off lateral branched caeca, and a short rectum. Mouth and anus are generally on the ventral surface, the former anterior, the latter posterior in position. There are no nephridia. The majority are hermaphrodite. The testes are ventral, paired, and branched except in the dioecious forms, and the male apertures are lateral, and placed externally to the third pair of parapodia. The ovaries are represented by a number of caeca on the dorsal surface; an oviducal tube opens into the dorsal aspect of the rectum. *M. cysticolum* has rudimentary testes; *M. tenuispinum*, *inflator*, *Murrayi*, are dioecious, i.e. either male or female. *M. glabrum*, though hermaphrodite, has small 'complemental' males, like certain hermaphrodite *Cirripedia* (p. 537). *M. glabrum* and *cirriferum* have larvae provided with a post-oral and a prae-anal band of cilia, with a larval supra-oesophageal ganglion, and two bundles of provisional setae; they closely resemble the larval *Nereis Dumerilii*. The position of the *Myzostomidae* in the class Chaetopoda must accordingly be regarded as a settled fact.

*Stelechopus* differs from *Myzostoma* in being elongate, in the parapodia not being radially arranged, in the absence of suckers and cirri, and in the absence of lateral caeca to its alimentary canal; ? hermaphrodite.

Von Graff, Challenger Reports, x. 1884; Id. Das Genus *Myzostoma*, Leipzig, 1877. Suckers, Niemiec, Recueil Zool. Suisse, ii. 1885. *Development*, Beard, Mitth. Zool. Stat. Naples, v. 1884.

*Archi-Chaetopoda* = *Saccocirridae*. This order is represented by the marine *Saccocirrus papillocerus* from the bays of Sebastopol and Marseilles. It has a

small prostomium, a large peristomium, a segmented body, which terminates in two processes armed with adhesive papillae. The two prostomial tentacles contain each a tube with muscular walls, which terminates in the peristome in a saccule. The two tubes are connected by a cross branch. Each somite is provided with a pair of latero-dorsal bundles of setae contained in a sheath, capable of protrusion and retraction. Oblique dorso-ventral muscles are well developed, and cut off two lateral coelomic chambers from a median chamber. Transverse septa are present. The nervous system is wholly contained in the hypodermis. It consists of a supra-oesophageal ganglion, oesophageal commissures, and two ventral cords, the latter being connected by a single transverse commissure in the peristome. Ganglionic (hypodermic) cells cover the supra-oesophageal ganglion above and below, the ventral cords only on their external surface. Two pigmented eye-spots are contained in the supra-oesophageal ganglia, and there is a pair of large ciliated cephalic grooves. The mouth is ventral, the anus dorsal and terminal. The digestive tract consists of an oesophagus with an intestine constricted where it traverses the septa. Both are ciliated throughout. A dorsal vessel has been observed. A pair of nephridia are present in each somite, and traverse the septa, as in all *Oligochaeta*. Their external apertures are near the setigerous tubes. The sexes are separate. The testes and ovaries are small cellular masses affixed to the posterior faces of the septa in the intestinal region. Their cells are detached and ripen in the coelome. The sexual products are conveyed outwards by the nephridia. The nephridial apertures in the sexual somites of the male are papilliform, and probably copulatory. The sexual somites of the female contain a pair of vesicles, which are filled with spermatozoa; their ciliated ducts open latero-ventrally.

Marion and Bobretzky, *Annélides du Golfe de Naples*, A. Sc. N. (6), ii. 1875, p. 69. *Nervous system*, Fraipont, *Archives de Biol.* v. 1884. *Larva*, see Claparède and Metschnikoff, *Z. W. Z.* xix. 1869, p. 175 ('an undetermined Spionid larva'). *Development*, Repiachoff, *Z. A.* iv. 1881.

The classification of the Chaetopoda is as follows—

I. *Polychaeta*: marine, with the setae implanted in parapodia, there being many setae in a bundle; antennae and palpi usually present on the prostomium; cirri and branchiae on the somites of the body. The sexes, as a rule, separate; development accompanied by a metamorphosis.

(a) *Errantia*: free and carnivorous. Prostomium large and more or less independent; usually furnished with eyes and well-developed antennae; body seldom divided into regions; parapodia large; pharynx generally protrusible. *Aphroditidae*, *Eunicidae*, *Nereidae*, *Syllidae*, &c.

(b) *Tubicola* s. *Sedentaria*: vegetable feeders; tubicolous; the tube sometimes fixed. Prostomium small; body frequently divided into regions; parapodia small; pharynx short, sometimes eversible, but never armed with teeth. *Capitellidae*, *Arenicolidae* (= *Telethusidae*), *Chaetopteridae*, *Chlorhaemidae*, *Terebellidae*, *Serpulidae*, &c.

II. *Oligochaeta*. No antennae, parapodia, cirri, or branchiae; setae sometimes absent; hermaphrodite; sexual organs restricted to a limited number of somites; special sexual ducts present; ova laid in a cocoon; no metamorphosis in



development; aquatic; limicolous or terrestrial<sup>1</sup>. *Aphanoneura* (= *Aeolosomidae*), *Naidomorpha*, *Chaetogastridae*, *Discodrilidae* (= *Branchiobdella*)<sup>2</sup>, *Enchytraeidae*, *Tubificidae*, &c., *Lumbricidae*, &c.

III. *Chaetopoda ectoparasitica*, ante, p. 609.

IV. *Archi-Chaetopoda*, ante, pp. 609-10.

For lit. of *Oligochaeta*, see pp. 200, 208, 212; add. Stolc, 'Naidomorpha,' Z. A. ix. 1886; Benham, 'Studies,' &c., Q. J. M. xxvii. (1), 1886.

*Polychaeta*, Ehlers, Borstenwürmer, Leipzig, 1863-68; Claparède, Annélides Chétopodes du Golfe de Naples, Geneva, 1868; Supplement, 1870; Id. Recherches sur la Structure des Annélides Sédentaires, 1873 (or in Mémoires de la Société de Physique de Genève, vols. xix., xx., xxii.); Marion and Bobretzky, Annélides du Golfe de Marseilles, A. Sc. N. (6), ii. 1875; Marenzeller, Adriatic Annelids, SB. Akad. Wien, lxix. 1874, lxxii. 1875, lxxxix. 1884, all Abth. 1; McIntosh, Annelids of Challenger Exped., Challenger Reports, xii. 1885; Langerhans, Wurmfauna von Madeira, Z. W. Z. xxxii. 1879; xxxiii. 1880; xxxiv. 1881; xl. 1884.

De Quatrefages, Histoire Nat. des Annelés, 2 vols. with atlas, Paris, 1865.

*Polynoe clava*, Bourne (A. G.), Tr. L. S. ii. pt. 7, 1883; *P. cirrata*, Kallenbach (Kieler dissert.), Jena, 1883. *Oligognathus Bonelliae*, Spengel, Mitth. Zool. Stat.

<sup>1</sup> The *Oligochaeta* were formerly divided into the *Terricola* and the *Limicola*. The *Terricola* were distinguished by the presence of a sub-neural blood-vessel, a capillary network surrounding the nephridia, a typhlosole, the presence of nephridia in the same somites as the sexual ducts. But the discovery of new forms and the fact that in the *Limicola* the nephridia of the genital somites atrophy when the genital ducts develop, have broken down the division. See the account of *Lumbricus*, pp. 196-212.

<sup>2</sup> *Branchiobdella*, which is usually classed among Hirudinea, is placed by Vejdovsky among *Oligochaeta*. There is one species, *B. varians* (Voigt), with several local varieties. It is small (3-12 mm.), parasitic on *Astacus*, but not in England. Of the eight middle somites, seven are formed of two rings, one large, one small. There is a posterior sucker formed by the modification of post-anal somites. The coelome is roomy and divided by transverse septa. Large cutaneous glands open on the head and sucker, and secrete a sticky adhesive substance. The sub-oesophageal ganglion corresponds to four embryonic ganglia, and there is concentration of ganglia again at the posterior extremity of the cord. There is a pair of large stomatogastric ganglia as in *Oligochaeta*. The ganglion cells form prominent masses as in Leeches. There are tactile setae on the head. The buccal cavity is armed with two opposing chitinous teeth, one dorsal, one ventral. Glands open into it. The anus is dorsal. Chloragogen cells (p. 202) are present. There is a dorsal and ventral blood-vessel connected by seven transverse anastomoses, five anterior, two posterior, and an intestinal sinus. The blood-system is closed, the blood colourless in young, yellow or red in adult, specimens. There are two pairs of nephridia, one posterior, the other anterior; and the members of the latter pair belong to different but successive somites. Testes and ovaries appear to be derived from peritoneal cells; the former are attached to the posterior aspect of a septum, the latter to the sides of the intestine in the second somite behind the testes. The vas deferens is composed of two ciliated funnels and ducts, which perforate a septum, unite, open into a glandular tube some distance from its end. A median and protrusible penis is continuous with the gland-tube. The oviducts are represented by two slits situated each on the apex of a papilla and leading into a short wide tube. The genital products appear to be set free and to ripen in the coelome. There is a median azygos spermatheca in the testicular somite. The ova are laid singly in a delicate case, which is attached by a pedicle to the *Astacus* harbouring the worm.

Voigt, Arb. Zool. Zoot. Inst. Würzburg, vii. 1885; viii. 1886. Dorner, Z. W. Z. xv. 1865. Lemoine, French Association for Advancement of Science, Reims, 1880. *Development*, Salensky, Archives de Biol. vi. Pt. i. 1885.

Naples, iii. 1883. *Typhloscolex*, Greeff, Z. W. Z. xxxii. 1879. *Alciopidae and Tomopteridae*, Id. Z. W. Z. xlii. 1885, with lit. quoted. *Polyopthalmus*, Meyer, A. M. A. xxi. 1882. *Capitella capitata*, Fischer, Marburg, 1884 (cf. Z. A. vi. 1884). *Scoloplos armiger*, Mau, Z. W. Z. xxxvi. 1882. *Polydora ciliata* and *P. quadrilobata*, Jacobi (Kieler dissert.), Weissenfels, 1883. *Magelona*, McIntosh, Z. W. Z. xxx. 1878 (cf. A. N. H. (4), xx. 1877). *Terebellides*, Steen, J. Z. xvi. 1882. *Manayunkia*, Leidy, Proc. Ac. Nat. Hist. Philadelphia, 1883.

*Tube of Sabella*, Macé, A. Z. Expt. x. 1882; of *Onuphis*, Schmiedeberg, Mitth. Zool. Stat. Naples, iii. 1883.

*Gills of Serpula*, &c., Örley, Mitth. Zool. Stat. Naples, v. 1884. *Branchial skeleton of Sabella*, Viallanes, A. Sc. N. (6), xx. 1886.

*Muscular tissue*, Rohde, Schneider's Zool. Beiträge, i. 1885.

*Nervous system*, Pruvot, A. Z. Expt. (2), iii. 1885; of *Eunice Harassii*, Jourdain, A. N. H. (5), xiii. 1884. Cf. Semper, Arb. Zool. Zoot. Inst. Würzburg, iii. 1876-77, p. 143.

*Organs of special sense. Tactile setae*, Vejdovsky, System der Oligochaeten, 1885, p. 96; Langerhans, Z. W. Z. xxxiii. 1880, p. 271. *Lateral line organs*, &c., in *Capitellidae*, Eisig, Mitth. Zool. Stat. Naples, i. 1879; in *Polyopthalmus*, Meyer, op. cit. *supra*. *Eyes*, Carrière, Sehorgane der Thiere, Leipzig, 1885; cf. Graber, A. M. A. xvii. 1880; of *Hyalinaecia*, Pruvot, A. Z. Expt. (2), iii. p. 262. *Otocysts in Arenicola*, Jourdain, A. N. H. (5), xiii. 1884; in *Aricia*, Langerhans, Z. W. Z. xxxiv. p. 88.

*Digestive tract. Poison tooth of Syllidae*, Langerhans, Nova Acta Cur. 42, 1881, p. 95. *Glands of oesophagus*, Graber, SB. Akad. Wien, lxvii. Abth. 1, 1873. *Gizzard of Syllis*, Haswell, Q. J. M. xxvi. 1886. *Siphon of Capitellidae*, Eisig, Z. A. 1, 1878; Fischer, op. cit. *supra*. *Air-vesicles of Hesionidae and Syllidae*, Eisig, Mitth. Zool. Stat. Naples, ii. 1881. *Secretion of caeca in Aphrodite*, Krukenberg, Untersuch. Physiol. Inst. Heidelberg, ii. 1882, p. 353.

*Vascular system of Aphrodite*, Selenka, Archiv. Nederl. f. Zool. ii. 1874-75; of *Polynoe vasculosa*, Claparède, Supplement (*supra*). *Blood corpuscles*, Bourne and Blomfield, Q. J. M. xxi. 1881. *Blood of Arenicola*, Krukenberg, Vergleich. Physiol. Studien, ii. 2, 1882, p. 87. *Chlorocruorin*, MacMunn, Chromatology, &c., Q. J. M. xxv. 1885.

*Nephridia and sex organs*, Cosmovici, A. Z. Expt. viii. 1879-80; of *Capitellidae*, Eisig, Mitth. Zool. Stat. Naples, i. 1879. *Ovaries and ducts of Endrilus*, Beddard, Z. A. ix. 1886.

*Development*, Salensky, Archives de Biol. iii. 1882; iv. 1883; of *Serpula*, Conn, Z. A. vii. 1884; *Eupomatus*, Hatschek, Arb. Zool. Inst. Wien, vi. 1885. *Worm larvae*, Fewkes, Bull. Mus. Harvard, xi., No. 9, 1883.

*Viviparous Syllis*, &c., Krohn, A. N. 35 (1), 1869. *Egg-carrying Syllidae* (= *Exogoneae*), Viguier, Animaux inférieurs de la baie d'Alger, A. Z. Expt. (2), ii. 1884.

*Asexual reproduction: in Oligochaeta*, Semper, Arb. Zool. Zoot. Inst. Würzburg, iv. 1877-78; cf. op. cit. iii. 1876-77, p. 161, and Vejdovsky, Oligochaeten, p. 161; *Lumbriculus*, von Bülow, A. N. 49, 1882; in *Syllidae*, Langerhans, Z. W. Z. xxxii. 1879, pp. 519-522; in *Autolytus*, Greeff, A. N. H. (4), i. 1868 (with lit.); in *Syllis ramosa*, McIntosh, Challenger Reports, xii. 1885, p. 198; in *Protula*, Huxley, Edinburgh New Phil. Journal, i. (n. s.), 1855.

*Metamorphosis of Nereis Dumerilii*, Claparède, Supplement (*supra*); on *Hetero-*

*nereis*, cf. also Ehlers, *Borstenwürmer*, 1868, p. 451, &c.; and Bobretzky, A. N. 37, (2), 1871, p. 385.

*Powers of reparation*: in *Diopatra*, Ehlers, Akad. programme, Erlangen, 1869; cf. A. N. 35 (2), p. 244; in *Spio*, Bobretzky, A. N. 37 (2), 1871, p. 385; cf. de Quatrefages, *Hist. Nat. (supra)*, p. 124; in *Oligochaeta*, p. 208-9 *ante. Phosphorescence*, p. 201, and p. 208 with note 1.

*Freshwater Polychaeta of Trinidad*, von Kennel, Arb. Zool. Zoot. Inst. Würzburg, vi. 1883. *Manayunkia*, Leidy (*supra*). *Boring Chaetopoda*, Ray Lankester, A. N. H. (4), i. 1860; McIntosh, *ibid.* ii. *Pelagic forms*, Viguier, C. R. 101, 1885; Greeff, Z. W. Z. xxxii. 1879.

### ARCHI-ANNELIDA.

The name *Archi-Annelida* was employed originally by Hatschek as an ordinal name for the *Polygordiidae*, a family with a single genus, *Polygordius*, to which he added subsequently the genus *Protodrilus*. Foettinger has more recently still added a second family, *Histriodrilidae*, represented by the parasitic *Histriodrilus Benedeni* (= *Histriobdella Homari*). All the Archi-annelids are marine; all have a small pro- and a large peri-stomium; the somites of the body are similar to one another, especially in the *Polygordiidae*, and are but feebly marked externally. There are no setae, no parapodia, cirri or branchiae, but the head carries two or more tentacles. The muscles form a single layer of longitudinal fibres disposed in four bands, two dorso-lateral, two ventro-lateral, the latter widely separate. *Polygordius Villoti* is stated by Perrier to have circularly disposed fibres. The nervous system is retained in the hypodermis. A pair of ciliated grooves is present on the head. The oesophagus is restricted to the peristomial somite, and there is a simple intestine. A muscular sub-oesophageal bulb or proboscis lies beneath the oesophagus and at the posterior margin of the mouth in *Histriodrilus* and *Protodrilus*. Simple nephridia are present. *Histriodrilus* and *Polygordius* are of separate sexes; *Protodrilus* is hermaphrodite.

The *Histriodrilidae* are the higher group, inasmuch as there are individual nerve ganglia and special (?) genital ducts. The *Polygordiidae* have an intra-muscular nerve-plexus connected to the cells of the hypodermis, and oblique dorso-ventral muscles are present in each somite, as in many *Polychaeta*. *Polygordius*, like some Nemertea, is apt to break into fragments when irritated or injured.

*Histriodrilus Benedeni* (= *Histriobdella Homari*) is parasitic upon the Lobster, the eggs of which it devours. It is a minute worm 1.4 mm. long. There is a distinct head, a body composed of three narrow somites, a sexual enlargement which appears to include two (? 3) somites followed by three short somites. The head carries a median and two laterally placed pairs of sensory tubercles, and a pair of short limbs. The last somite

carries a larger pair of posterior limbs. The hypodermis is composed of nucleated protoplasm. The nervous system consists of cerebral ganglia, oesophageal commissures, and a pair of ventral cords which fuse in each somite to form a ganglion. Organs of special sense are the sensory setae of the cephalic tubercles, and of a similar tubercle attached to each posterior limb. The digestive tract is ciliated and consists of an oesophagus, stomach-intestine and short rectum. The mouth is ventral, the anus terminal; both are surrounded by cilia. The oesophageal bulb is armed with three chitinous jaws. The three first somites of the body possess each a pair of ciliated nephridial tubes. A fourth pair occurs close to the third in the female, but close to the ventral genital opening in the male, which has also a fifth pair in the first of the three posterior somites. The sexes are separate. Testes and ovaries are formed by the growth of splanchnopleural coelomic epithelium. The genital ducts in the female are a pair of wide ciliated tubes opening each into a dilatation in which sperm has been observed, and this in its turn into a second dilatation. The external apertures are lateral like the nephridial, and the hypodermic cells surrounding them enlarged. The latter probably secrete the egg-shell. The male appears to possess a pair of lateral evaginable penes. A median ventral genital opening leads into a canal which bifurcates, each of its branches ending in a vesicle. Sperm has been observed in these vesicles. Internal openings to the male ducts have not been observed. Vascular system absent (?).

Foettinger, Archives de Biol. v. 1884.

The family *Polygordiidae* includes the two genera *Protodrilus* and *Polygordius*. The species of the former genus are of minute size, provided with a longitudinal ventral and ciliated furrow, a muscular sub-oesophageal bulb, and are hermaphrodite. The best known is *P. Leuckarti* from Messina, which is about 4 mm. long. The segmentation of the body is marked only by fine lines, by bands of cilia and internal septa; the last somite carries a pair of terminal glandular adhesive lobes. The head has a pair of long tentacles or palpi. Cilia are found on the tentacles, ventral aspect of the head, in the ventral groove, as a double pre-oral band, and five simple post-oral cephalic bands, as well as two bands, one at each end of every somite. The nervous system consists of a cephalic mass, two oesophageal commissures, two ventral cords connected from place to place by transverse fibrous commissures, but separated by the ventral groove. A gradual transition between ganglion cells and ordinary hypodermis cells is observable. The mouth is ventral, the anus terminal. The digestive tract is ciliated, and consists of oesophagus with sub-oesophageal bulb and intestine. There is a dorsal and ventral blood-vessel. A contractile bulb developed on the

former drives the blood into the tentacles. The afferent tentacular vessel is contractile, the efferent not so. The latter fuses with its fellow to form the ventral vessel. Lacunae in the walls of the intestine put the dorsal and ventral vessels in communication. The blood is feebly red when in mass. There is a pair of nephridia in each fully developed somite, which traverse the septa as in *Oligochaeta* and open laterally. The seven first somites contain paired ovaries, the next succeeding testes.

Two eye-specks and otocysts are stated to be present in *P.* (= *Polygordius*) *flavocapitatus*, and *P. Schneideri*. The former is also said to have the coelome traversed by a network of connective tissue fibres, and a special oviducal aperture in the last somite.

The species of the genus *Polygordius* are larger than the species of *Protodrilus*. *P. lacteus* is 40 mm. long, *P. Villoti* 1 dm. The cephalic tentacles are short, and at the apex of the prostomium. The posterior somites are distinctly delimited. *P. lacteus* has the anus surrounded by eight tooth-like processes, and a short distance in front of it the body is begirt by a circle of twenty-four adhesive papillae. The cerebral ganglion in *P. neapolitanus* is divided into three lobes, anterior, middle and posterior. The oesophageal commissures originate from the middle lobe, and are united on the ventral aspect by a transverse commissure. From this point onwards there is a single median cord due to the fusion of the two larval cords. Remnants of the ciliated longitudinal furrow which divides the two cords of the larva are to be found within this cord as fine canals. The mouth is ventral; there is an oesophagus and ciliated intestine, the latter constricted by the transverse septa. The blood-vascular system consists of a dorsal vessel which gives origin in each somite to a pair of transverse vessels. The latter end caecally with the exception of the first pair which are united ventrally. The blood is red. There is a pair of nephridia in each somite. The sexes are separate, and the genital products are developed in the posterior somites.

Perrier states that in *P. Villoti* the vicinity of the mouth, together with a small part of the last somite are ciliated, that a ventral vessel is probably present, and that the genital products escape by the nephridia.

*Protodrilus* appears to develop direct (Repiachoff). *Polygordius*, on the contrary, passes through a metamorphosis. The larva is a Trochosphere, and the body grows as does that of an ordinary Chaetopod. There is a pair of remarkable head-kidneys; each consists (Fraipont) of a horizontal ciliated intracellular tube terminating in a ciliated enlargement. A vertical branch soon appears similarly terminated. The enlargements multiply by division, and there are usually two to the vertical, three to the horizontal branch. Each of them carries several radiating caecal tubules representing aborted 'nephridial canals of the second order,' &c. (Fraipont). The tubules in *P. neapolitanus* are supported by a funnel-shaped membrane

According to Hatschek a longitudinal canal is formed in connection with each cephalic kidney. Segmental nephridial funnels develop in each somite in continuity with this canal, which then disappears, each nephridium opening externally by its own pore. The young *Polygordius* has a pair of eye-specks.

*Species of Protodrilus and Polygordius*, Fraipont, Archives de Biologie, v. 1884, note p. 250; the names as given by Fraipont have been followed here.

*Protodrilus Leuckarti*, Hatschek, Arb. Zool. Inst. Wien, iii. 1880. *P. purpureus*, Schneider, Archiv f. Anat. und Physiol. 1868, p. 56. *P. flavocapitatus*, Uljanin, apud Hoyer, Z. W. Z. xxviii. 1877, p. 389; *development of*, Repiachoff, Z. A. iv. 1881. *P. Schneideri*, Langerhans, Z. W. Z. xxxiv. 1880, p. 125.

*Polygordius lacteus*, Schneider, loc. cit. *supra*. *P. Villoti*, Perrier, C. R. 80, 1875. *Development*, Hatschek, op. cit. *supra*, i. 1878; *of head*, Id. op. cit. vi. (1), 1885; Fewkes, Bull. Mus. Harvard, xi. (No. 9, 1883), p. 195; *head-kidney*, Fraipont, op. cit. *supra*.

*Nervous system of Archi-annelida*, Fraipont, op. cit. *supra*. This author is stated to be preparing a monograph of the genus *Polygordius* for 'The Fauna and Flora of the Gulf of Naples.'

#### CLASS GEPHYREA.

*Vermes with a sub-cylindrical non-segmented body, usually brightly coloured. The fore-part of the body is either invaginable, and provided with tentacles, or prolonged into an extensile prostomium, which is readily cast off. Setae may be present as an anterior ventral pair, and one or two posterior circlets. The mouth is anterior, or at the base of the prostomium; the anus dorsal and anterior, or terminal and posterior. The nervous system consists of a peripharyngeal band, with or without a supra-oesophageal swelling, and of a ventral non-ganglionated cord. There are no specialised organs of respiration. A vascular system is usually present; the coelome large. Specialised corpuscles tinged with haemoglobin or haemerythrin are frequently found in the coelomic fluid, and sometimes in the vascular. Nephridia are usually present. The sexes are separate, the male sometimes degenerate; and the genital products are either shed into the coelome and taken up by the nephridia; or the glands are continuous with their ducts. Exclusively marine and generally distributed.*

Of the two sub-groups of Gephyrea, the *G. achaeta* and *G. chaetifera*, the former contains the families *Sipunculidae* and *Priapulidae*, the latter the *Echiuridae*. The *Sipunculidae* have the forepart of the body invaginable, and this 'introvert,' often termed proboscis, is of considerable length, and usually slender as compared with the rest of the body. The introvert is generally covered with hooks, except in the genus *Sipunculus*<sup>1</sup>. There

<sup>1</sup> Bülow found that the anterior part of the introvert was regenerated after removal in 3-5 weeks' time in *Phascolosoma* and *Aspidosiphon* (Biol. Centrblatt. iii. p. 14). *Sipunculus* has often

are, with the exception of two genera, oral tentacles variable in form surrounding the mouth, either in a complete or incomplete ring, or aggregated in bundles, which may be entirely dorsal to the mouth. A pair of ciliated tubercles may lie above the supra-oesophageal ganglion. The hind-end of the body is either expanded or pointed and narrow. The *Priapulidae* are cylindrical in shape, the introvert is short and not slender, and there are no tentacles. The mouth is surrounded by chitinous teeth, long and curved in *Halicryptus*. *Priapululus* has a caudal appendage (double in *P. bicaudatus*) which is ventral to the anus, hollow, communicating with the coelome, and beset with hollow papillae. The *Echiuridae* have a long prostomium developed from the larval prostomium, and often termed proboscis, capable of great extension and very mobile, at the base of which the mouth lies ventrally. It is bifid at its apex in *Bonellia*. The body is cylindrical and tapers posteriorly. There is a pair of ventral chitinous hooks placed anteriorly in *Echiurus*, *Thalassema*, and *Bonellia*. *Echiurus Pallasii* is also provided with two posterior, nearly complete circles of setae; *E. uncinatus* with one; but in some species of the genus the circles in question are wanting altogether. The female *Hamingia* has no setae. The male in this genus as well as in *Bonellia* is minute, and Planarian in aspect.

The integument is composed of a cuticle, a hypodermis, and muscle layers. A layer of connective tissue, or cutis, may underlie the hypodermis, as in *Sipunculus* and *Echiuridae*. The cuticle is chitinous, and sometimes cast off and renewed (*Echiurus*). The hypodermis consists of a single layer of cells usually close-set and columnar, sometimes stellate, the intervals being occupied by a clear material (*Priapululus*, *Halicryptus*). The colouring-matter of the animal is contained in them. The green hue of *Bonellia* is due to a peculiar pigment known as Bonellein, which is not identical with chlorophyll as usually stated. It may also be the pigment of the green-coloured *Hamingia*. Pigment cells are found in clumps in the cutis, &c. The cuticle and hypodermis form together the various processes,—papillae, hooks, plates bearing papillae, which occur in different genera. The spines of the *Echiuridae* are formed in sacs of invaginated hypodermis, those of the posterior circles in *Echiurus* from a single cell. Glands are generally present, usually unicellular, sometimes bi- or multicellular as in *Sipunculus nudus*. The musculature of the body consists of an external circular layer followed in *Sipunculidae* by a layer of oblique and then of longitudinal fibres; in *Priapulidae* by a layer of longitudinal fibres alone; in *Echiuridae* by a layer of longitudinal and of circular (Greeff) or oblique (Spengel) fibres. The muscles of the different layers

been said to possess a posterior terminal pore opening into the coelome. There is a depression, but no pore; and the larva, as figured by Hatschek, has a bundle of sensory hairs at the spot in question.

may be disposed in parallel bands, sometimes connected by anastomotic bundles, e.g. in *Sipunculus*, some species of *Phascolosoma*; or one layer only may be so disposed, e.g. the circular muscles of *Priapululus* and *Halicryptus*; or all the layers may be continuous, e.g. in *Echiurus*. But species in the same genus may vary in this respect. The musculature is covered internally like all the organs of the body by a peritoneal epithelium which may be uniformly ciliated (*Sipunculus*, *Phascolosoma*).

The nervous system consists of a median ventral cord, and of a pharyngeal ring, which extends in the *Echiuridae* into the proboscis, coursing along its edges. In *Priapululus* and *Halicryptus* the ring and cord are in continuity with the hypodermis, in which the nerves also run; in other cases they lose this connection, and lie internally to the muscular layers. The cord is never ganglionated, and it is only in the *Sipunculidae* that a bilobed supra-oesophageal swelling is developed. In *Echiurus* and *Thalassema* it is traversed by a fine canal. The ganglion cells are evenly distributed either as two lateral bands, or more rarely as a single ventral band. The nerves originate as a rule from the cord opposite, or nearly opposite to one another, and in *Sipunculus nudus*, *Echiurus Pallasii*, *Thalassema erythrogrammon*, they unite dorsally, thus forming complete rings. The cord may bifurcate posteriorly, as in *Sipunculus nudus*<sup>1</sup>. A plexus of nerve-fibres has been observed in the same animal in the cutis, with terminal branches in connection with small groups of elongated hypodermis cells. A fine pore may perforate the cuticle above these groups. The integumental spines of the *Priapulidae* are cuticular elevations lined with elongated hypodermis cells, and in *Priapululus caudatus*, according to Scharff, some or all of the cells end in projecting sensory hairs<sup>2</sup>. The papillae of *Echiuridae* consist of thickenings of the cutis, into which a nerve penetrates and branches; its branches have interpolated ganglion cells, and end in the ordinary hypodermis cells (Greeff). Two or more pigment specks, representing eyes, lie on the supra-oesophageal ganglion in *Phascolosoma*. Eye-specks are also present in *Phymosoma*.

The mouth is anterior and terminal in the *Sipunculidae* and *Priapulidae*, at the base of the prostomium and surrounded by it in *Echiuridae*. The anus is dorsal, and more or less anterior in the *Sipunculidae*, terminal

<sup>1</sup> There is a space between the two sheaths of the ventral nerve-cord in *Sipunculus nudus*, filled in prepared specimens by a coagulum with nuclei and pigment clumps in suspension, but no vascular elements. Hence it is *not* a blood-vessel (Andreae). A vessel or blood-space is said by Greeff to inclose the nerve-cord of *Echiurus*, but Spengel, who investigated the same animal, did not find anything of the kind, and professes himself unable to explain Greeff's figures. In addition to the facts given in the text, Spengel states that in *Echiurus* transverse nerves pass across the proboscis from one side of the nerve-ring to the other, and that in the young animal the cord has a ganglionated aspect, but the interganglionic gaps are irregular. See p. 624 *post*.

<sup>2</sup> The wart-like papillae which cover the dorsal aspect at the posterior extremity of the body in *Priapululus caudatus* are glandular, according to both Apel and Scharff.



in other Gephyrea. The digestive tract itself takes a straight course from mouth to anus in *Priapululus* (except in *P. glandifer*) and *Halicryptus*; it is convoluted in *Echiuridae*, principally in side to side loops, whereas in the *Sipunculidae* it is coiled in a close dextral spiral, except in certain tubicolous forms, in which the coils are loose. The axis of the spiral is generally occupied by a muscle, usually attached in front close to the anus, and frequently behind as well, at the apex of the body. From this muscle fibres pass to the walls of the tract. Muscle-fibres, especially well-developed in *Echiuridae*, also attach the tract to the body-walls. The pharynx and the rectum are always provided in *Gephyrea achaeta* with specially developed bands, which attain great prominence as the retractor muscles in connection with the former. The retractors in question are derived from the longitudinal muscle-layer of the body; are short in the *Priapulidae*, of considerable but variable length in the *Sipunculidae*. In the last-named there is either a single ventral retractor, or two ventral, or two ventral and two dorsal. The tract itself is divisible in *Sipunculidae* into a muscular pharynx, intestine, and extremely short rectum. In *Echiuridae* it consists of an anterior ('buccal') region, which ends at the spot where the dorsal blood-vessel forms a peri-intestinal ring, of a middle region of great extent, in which the longitudinal muscle-layer is internal to the circular instead of the reverse as is usual, and of a short rectum. In the Echiurids, *Bonellia*, *Thalassema*, *Echiurus*, and possibly *Hamingia*, a siphon, or collateral intestine, comparable to the structure seen in some Echinoids, extends for the greater part of the length of the middle region (*supra*) on its ventral aspect. A band of longitudinal muscle-fibres underlies the siphon. The inner aspect of the pharynx is armed in *Priapululus* and *Halicryptus* with numerous teeth, analogous in structure with the spines of the body; the cuticula lining it is fairly thick, as is that of the rectum, and both alike are shed when the outer cuticle is cast off. The tract is ciliated throughout in *Echiuridae*, and there is a ventral furrow with especially long cilia in its middle region. So, too, in *Sipunculus nudus*, according to Keferstein. A delicate cuticle lines the tract in *Priapulidae*. *Thalassema* has a ventral caecum at the end of the middle region, which has been found filled with a gelatinous substance in *Th. erythrogrammon*. The rectum in the same genus is dilated terminally, and a layer of peculiar cells underlies its peritoneal epithelium. A caecum is sometimes present at the commencement of the rectum in Sipunculids, and tufts of branched caeca close to the anus. But in *Echiuridae* with some exceptions (*Saccosoma*, *Epithetosoma*), there is always a pair of anal caeca, the branchiae of Greeff, or posterior nephridia appended to the rectum and opening into it. They have muscular walls, and communicate with the coelome by means of ciliated funnels with short stalks. In *Bonellia viridis* and *Hamingia*, they bear a number of branched stems, each branch ending in a funnel. The

branched stems are replaced by simple stems in *B. minor*. Scattered ciliated cells occur in the epithelium of the caeca in *Echiurus Pallasii* and *Thallasema erythrogrammon*. It is possible that these structures serve two functions, (1) the removal of an excess of water from the coelome, (2) the formation of excretory products by the epithelium of the caeca themselves<sup>1</sup>. Large granules are found in their lining cells in *B. minor*, and coloured drops or granules are massed in the groups of larger cells observable in *Echiurus Pallasii*.

A vascular system is absent in *Priapulidae* and a few genera of *Sipunculidae* and *Echiuridae*. When present it is a closed system. In the *Sipunculidae* it usually consists of a dorsal contractile vessel closely applied to the fore-part of the digestive tract; but in some species of *Sipunculus*, e. g. *S. nudus*, a second similar vessel is applied to the ventral aspect of the same region. There is in many Sipunculids a peripharyngeal vascular ring or plexus. Vessels from the ring or plexus enter the tentacles, but in the lobed tentacles of *Sipunculus* they are replaced by a plexus. Branches have also been observed passing from the dorsal vessel to the rectum in some cases. Caeca, simple or slightly branched, may be appended to the dorsal vessel in a single or double row. Ciliated cells are found here and there in the epithelial lining of the vessels, or a band of ciliated cells in the dorsal vessel. In the *Echiuridae*, starting from a peri-intestinal ring or sinus (*supra*, p. 619), a vessel courses along the dorsal surface of the oesophagus and pharynx to the apex of the prostomial lobe. Here it bifurcates; a branch lies on either side of the prostomium, surrounds the pharynx, and then the two fuse and form a ventral supra-neural vessel which ends blindly at the posterior end of the nerve-cord. A neuro-intestinal vessel connects the ventral vessel to the peri-intestinal ring. The origin of the dorsal vessel is sometimes dilated, and its walls muscular. Contractions were observed in it by Greeff<sup>2</sup>.

The coelomic fluid is sometimes colourless, but milky, as in *Priapululus* and *Halicryptus*, sometimes coloured pink or red. Amoeboid corpuscles are always to be found in it, and appear to be the sole kind possessed by *Echiurus*. Spherical or biconcave cells coloured, or, as in *Priapululus* and *Halicryptus*, colourless, may be present as well. There appear to be no less than three blood pigments occurring in Gephyrea; a brownish pig-

<sup>1</sup> The cilia of the funnels are said to cause a current solely outwards from the coelome in *Bonellia viridis* (de Lacaze Duthiers). The asserted absence of funnels in some instances is probably due to the examination of specimens preserved in spirit without previous preparation. The anal caeca in question probably acquire their connection with the rectum. See account of male *Bonellia* and the development of *Echiurus*, p. 623, and p. 624. In this case they are to be regarded as homologous serially with the anterior nephridia described further on.

<sup>2</sup> Daniëlsen and Koren ascribe to *Hamingia arctica* a vascular system differing in some respects from the account given in the text; but Horst finds in *H. glacialis* (probably the same species) a system wholly conformable to it.

ment in small clumps in the amoeboid cells of *Echiurus*, and the spherical corpuscles of *Thalassema Neptuni*; haemoglobin in the spherical corpuscles of the last named, and in *Hamingia arctica*; a pink or red pigment not yielding any absorption-bands, but the colour of which is intensified by contact with air or oxygen in the biconcave discs of *Sipunculus nudus*; it is termed haemerythrin by Krukenberg. The pink pigment contained in similar corpuscles in other species of *Sipunculus*, in some species of *Phascolosoma*, and of *Bonellia minor*, has not been investigated spectroscopically<sup>1</sup>. The coelomic fluid of *Sipunculus* and *Phascolosoma* also contains remarkable structures moving freely in it—the ‘Töpfchen’—which are shaped like a bell, with a ciliated mouth. They appear to be coelomic cells detached from some portion of the alimentary canal, &c. The liquid in the blood-vessels is corpusculated, and the corpuscles resemble those of the coelome in *Sipunculus nudus* and *Echiurus*. The ‘Töpfchen’ are said to occur in it in the former (Brandt). In *Thalassema Neptuni*, however, it is colourless, and does not contain ‘corpuscles similar to those of the coelome’ (Lankester).

With the exception of the *Priapulidae* all Gephyreans possess organs known as genital or uterine pouches, segmental organs, or anterior nephridia, which open outwards anteriorly on the ventral surface. The genus *Bonellia* possesses but a single organ, as is sometimes the case in *Hamingia arctica*; so too *Saccosoma*, *Epithetosoma*, and tubicolous *Sipunculidae*<sup>2</sup>. Other *Sipunculidae*, and *H. arctica* as a rule, possess a single pair, *Echiurus* two, the various species of *Thalassema* one, two, three, or four pairs, one behind the other. The external apertures of these organs lie one on either side of the ventral nerve-cord, and behind the ventral hooks in Echiurids; but when three pairs are present, the first usually opens in front of and a little laterally to those structures (Lampert). The walls of the organs are muscular, and except at the period of sexual activity, when they are much distended with sperm or ova, they are small in size. Internal openings into the coelome have not been found in all Sipunculids. In others, and in Echiurids, they are present. In *Sipunculidae* they may be

<sup>1</sup> The brown pigment of *Echiurus* is probably identical with that occurring in other parts of the body, e.g. in the walls of the anal caeca. The pink pigment of *Sipunculus nudus* tinges, according to Ray Lankester, the sheath of the nerve-cord and a band underlying the alimentary canal. The same authority states that in *Th. Neptuni* haemoglobin is present in the muscles of the middle region of the body, in the thick coelomic epithelium covering the mesenterial bands of the alimentary canal and of the anterior nephridia. Orange-red granules are plentiful in the same animal in the coelomic epithelium of the vessels, of the sheath of the nerve-cord, of the median ventral line of the intestine, of the four anterior nephridia, and the anal caeca. So too in *Echiurus Pallasii*. Sluiter states that the alcohol in which a specimen of *Th. erythrogrammon* was preserved gave the spectrum of haematin, indicating the existence of haemoglobin in the living animal.

<sup>2</sup> De Lacaze Duthiers found a pair of organs in a single specimen of *B. viridis*. See p. 74, A. Sc. N. (4), x. 1858. The single organ is usually that of the right side in *B. viridis*, of the left in *B. minor*.

situated on the wall of the sac, close to the outer opening (*Aspidosiphon fuscus*, several species of *Sipunculus* including *S. nudus*, *Phascolion Strombi*); or near its apex (*Sipunculus edulis*, *Phascolosoma nigritorquatus*, *Ph. falcidentatus*), and are either funnel-shaped or bilobed. They are always anterior, near the external aperture in *Echiuridae*, and are either simple funnels (*Bonellia*, *Hamingia*?), bilabiate funnels (*Echiurus Pallasii*, *Thalassema Neptuni*, &c.), or they are drawn out on each side into a long gutter, which is twisted into a spiral (*Echiurus uncinatus*, many species of *Thalassema*). The funnels are ciliated in the *Echiuridae*, and there can be little doubt that such is the case in *Sipunculidae* also. The homology of these organs with nephridia is undoubted, but it is by no means a settled fact that they are excretory in function.

The sexes are said to be separate, and are undoubtedly so in most cases, the possible exceptions being among *Sipunculidae*<sup>1</sup>. The genital organs of the *Priapulidae* consist of two ducts, one right, the other left, opening posteriorly near the anus, and attached by a ventral mesentery to the body-walls. The lobulated genital gland lies on either side this mesentery in the female, but nearly surrounds the duct in the male. The main duct gives off lateral branches which divide repeatedly, and in the female anastomose. The ova take their origin from isolated cells of the epithelium, which grow at the cost of their neighbours; the sperm from the epithelium at the base of short caeca appended to the canals. In all other Gephyreans the genital products are found floating in the coelome. In the *Sipunculidae* little is really ascertained as to the genital glands. In *Sipunculus edulis* and *Phascolosoma nigritorquatus* the ovaries are small sausage-shaped bodies, placed in a row between the dorsal retractor muscles of the pharynx, attached to them and to the alimentary canal. They consist of fibrous sacs, which are eventually burst by the growing cells they contain. The testes are not known. In *Aspidosiphon fuscus* both ovaries and testes have the form of mesenterial folds attached behind the ventral retractors of the pharynx on either side the nerve cord, between two bundles of circular muscles. The ova are detached, and ripen in the coelome; the sperm is formed *in situ*, and then detached. In *Phascolosoma falcidentatus* the ovaries are similar to those of *Aspidosiphon*, similarly placed, but attached between the longitudinal muscles. Its testes are not known. As a rule, the ova and the cells from which the sperm originates, are set free at an early period into the coelome, hence 'swimming ovaries

<sup>1</sup> Sperm and ova may alike be found floating in the coelome of *Sipunculus nudus*, but according to Brandt, most individuals of this species contain either ova or sperm. The simultaneous presence of both products he explains as possibly due to an abnormality, unless it be supposed that the animal is hermaphrodite, and that the two products ripen as a rule at different times, but occasionally at the same time. A Gregarine, *Monocystis Sipunculi*, is not uncommon in the coelome of the species in question. A Gregarine occurs also in *Echiurus Pallasii* and *Thalassema Neptuni*.

and testes.' In the *Echiuridae* the glands are formed at the posterior end of the ventral vessel, and from the coelomic cells which constitute its walls. In *Thalassema* and *Echiurus* the young ova and corresponding male cells are simply enlarged superficial coelomic cells, which are set free and develop into ova and sperm. In *Bonellia* each cell-mass thus liberated, consists of an envelope of delicate coelomic epithelium inclosing a mass of cells, one of which is larger and becomes ovum, whilst the rest supply it with secondary yolk. The Gephyrean egg is inclosed in a membrane which is generally striated.

The dimorphic male of *Bonellia viridis* has the following structure. It is a Planarian-like organism, 1-5 mm. long, pointed at each end. The hypodermis consists of a layer of ciliated cells with a delicate cuticle. The muscular layers of the body-wall are an outer circular, a spiral and an internal longitudinal layer (Spengel), with a mass of vacuolated cells lodged in a cell reticulum, and covered internally by flat coelomic epithelium, which is reflected over the intestine and vesicula seminalis. Dorso-ventral bundles of fibres placed at regular intervals and projecting into the coelome, give an appearance of septa. The coelome does not extend up to each end of the body. The nervous system consists of a peri-intestinal ring and ventral cord. The intestine ends blindly in front and behind, and is attached at both ends by muscle-fibres to the body-walls. Its own walls consist of a single layer of cells; its contents are fatty. Two simple excretory organs, the homologues of the anal caeca of the female, are situated posteriorly, one on either side, in front of the end of the intestine. Each of them consists of a tube with sparsely ciliated walls hanging in the coelome, into which it opens by a ciliated funnel. Its external pore is minute. The spermatozoa are formed from peritoneal cells, and are differentiated from an outer layer of cells surrounding a central cell, the latter undergoing atrophy. The vesicula seminalis opens at the anterior apex of the body. Its duct is narrow, and passes inwards through the nerve-ring, when it enlarges into an elongated sac. The sac opens into the coelome by a ciliated funnel, which Spengel believes communicates with the sac itself, not terminally but laterally. The male larva clings to the under side of the prostomium of the female, and migrates thence into the mouth, where it undergoes its final changes. It then wanders into the outer chamber of the uterine pouch, which in *B. minor* at least is cut off by a fold from the inner portion where the ova accumulate. The males of *B. viridis*, and of *Hamingia*, are found in the same place. They are furnished with a pair of chitinoid hooks, placed anteriorly and ventrally<sup>1</sup>.

The larva of *Echiurus* is a typical Trochosphere. The most important features

<sup>1</sup> Spengel's male *Bonellia* with a pair of ventral hooks probably belonged to *B. minor*. Cf. p. 411 of his paper, cited below.

of its development are the following. There is a large prostomium, which becomes the 'proboscis' of the adult. The mouth is ventral, the anus posterior and terminal. There is a double praeoral ring of cilia, a postoral ring, and between the two a ciliated adoral zone, which is continued as a ciliated ventral furrow from mouth to anus. There is also praeanal ciliated ring. The mesoderm is segmented. Fifteen somites with a terminal piece are indicated by septa internally, by ciliated rings externally. These rings are replaced in the young *Echiurus* by zones of spinous tubercles, and in somites fourteen and fifteen by the circles of setae. Four zones of tubercles are formed anteriorly, in addition to the first of the series referred to. The nervous system is developed (1) from an ectodermal thickening at the apex of the prostomium, from which commissures grow down to become connected with (2) the ventral cord. The latter arises at first as segmentally-arranged thickenings of the epiblast, which subsequently fuse. The fibres of the cord are derived from the cells of the ventral furrow, which is perhaps invaginated. There is a pair of provisional cephalic nephridia, ciliated, branched, and the terminations of the branches ending in aborted flame-cells. The anal sacs originate from the mesoblast as two tubes, opening by an internal funnel and an external pore, situated close to the anus. Their communication with the rectum in the adult is therefore secondary.

*Thalassema mellita* (Conn) has an invaginate gastrula. A ciliated band appears round the blastopore, and is replaced in the Trochosphere by a praeoral ring or row of long powerful cilia. A postoral and praeanal band are subsequently formed, and a ventral ciliated furrow. A group of stiff cilia (? sense hairs) mark the apex of the prostomium. The alimentary canal is formed entirely from the invaginated archenteron. The blastopore persists as the mouth. The mesoderm forms two ventral bands (as in *Echiurus* and Chaetopoda), but stellate mesodermal cells are also derived from the hypoblast, as in Holothurians, &c.

The larva of *Bonellia viridis* possesses two rings of cilia: it also becomes ciliated all over. The mouth probably appears *behind* the first ring, but is formed after its disappearance. The ventral cord shows no ganglionic rudiments. The anal pouches are said to develop from the rectum (Spengel).

*Sipunculus nudus* has an invaginate gastrula. During development the epiblast forms an *amnion*, which does not cover the apex of the prostomium, indicated by a tuft of long cilia. There are no traces of somites. A postoral band of cilia is present, and the anterior nephridia (uterine pouches) appear early. The anus and proctodaeum are dorsal and at first nearly posterior, but the real posterior apex of the body is denoted by a group of sense cells with hairs. The ventral cord is an epiblastic thickening. There is a glandular appendage opening at the posterior margin of the mouth, and a pharyngeal apparatus attached to the ventral wall of the oesophagus. Both structures are lost during the growth of the larva. Ciliated organs, like the Töpfchen, but not free, appear very early in the parietal coelomic epithelium of the body. During the growth of the larva, the prostomial process becomes shorter and shorter, and the anus more and more dorsal. The tentacles appear on either side of the mouth, and have no connection with the postoral ring of cilia.

In *Phascolosoma elongatum* there is an invaginate gastrula. The apex of the prostomium bears sensory cells with hairs. A postoral ring of long cilia appears,

and later on a second ring of finer cilia. The body has three pairs of setae, of which the posterior appears first, then the anterior, and lastly the middle. The first circle of hooks on the 'introvert' appears between the two bands of cilia, just behind the mouth. The zona radiata of the egg becomes the larval cuticle.

The development of *Sipunculus* is, according to Hatschek, a remarkably abbreviated one. That of *Echiurus* is Chaetopodan, and shows very distinct traces of a metameric condition, but the somites disappear very early. Hatschek therefore proposes to separate the *Echiuridae* from the other Gephyrea. It is, however, possible that if the development of *Sipunculus* is abbreviated, it is so to a much greater degree than is that of *Echiurus* when compared with a typical Chaetopodan. In other words, it has lost even traces of what is most clearly preserved in the life-history of *Echiurus*. The existence of an embryonic membrane shows great specialisation. It is therefore, perhaps, advisable to retain all the forms provisionally in the same group until something is known as to the ontogeny of other Sipunculids. Moreover, it is by no means certain that the *Sternaspidae*, which are variously regarded as belonging to the Gephyrea or Chaetopoda, may not prove to be a connecting link between the two classes.

*Sternaspis scutata* has been investigated by Vejdovsky and Rietsch. Its chief features are the following. The body is elongated, its fore-part retractile by special muscles. It is segmented, and divisible into an anterior region with seven rings, and a posterior with eight or more rings. It is covered by a cuticle and delicate cirri. All the somites carry setae except 5, 6, 7, but those of somites 8-15 never pierce the cuticle. The cuticle is thickened posteriorly and ventrally into a bilobed shield, the edges of which are set round with bundles of setae. There is a circular and longitudinal muscle-layer, the latter internal. The nervous system consists of a pair of supra-oesophageal ganglia, fibrous commissures, and a ventral cord, which is not segmented. The digestive tract has a pharynx, oesophagus, crop, an intestine disposed in longitudinal coils, and a rectum. Mouth and anus are terminal. A dorsal blood-vessel corresponds to the fore-part of the digestive tract; it forms a peripharyngeal ring and a ventral vessel, from which numerous lateral branches pass off. The capillary system is well developed; the blood, a red plasma. Excretory organs are present as two brown lobed sacs attached to the skin between somites 6-7, but devoid of external aperture (?). Two posterior and dorsal bundles of long contractile cirri, each traversed by a looped vessel connected both to the dorsal and ventral vessels, constitute special respiratory organs. The sexes are separate. The genital ducts open between somites 8-9 by long tubes, and receive the sexual products direct from the glands. The ova and sperm originate from cells covering the branches of vascular capillaries. The ovum undergoes complete segmentation; the gastrula is epibolic. The larva is ciliated, with an anterior tuft of long cilia, and a large prostomium. Sluiter has investigated an Indian species (*St. spinosa*). He found a bifid prostomium, which the animals throw off in about a minute; the dorsal vessel bifurcated, and entering the prostomium; the two returning vessels united round the pharynx to form a ventral vessel. There were minute external apertures to the excretory organs.

Vejdovsky, Dk. Akad. Wien, xliii. 1882; Rietsch, A. Sc. N. (6), xiii. 1882; Sluiter, Tijdsch. für Nederl. Indie, xli. 1882 (cf. Naples Zool. Jahresbericht, 'Vermes,' p. 287).

The *Gephyrea* are classified as follows—

1. *Gephyrea Achaeta*: unisegmental (?); fore-part of the body invaginable by means of special retractor muscles; no setae, at least in the adult; mouth anterior and terminal.

(a) *Sipunculidae*: tentacles usually present at the oral extremity. Nervous system with supra-oesophageal swellings. Alimentary canal spirally coiled as a rule, rarely disposed in loops; anus dorsal and anterior. Vascular system rarely absent; closed; enters tentacles; blood moved by cilia as well as by one or two contractile vessels. An anterior pair of nephridial sacs, which serve as genital ducts. Genital products set free into coelome, where they mature. Sexes separate (? always). Ova with a zona radiata. Prostomium of larva aborted; larval setae in *Phascolosoma*. Free, or living in shells or tubes, e.g. *Phascolosoma*, *Sipunculus*, &c.

(b) *Priapulidae*: introvert short. Nervous system in continuity with hypodermis. Pharynx armed with chitinous teeth. Alimentary canal either straight or slightly looped; anus terminal. No vascular system nor anterior nephridia. Sexes separate; genital apertures posterior on either side of the anus; ducts continuous with the glands. *Priapulus* with ventral caudal appendage, single or double, beset with papillae; *Halicryptus*.

2. *Gephyrea Chaetifera*: multisegmental, but segmentation lost in adult. A long extensile prostomium, with the mouth at its base. A pair of ventral anterior setae. Nervous and vascular systems extend into the prostomium. Alimentary canal convoluted; anus terminal; a pair of posterior nephridia open into the rectum. One to four pairs of anterior nephridia present, and act as genital ducts. Sexes separate; genital products set free into the coelome. A minute Planarian-like male in the genera *Bonellia* and *Hamingia*. Live in mud or sand, or holes in rock, or shells.

*Echiuridae*: *Echiurus*, *Thalassema*, *Bonellia* with bifid prostomium; *Hamingia*.

*Gephyrea in general*, Danielssen and Koren, Den Norske Nordhavs Expedition, iii. 1881 (cf. A. N. H. (5), vi. 1881, p. 462); *Iid. Fauna Littoralis Norwegiae*, pt. 3, 1877.

*Sipunculidae*, Die Sipunculiden, De Mace, Bülow, and Selenka, 1884 (with lit.) in Semper's Reisen im Archipel der Philippinen, Part II, iv. pt. 1. *Golfingia*, Ray Lankester, Tr. L. S. (2), ii. pt. 16, 1884 (key to genera). *Sipunculus nudus*, Andreae, Z. W. Z. xxxvi. 1882 (with lit.); Keferstein, Z. W. Z. xv. 1865; *development of*, Hatschek, Arb. Zool. Inst. Wien, v. 1884. *Phascolosoma*, Keferstein, Z. W. Z. xii. 1862-63, p. 35; *development of*, Selenka, Z. W. Z. xxv. 1875. *Aspidosiphon*, &c., Sluiter, Beiträge, &c., Nat. Tijdschrift. Nederl. Indie, 43, 1883. *Segmental and sex organs*, Sluiter, Tijdschrift Nederl. Dierk. Vereen. vi. 1882-85. *Blood corpuscles and 'Töpfchen'*, Brandt, Mémoires de l'Acad. Imp. St. Pétersburgh (7), xvi. 1871. *Blood-colouring matter*, Ray Lankester, P. R. S. xxi. 1873, p. 80; Krukenberg, Vergleich. Physiol. Studien, i. pt. 3, 1880, p. 82.

*Priapulidae*, Apel, Z. W. Z. xlii. 1885; *skin and nervous system*, Scharff, Q. J. M. xxv. 1885; Ehlers, Z. W. Z. xi. 1861-62; Horst, Arch. f. Nederl. Zoologie, Suppl. i. 1881.

*Echiuridae*: *monograph*, Rietsch, Recueil Zool. Suisse, iii. 1886; Greeff, Nova Acta, 41, 1879. *Echiurus*, Spengel, Z. W. Z. xxxiv. 1880; *development of*, Hatschek, Arb. Zool. Inst. Wien, iii. 1881. *Thalassema*, Ray Lankester, Z. A. iv. 1881;



Lampert, Z. W. Z. xxxix. 1883; Sluiter, Tijdschrift Nederl. Indie, 43, 1883; *development of*, Conn, Studies Biol. Lab. Johns Hopkins Univ. iii. pt. 7, 1886. *Bonellia*, Rietsch (*supra*); de Lacaze Duthiers, A. Sc. N. (4), x. 1858; *development of, and male*, Spengel, Mitth. Zool. Stat. Naples, i. 1879; *figure of male*, Selenka, 'Gephyrea,' Challenger Reports, xiii. 1885, Pl. ii., figs. 7-10. *Bonellein*, Krukenberg, Vergleich. Physiol. Studien (2), ii. 1882. *Hamingia*, Ray Lankester, A. N. H. (5), xi. 1883.

## CLASS HIRUDINEA.

*(Discophora).*

*Multisegmental Vermes, in which the original somites are masked by the development of secondary annuli. The posterior somites are always fused to form a terminal sucker. The original coelome is obliterated for the most part by a growth of connective tissue, and is represented by a series of sinuses and channels with which the true blood-system communicates. The mouth is anterior and ventral, and the anterior extremity of the body in which it lies is, often marked off as a more or less efficient sucker. The anus is dorsal and anterior to the posterior sucker. Hermaphrodite. The genital openings are median and ventral; the male in front of the female. For the most part aquatic, parasitic, and blood-sucking.*

The ventral surface of the body is flattened, the dorsal convex. The animal creeps by alternately attaching and detaching the anterior and posterior extremities or suckers, and swims by undulations of the body. The body is segmented. The *Hirudinidae* possess twenty-six somites, and these somites in them as well as in all other Leeches are annulated. A variable number of annuli, or rings, belong to a somite, e.g. in *Hirudo* five, *Pontobdella* four, *Branchellion* three. In the cephalic and posterior regions of the body, the number in the somite is less, and may most anteriorly be reduced to a single ring. A first annulus in the middle region of the body contains a nerve ganglion and a nephridial funnel, and it may be marked externally by peculiar arrangements of colour, of integumental papillae, or by the presence of segmental sensory papillae. The anterior extremity of the body is more or less expanded, and its annulation lost in the Leeches with a pharyngeal proboscis (*Rhynchobdellidae*), but whether expanded or not, it always acts as a sucker. The two or three somites which contain the genital openings constitute the clitellum, and at the reproductive season secrete on their surface the cocoon in which the ova are contained. These genital somites are the ninth, tenth, and eleventh in *Hirudo* (Whitman); the sixth and seventh post-oral of *Pontobdella* (A. G. Bourne). The marine *Branchellion Torpedinis* has a pair of lateral foliaceous expansions to each annulus of the middle and posterior regions of

the body. Similar folds are found in *Lophobdella* from the mouth of the Crocodile, &c. *Acanthobdella* has setae.

A delicate elastic cuticle, which is moulted and renewed at intervals, covers the body. It is pierced by the orifices of the cutaneous glands, nephridia, &c. The epidermis consists of a single layer of cells, between which there penetrate in all *Gnathobdellidae* and some *Rhynchobdellidae* processes of pigmented connective tissue cells together with blood capillaries. There are numerous integumental unicellular glands of various kinds; mucous glands which either retain their position in the epidermis, or when large intrude into the dermis; prostomial glands in *Gnathobdellidae*, opening round the buccal cavity; salivary glands opening into the pharynx; and clitellar glands opening on the clitellar somites; all deeply placed in the dermis and provided with long ductules. The body-walls are composed of an external circular and an internal longitudinal layer of muscles, with an interposed diagonal layer in some instances. These layers are imbedded in a plentiful connective tissue, which forms also a superficial sub-epidermic coat, and consists of a variably developed jelly-like matrix containing cells of various kinds, among them branched connective tissue and pigment cells (see p. 215). Dorso-ventral and radial muscle bundles take the place of the septa of Chaetopoda.

The nervous system consists of a paired supra-oesophageal ganglion, connected by a very narrow oesophageal commissural ring with the first ganglion of the ventral chain, which consists in most Leeches of twenty-three ganglia, united by longitudinal commissures. The first or sub-oesophageal and the terminal ganglion are formed by the fusion of several embryonic ganglia (p. 219-20). The ganglionic cells have a tendency to form projecting masses on the surface of the ganglia. In *Hirudo* there are three minute ganglia connected one with each of the three jaws. A sympathetic nerve is in relation with the stomach. A variable number of eyes are present on the anterior cephalic annuli and of *Piscicola* on the posterior sucker. They are entirely absent in some terrestrial forms (*Typhlobdella*, *Cylicobdella*, *Macrobdella*). Eye-like organs, but devoid of pigment and known as 'segmental papillae,' are found on the first annulus of each somite, and sometimes on the posterior sucker in *Gnathobdellidae*. They occur in *Clepsine*, and it is possible that they exist also in other *Rhynchobdellidae*. Sense organs or goblet-shaped bodies, with a structure closely resembling eyes, are scattered in large numbers over the cephalic annuli of some Leeches, and on the lips<sup>1</sup>.

<sup>1</sup> According to Whitman (Leeches of Japan, Q. J. M. xxvi. pp. 396-410), the goblet organs of the lip consist of a clump of elongated hypodermis cells, and of a nerve distributed to the base of the clump in which there are what appear to be ganglion cells. Clear, nucleated, and vacuolated cells are found scattered along the nerves going to these organs. The segmental organs and the scattered sense-bulbs of the head, on the contrary, have a number of vacuolated cells grouped round the clump

The alimentary canal consists of a pharynx, oesophagus, proventriculus, digestive stomach, intestine, and rectum. The pharynx has muscular walls, with the muscles arranged as radiating and circular fibres, very largely developed in the *Rhynchobdellidae*, where it and the part of the body which lodges it, constitute the retractile proboscis characteristic of the group. In the typical *Gnathobdellidae* the radiating muscles of the pharynx form three prominent ridges which have their cuticle produced into the three well-known toothed jaws. The Australian Land Leeches (*Geobdella*, Whitman) possess only the two lateral jaws. In other cases, e.g. *Trocheta*, the jaws are quite rudimentary, or even, as in *Leptostoma edentulum*, lost altogether<sup>1</sup>. There is an oesophageal tube, short in *Hirudo*, longer in most other Leeches, thrown into folds in *Clepsine* when the proboscis is retracted. The proventriculus is a feebly muscular tube with lateral paired caeca in most *Hirudinea*, the number of pairs not being the same in all instances<sup>2</sup>. The last pair bends backwards parallel to the axis of the body. *Aulostoma* and one or two others possess this last pair alone. *Pontobdella* has a single median ventral caecum underlying the stomach, whilst *Trocheta* and *Nepheleis* are devoid of caeca altogether. The stomach is a relatively short tube: its calibre varies and is sometimes very small. In *Clepsine* it has four pairs of lateral caeca. It is followed by a short intestine and a rectum which ends in an anus placed dorsally and in front of the sucker, except in *Acanthobdella*, where it lies in the sucker itself.

The circulatory system of the *Rhynchobdellidae* consists of four longitudinal vessels with muscular walls, viz. a dorsal, double in *Branchellion*, a ventral and two lateral, one on either side. In *Branchellion* a branch from each lateral vessel passes outwards into the first pair of branchial leaflets, and into every third succeeding pair. It ends by an open mouth in a dilatation which communicates with the lateral coelomic sinus. Similar but rudimentary dilatations are present in *Pontobdella*, *Piscicola*, and *Clepsine*. In the *Gnathobdellidae* the pair of lateral vessels are alone present. The vascular system is connected with the coelome in the *Rhynchobdellidae* probably only in the branchial dilatations or their rudiments; in the *Gnathobdellidae* with the spaces of the botryoidal tissue (p. 218), and through them with the remnants of the coelome. The coelome is much restricted by a

of elongated hypodermis cells. In the eyes the vacuolated cells become very numerous; they are surrounded externally by a coat of pigment cells, and the axis of the eye is occupied by what appears to be a string of hypodermis cells detached from the cap of short hypodermis cells which covers the centre of the organ superficially. In *Clepsine*, according to the same authority, there are six dorsal and four ventral rows of segmental papillae. The term goblet-organ is a misnomer. The centre of all three sets of organs projects naturally, but it may be and is depressed by their retraction. The eyes and segmental organs are, so far as can be judged, visual organs in the sense of appreciating the difference between light and shade, and they are perhaps also tactile. The goblet-organs of the lips are probably both gustatory and tactile. See p. 215, *ante*.

<sup>1</sup> See Whitman, *op. cit.* p. 388.

<sup>2</sup> The caeca extend into the branchial folds of *Lophobdella*.

growth of connective tissue, which splits it up into sinuses and channels, a process termed diacoelosis. This tissue may in its turn undergo metacoelosis, i. e. become secondarily hollowed out, a process most marked in *Nepheleis* and *Trocheta* (Bourne). There are four main sinuses in the *Rhynchobdellidae*, a dorsal, a ventral which always lodges the nerve-cord, and two lateral. The dorsal and ventral sinuses are alone present in *Gnathobdellidae*, and the former is sometimes absent (*Nepheleis*, *Trocheta*). Coelomic epithelium is found lining the sinuses in the former group, but not in the latter. There are other remnants of the coelome round the generative organs, &c., but different Leeches vary much in these points. The blood is colourless in *Rhynchobdellidae*, but in the *Gnathobdellidae* the plasma is red with haemoglobin. There are colourless amoeboid corpuscles, and in some *Gnathobdellidae* at least nuclei set free from the excavated connective tissue cells.

The excretory system consists in *Pontobdella* of a network of tubules lying within the muscular layers, continuous from side to side of the body, and provided with ten pairs of segmentally arranged nephridial funnels and as many external openings. There appears to be a similar network in *Branchellion* and *Piscicola*. The latter has also ten pairs of external apertures. In *Clepsine* and other Hirudinea, so far as is known, the nephridia are paired organs, independent of one another, and complicated in structure. In *Hirudo* and its immediate allies, the nephridial duct terminates in a contractile vesicle which opens externally. The ciliated nephridial funnel is rudimentary in *Hirudo*, *Haemopis*, *Haemadipsa*, or occasionally occluded as in *Pontobdella*. It lies in a blood, i. e. coelomic sinus; the ventral sinus in *Clepsine*; a dorso-ventral sinus in *Pontobdella*; a small isolated remnant of a sinus in *Hirudo*, &c.; or in a metacoelome excavated in botryoidal tissue, as in *Nepheleis* and *Trocheta*. The ductules in the secreting part of the gland ramify in the gland-cells. The external nephridial aperture is ventral or marginal in *Haemadipsa japonica*, and on the first annulus of a somite in *Pontobdella*, on the last in *Hirudo*<sup>1</sup>.

The Hirudinea are hermaphrodite. The apertures of the male and female organs lie near one another in the median ventral line, the male in front of the female. The testes vary in number from five to twelve pairs segmentally arranged, or a much larger number not arranged segmentally as in *Nepheleis*, and connected, each testis by a separate duct, to a common

<sup>1</sup> Whilst the Leech, and more especially the Land Leech of Japan, is engaged in sucking, a clear fluid covers it and may fall in drops. It is derived chiefly if not entirely from the nephridial vesicles, and may be seen to exude from their external pores. The organs in question may therefore serve as a storehouse of liquid to moisten the skin. They are peculiarly large in the Land Leech, and the three pairs opening within the limits of the clitellum have a thick cubical epithelium disposed in folds. It is possible that they furnish some of the liquid contents of the cocoon. The epithelium of the vesicles in other parts of the body is a pavement epithelium. See Whitman, op. cit. p. 327, pp. 338-346. The Japanese Land Leech leaves a slimy track like a snail's behind it as it crawls.

longitudinal vas deferens on either side of the body. The two vasa deferentia are either coiled or dilated at their anterior extremities, and unite in the middle line. The *Gnathobdellidae* have a protrusible muscular penis; the *Rhynchobdellidae* a short eversible sac. Attached prostatic glands are present in both cases. The female organs consist of a pair of ovaries, a pair of ducts which unite, and in *Gnathobdellidae* form a long unpaired portion, or utero-vagina. The ducts of both testes and ovaries develop independently of the glands in *Clepsine* (Nusbaum). The true ovaries of *Hirudo* are two solid bodies, inclosed each in a capsule which is a part of the coelome, and into which the two oviducts open. The epithelium of the ovarian sac itself produces the ova and yolk-cells of *Pontobdella* and the egg-strings of *Nephelis*. The similar strings of *Clepsine* probably have a similar origin. There is a sexual congress, except perhaps in *Clepsine*, where it is possible that self-fertilisation occurs<sup>1</sup>. The spermatozoa are inclosed in a spermatophore. The ova are laid together with albumen in a cocoon, which is secreted by the glands of the clitellum (*supra*), and which is stripped off by the withdrawal of the fore part of the body of the parent. But in *Clepsine* the ova are united by the secretion of the glands of the ventral surface of the clitellum, and are thus attached in a mass to some foreign object in the water; the parent broods over the mass, and the young when hatched attach themselves to its body. *Nephelis* affixes its cocoon to water plants, but the cocoon of *Hirudo* and *Aulostoma* is laid in damp earth. Segmentation is unequal. A remarkable metamorphosis occurs in some instances (*Aulostoma*, *Nephelis*). The larval ectoderm, muscle-layers, nervous-layer (?), of reticulated cells, are thrown off, a new pharynx is formed, and with the exception of the epithelium of the mesenteron, the whole body of the future Leech is derived from paired mesodermal rudiments, two cephalic, and two for the body. There are two pairs of provisional kidneys. The young Leech has a coelome with septa corresponding to the somites. A number of posterior somites fuse to form the sucker.

The Hirudinea live for the most part in water, fresh or salt; some, however, are terrestrial, like the widely-spread Land Leeches (Ceylon, the Himalayas, Java, Sumatra, various East Indian Islands, Japan, New South Wales, Queensland, Trinidad, and South Chili), or subterranean forms such as the European *Trocheta* and the South American *Cylicobdella*, and *Macrobodella Valdiviana*, which is the largest Leech known, and is said to attain a length of two and a-half feet. The majority are parasitic, and suck the blood of animals (Vertebrates, Snails); some are carnivorous like *Aulostoma*, *Trocheta*, *Macrobodella*.

<sup>1</sup> The somite behind the clitellum in *Macrobodella*, i. e. the twelfth, bears on its ventral aspect a swollen oblong area, within which open twenty-four gland pores. These glands may possibly subserve copulation (Whitman, op. cit. p. 379).

The Hirudinea are classified as follows—

1. *Rhynchobdellidae*: body elongate, cylindrical, or flat, with well-marked anterior as well as posterior suckers; fore-part of the body retractile, and constitutes a proboscis. *Piscicola*, *Pontobdella*, *Branchellion*, *Clepsine*, &c.

2. *Gnathobdellidae*: no proboscis. Anterior end of the body more or less expanded; mouth sucker-like; pharynx usually armed with three jaws; blood-plasma red. *Hirudo*, *Haemadipsa*, *Leptostoma*, *Trocheta*, *Aulostoma*, *Nephelis*, &c.

See lit. pp. 216; 218; 220; 223.

*Batrachobdella*, Viguier, A. Z. Expt. viii. 1879-80. *Lophobdellidae*, Poirier and Rochebrune, A. N. H. (5), xiv. 1884.

*Generative organs of Pontobdella*, Dutilleul, C. R. 102, 1886; *development in Clepsine*, Nusbaum, Z. A. viii. 1885.

*Development: Germ-layers in Clepsine*, Whitman, Z. A. ix. 1886; Bergh, *ibid.* *Metamorphosis of Aulostoma*, Bergh, Arb. Zool. Zoot. Inst. Wurzburg, vii. 1885; *of Nephelis*, Id. Z. W. Z. xli. 1885.

## CLASS ROTIFERA.

*Unisegmental Vermes with a retractile trochal apparatus at the anterior end of the body, and a posterior foot which is a ventral process of the body. There is a single ganglion dorsally placed, a pair of nephridial tubes, and a coelome. Circulatory organs are absent. The sexes are separate, and the male with rare exceptions arrested in development. Parthenogenetic (?)*

The body is protected by a cuticle secreted by an underlying layer of ectodermic protoplasm with scattered nuclei, i.e. by a syncytium. This cuticle is often delicate; gelatinous in *Notommata centrura*; sometimes thickened as a series of rings which gives to the body a segmented appearance, or as a variously shaped shield or lorica protecting the body more or less perfectly. A moult has been observed only in one instance (*Apodoides stygius*). One or two Rotifers are furnished with long spines, e.g. *Triarthra*; and *Pedalion mira* has six hollow processes, terminating in a number of feathered setae and containing muscles like the limbs of Arthropoda. Some few Rotifera develop round themselves a gelatinous case, which they inhabit permanently (*Flosculariadae*) or temporarily (*Philodina*), the origin of which is unknown. *Melicerta* fashions a case of pellets out of material collected in a ciliated groove below the trochal apparatus, and cemented together by a gland. The trochal apparatus is sometimes absent altogether, e.g. *Balatro*, or feebly developed, e.g. *Albertia*. It appears to consist typically of an internal prae-oral ring of long cilia, the trochus, and an external ring of finer cilia, the cingulum which leads into the mouth; the former is the homologue of the prae-oral ring of cilia in the Trochosphere, the latter of the adoral ciliated band, seen not in all but in many examples of the same larval form. Both rings may be interrupted dorsally, and the

trochus ventrally. The latter is sometimes lobed or broken up into isolated eminences. The cingulum forms five long processes fringed with stout cilia in *Stephanoceros*, or five knobs each with a bundle of long cilia, usually motionless, in *Floscularia*.

The foot is sometimes absent, e. g. *Asplanchna*. It may be short or long; sometimes transversely wrinkled, e. g. *Pterodina*, or segmented; it terminates with two styles, or in a disc, as in tubicolous forms and occasionally in free, e. g. *Pterodina*. It is in the latter case surrounded by cilia, as it is in tubicolous forms before they become attached. The coelome does not extend into it, but it contains two glands, the secretion of which serves for attachment.

There are muscles for the retraction and extension of both the trochal apparatus and the foot, disposed partly in a circular, partly in a longitudinal direction. They are colourless and sometimes striated. The jaw apparatus and the digestive tract have their special musculature. Connective tissue cells with fine processes unite the various organs which lie in a well-developed coelome. The latter is probably to be considered an archicoele. The blood (haemo-lymph) is clear, as a rule colourless, and often contains granules but no corpuscles.

There is a single dorsally placed nerve-ganglion composed of round cells. It lies above the pharynx and gives off nerves anteriorly as well as to the dorsal sensory organ or antenna (calcar). The latter is represented by a bundle of sensory hairs, sometimes borne upon a peduncle, and it may be double or probably divided. In many Rotifera there is a pair of similar but laterally placed organs, somewhat posterior in position, but not supplied directly from the ganglion. An unpaired or paired eye generally lies behind, upon, or in front of the ganglion. It consists of a reddish pigment, in which a clear lens is found imbedded in some species. Many Rotifers possess a remarkable globular or kidney-shaped mass of calcareous granules in connection with the ganglion, the significance of which is unknown.

The mouth is anterior, nearly terminal in tubicolous forms, but more or less ventral in others. The digestive tract is usually ciliated throughout. The mouth leads into an oesophagus, followed in *Flosculariadae* by a crop, but usually directly by a muscular pharynx or mastax containing the chitinous jaw-apparatus or 'trophi.' These consist of two hammer-like bodies, the mallei, which work against an incus or anvil. Each malleus consists of a manubrium jointed to an uncus; the incus of two pieces, rami, borne upon a single piece, the fulcrum. The shape of the 'trophi' is variable. The stomach is globular or cylindrical, and receives the secretion of two glands placed at its commencement and in some of a large simple or lobed glandular mass as well. The intestine is pyriform and opens into a rectum or cloaca, which also receives the duct of the nephridi and

the oviduct. It is rarely ciliated, and always opens dorsally. Both intestine and cloaca are absent in the *Asplanchnidae*. The mouth, oesophagus, and mastax originate from the stomodaeum; the cloaca from the proctodaeum; the stomach, its glands, and the intestine from the archenteron. The nephridia or excretory organs consist of a right and left tube, much convoluted in places, especially anteriorly. These tubes have nucleated walls and are probably intracellular. They are connected by a transverse canal close behind the ganglion in three or four Rotifers, *Lacinularia socialis*, *Floscularia* (sp.?), *Apsilus lentiformis*, *Hydatina senta*. They carry laterally a variable number of ciliated organs, each of which consists of a pyriform canalicule, lodging at its free broad end a flame-cell. The canalicule is closed (Plate), or has a lateral aperture (Eckstein). The two nephridia with a few exceptions end in a contractile vesicle which opens into the cloaca. Except in the *Philodinadae* the ovarium consists of a germarium and vitellarium (Plate), which are inclosed in a membrane. This membrane is continued into an oviduct which opens into the cloaca. *Seison* and the *Philodinadae* have a double, other Rotifera a single, ovarium.

The male resembles the female in structure in *Seison*. That of *Apodoides stygius* does so at first, but with the evolution of the generative organs the alimentary canal becomes reduced to a cellular cord. The male *Euchlanis* also resembles the female but with the same difference. In all other instances there is a dimorphism. The male is small, with the body pointed posteriorly, a simplified trochal disc, and a soft cuticle. The alimentary tract is represented by an irregular cellular cord. The ganglion is unchanged, but the tactile antenna is never stalked. The contractile vesicle of the nephridia may be absent even when present in the female, and then the two vessels have been observed opening on the penis in *Hydatina senta*: they may unite with the vas deferens. The testis is single, variable in shape; its duct ciliated, and either ending in an invaginable dorsally placed penis, e. g. *Hydatina*, *Brachionus*, &c., or in the posterior pointed termination of the body, e. g. *Conochilus*. In coitus the penis is inserted at any spot into the coelome, in which the spermatozoa move about freely for a time but after a time perish. The female is therefore parthenogenetic (Plate). The male has not been seen as yet in the *Philodinadae*.

The ova are of three kinds, small male ova, thin-shelled summer ova, and thick-shelled winter or, better, resting ova; and a given female lays only one kind (Plate). The ova are sometimes laid and then either float loose or are attached to water-plants or to the mother. The *Philodinadae* are viviparous, as are some other forms. The ovum then develops in the oviduct or in the coelome, as in *Rotifer vulgaris* (Zacharias). How the young Rotifer escapes from the parent in this latter case is unknown. There appears to be an epibolic gastrula.



*Rotifera* inhabit both fresh and salt water and damp moss. Some are parasitic, either externally, as *Seison* on *Nebalia*, or internally, as species of *Albertia* in the coelome of *Lumbricus* and the intestine of Slugs (*Limacidae*). They are said to resist the effect of drying. The *Philodinadae* certainly can do so, as they surround themselves with a gelatinous layer. The affinities of the class are doubtful, but certain resemblances to the Chaetopodan Trochosphere are to be traced.

Hudson and Gosse, 'The Rotifera,' London, 1886.

*Die Rotatorien der Umgegend von Giessen*, Eckstein, Z. W. Z. xxxix. 1883. *Beiträge zur Naturgeschichte der Rotatorien*, Plate, J. Z. xix. 1886 (with literature quoted). *An attempt to re-classify the Rotifers*, Hudson, Q. J. M. xxiv. 1884<sup>1</sup>.

*Pedalion*, Hudson, Q. J. M. xii. 1872. *Trochosphaera*, Semper, Z. W. Z. xxii. 1872. *Rotifer vulgaris*, Zacharias, Z. W. Z. xli. 1884; A. N. H. (5), xv. 1885. *Asplanchna*, Hudson, Journ. R. Micr. Soc. (2), iii. 1883. *Melicertidae*, Joliet, A. Z. Expt. (2), i. 1883.

*Chitinous parts of mastax*, Gosse, Ph. Tr. 146, 1856.

*Nephridia*, Plate, op. cit. pp. 56-7, 76-7, 98-100.

*Power of resisting drought*, Gavaret, A. Sc. N. (4), xi. 1859; Davis, Slack, and Hudson, Monthly Microscopical Journal, xi. 1873; and *winter habits*, Cubitt, op. id. v. 1871.

*Egg formation and development*, Tessin, Z. W. Z. xlv. (1 and 2), 1886.

## CLASS NEMERTEA.

### (*Nemertini*: *Turbellaria Rhynchocoela*.)

*Unisegmental Vermes, with a ciliated ectoderm; a pair of cephalic ciliated pits or grooves; a protrusible proboscis, placed dorsally to the oesophagus, opening above the mouth, and surrounded by nervous cerebral commissures. Two main nervous cords extend from the cerebral ganglia, one on either side, to the posterior end of the body, and are sometimes united by a supra-anal commissure. There is a coelomic blood-vascular system. A pair of nephridia is situated in the anterior or oesophageal region. The generative organs are simple and paired, and extend in a series down either side of the body. The sexes are as a rule separate. Development takes place with or without metamorphosis. Mostly marine.*

The body is frequently brilliantly coloured. It is usually elongated,

<sup>1</sup> Plate has recently proposed to divide the class into two groups, the *Aductifera* (= *Philodinadae*) and the *Ductifera*. In the former there are two ovaries but no oviducts. The trochal apparatus retains the primitive form of two rings, one behind the other; the posterior styles are 4-6 in number, and the four cement glands open on their apices; the nervous system has no lateral antennae, &c. The *Ductifera* have a single ovary (germarium and vitellarium) and an oviduct; the trochal apparatus is modified; the terminal styles are never more than two; there are one or two dorsal and two lateral antennae, &c. See Z. W. Z. xliiii. 1886, p. 233.

somewhat flattened or cylindrical in section, and endowed with marvellous contractility. The transparent pelagic *Pelagonemertes Rollestoni* and the parasitic *Malacobdella* are short and broad forms. The former has a posterior ventral sucker.

There is a delicate cuticle, which appears to bear the short numerous cilia; a cellular ectoderm, in which the cells are of different lengths; a basement membrane, and a cutis of connective tissue. The basement membrane in *Schizonemertea* lies between the ectoderm and the cutis, which is largely pervaded by longitudinal muscle fibres; whereas in the *Palaeo- and Hoplonemertea* it lies between the cutis and the muscular layers of the body. Many of the ectoderm-cells are glandular, and the gland-cells extend into the cutis. They secrete a plentiful mucus, with which are intermixed minute highly refracting rods. The animals are enabled to creep along the surface of water by means of this mucous exudation, and many, especially those which inhabit mud or sand, protect themselves by a coat or tube of it<sup>1</sup>. The muscular layers of the body are arranged in one of three ways. In the Palaeonemertean genera *Carinella* and *Cephalothrix* there is an outer circular, a median longitudinal, and an inner circular layer<sup>2</sup>. In the Palaeonemertean genera *Polia* and *Valencinia* and the *Schizonemertea* there is an external longitudinal layer of considerable thickness, a median circular and an internal longitudinal layer, whilst the *Hoplonemertea* possess only an external longitudinal and an internal circular layer. New layers seem to appear in individual specimens of large size, and variations in the mode of preparation cause differences of appearance (Hubrecht). The muscular tissue of *Borlasia* is red-coloured, but the source of the colour is not known. There is a plentiful nucleated and partly fibrous connective tissue between the muscle layers and muscle fibres, which appears also to fill the central region of the body, so that there is no coelome<sup>3</sup>. Bands of muscular fibres are disposed dorso-ventrally in the region of the intestine, passing between successive lateral intestinal coeca. Hence the body appears to be divided internally into a series of segments.

<sup>1</sup> The mucus is remarkable for possessing in some instances an acid reaction, in others an alkaline. See McIntosh, Monograph of British Annelids, pt. i.; Nemerteans, p. 45.

<sup>2</sup> *Pelagonemertes* and *Monopora* are stated to possess an outer circular and an inner longitudinal coat.

<sup>3</sup> The coelome of the larval *Lineus obscurus* is an archicoele, and is simply a persistent blasto-coele or segmentation cavity. So far as it persists in the adult, it is represented by the cavity of the proboscis sheath and the blood-vascular system (Hubrecht). In the *Pilidium*, on the contrary, the mesoblast eventually forms two solid masses in the head and two in the trunk; the former develop some irregular spaces, the future blood lacunae; the latter splits into a somatic and splanchnic layer. But the cavity between the two is eventually broken up by the growth of cell-processes. In the early stages of *Pilidium* the mesoblast is chiefly represented by branched cells imbedded in a gelatinous matrix between the epi- and hypo-blast, in which they are freely moveable. These cells appear to give origin eventually to the permanent mesoblast (Salensky).

The nervous system consists of a right and left cephalic ganglion connected *inter se* by two commissures, one thick, below the proboscis and its sheath, the other, thin, above them; they are prolonged backwards into two lateral nerve-cords. Both ganglia and cords consist of a peripheral layer of ganglion cells<sup>1</sup> and a core of fibres. The ganglia are simple in *Carinella*, *Cephalothrix*, and *Carinoma*. In other Nemertea each ganglion is divisible into a ventral lobe in direct continuity with the lateral cords, and a dorsal lobe, from which a posterior or third lobe is partially separated in *Polia*, *Valencinia*, and *Schizonemertea*. This third lobe in *Hoplonemertea* is connected to the main dorsal lobe by nerves alone, and it lies sometimes behind and sometimes in front of it, e.g. in *Oerstedtia*, *Amphiporus lactiflorens*, &c. The inner or postero-median side of the third lobe is formed of large cells different to those of the rest of the ganglion. They sometimes inclose a ciliated space. The cephalic ganglia give off various nerves, some to the apex of the head, a branch to the oesophagus, and from the upper proboscidian commissure a fine median nerve extending backwards in relation with the sheath of the proboscis. The lateral cords are placed towards the dorsal aspect of the body in *Langia* (*Schizonemertea*), towards its ventral aspect in *Drepanophorus* (*Hoplonemertea*). The supra-anal commissure is found in *Hoplonemertea*. The ganglia and lateral nerves of *Schizonemertea* are deeply tinged with haemoglobin. Dorsal and ventral nerves which branch dichotomously originate metamerically from the lateral nerves in *Hoplonemertea*. But in other Nemertea the lateral nerves are contained in a nervous sheath or plexus, which envelopes the body and in *Carinella* extends beyond the ganglia to the tip of the head, a region where definite nerves are found in *Schizonemertea*. The nervous system lies in *Carinella* immediately outside the muscular body-walls, in *Polia*, *Valencinia*, and *Schizonemertea* internal to the outer longitudinal muscular coat, and in *Hoplonemertea* within the body-walls.

The organs of special sense are small tufts of tactile hairs, sometimes seen at the apex of the head; long stiff isolated hairs on the surface of the body, observed only in young specimens; eyes sometimes absent, e.g. in mud-dwelling *Schizonemertea*, either numerous or restricted to four as in *Tetrastemma*, in structure either mere pigment specks or provided with a lens, a cellular vitreous body, retinal rods and a pigment sheath as in *Drepanophorus* and *Amphiporus*; and otocysts stated to occur in some *Hoplonemertea*. The two ciliated cephalic grooves situated on the head are probably not sensory organs. These structures are absent in *Cephalothrix* and *Geonemertes chalicophora*. In the Palaeonemertean *Carinella annulata* they form two simple shallow furrows at the level of the cerebral ganglia.

<sup>1</sup> In *Carinella* and *Cephalothrix* the ganglion layer is confined to one, the outer side of the fibrous core.

A ciliated canal leads inwards from each of them and enters the cerebral ganglia in *C. inexpectata*, or their posterior or third lobes in *Schizo-* and *Hoploneurtea*<sup>1</sup>. In the *Schizoneurtea* the groove is longitudinal and deep; in most *Hoploneurtea* transverse and often complicated by the addition of short longitudinal grooves present also in the Palaeoneurtean *Polia*<sup>2</sup>. The ciliated canal of *Hoploneurtea* is bifurcate.

The aperture by which the proboscis is extruded is anterior and terminal as a rule, and rarely lies within the mouth (*Akrostomum*, *Geonemertes palaensis*, *Malacobdella*, *Monopora*). It leads into a narrow canal. The proboscis proper commences just anteriorly to the ganglia. It is tubular, and is contained within a proboscis-sheath. The walls of the two structures are continuous in front, but elsewhere they are separated by a cavity filled with a liquid in which are suspended fusiform corpuscles, tinged with haemoglobin in *Cerebratulus urticans*. This cavity is completely closed. It is furnished in *Drepanophorus* with paired lateral diverticula commencing at the level of the nerve ganglia. The sheath lies dorsally to the digestive tract and usually reaches the posterior extremity of the body. Sometimes, e.g. *Carinella*, *Nemertes carcinophila*, it is extremely short. It has muscular walls, usually an outer circular and an inner longitudinal layer, whilst its cavity is lined by an epithelium. The proboscis also has muscular walls, an external and internal circular with an intervening longitudinal layer in *Palaeo-* and *Schizo-**neurtea*; an outer and inner longitudinal layer with an internal and circular layer in *Hoploneurtea*. The longitudinal muscles are continued beyond the posterior end of the proboscis as the retractor muscle, which is affixed to the sheath somewhere near its middle region. Numerous longitudinal nerves occur in the proboscis, as in *Amphiporus* and *Drepanophorus* (*Hoploneurtea*), or a nervous sheath, as in *Cerebratulus* (*Schizoneurtea*). The proboscis appears to be everted by the contraction of the sheath upon its contained liquid, but its eversion is only partial. The epithelium lining it is derived from the ectoderm. The surface of the eversible region is often covered with adhesive glandular papillae; its epithelium sometimes contains nematocysts as in *Carinella*, *Cephalothrix*, *Borlasia*, and especially *Cerebratulus*. The limit of the eversible region in *Hoploneurtea* is marked by an internal constriction due to a great development of muscular tissue (the muscular bulb), surrounding a cavity or reservoir, which communicates with both the eversible and non-eversible sections of the organ. A central, partially calcareous stylet, pointed, or in *Drepanophorus* serrated, is implanted close to the outer opening of the reservoir; and on either side of it a narrow duct leads to a single small

<sup>1</sup> Hence they have been supposed to possess a respiratory function in relation with the brain, especially in *Schizoneurtea*, where haemoglobin exists in the nervous substance.

<sup>2</sup> The Palaeoneurtean *Valencinia* has ciliated canals, but no grooves.

sac, rarely more, containing two or three calcareous stylets pointed at one end, at the other provided with a head like a nail's. Both central and lateral stylets can be thrown off and formed anew. The muscular bulb contains glands; its reservoir is filled with liquid which is perhaps poisonous. The non-reversible section of the proboscis has glandular walls and is filled with liquid. The function of the organ is doubtful. It may be in part tactile, in part offensive or defensive<sup>1</sup>.

The mouth is ventral, in front of the ganglia in *Hoploneurtea*, behind them in other Nemertea. It leads into a straight oesophagus with longitudinal muscular fibres in its walls; an intestine which, except in the adult *Carinella*, *Cephalothrix*, and *Carinoma*, is provided with short lateral and usually opposite caeca. The latter in *Pelagonemertes* number only thirteen pairs, are long and branched at their ends. Both oesophagus and intestine are ciliated and contain glands in their walls. The anus is terminal. There is a system of coelomic blood spaces communicating anteriorly in the head and posteriorly by a supra-anal commissure. The spaces in the head and oesophageal region of *Palaeo-* and *Schizo-nemertea* are lacunar, i. e. large and somewhat irregular in outline, whereas posteriorly they become vessels, i. e. smaller and either circular or oval in section, as they are throughout the whole system in *Hoploneurtea*. They are lined throughout by an epithelium, and the vessels generally possess a muscular wall of circular and sometimes also longitudinal fibres. There are two principal longitudinal and lateral spaces in *Carinella*, *Cephalothrix*, and *Carinoma*; there is added to these in *Polia*, *Valencinia*, and *Schizonemertea*, a median vessel placed above the digestive tract arising from an anterior lacunar connection between the two lateral spaces beneath the sheath of the proboscis, and partly imbedded in the lower wall of that sheath. The *Hoploneurtea* possess a looped vessel in the head, which passes anteriorly above the sheath of the proboscis, posteriorly below it, and at this point is connected with three longitudinal vessels, a median, dorsal, and two lateral. Transverse loops connect the three vessels in the region of each dorso-ventral set of muscles in *Polia*, *Valencinia*, all *Schizonemertea*, and most *Hoploneurtea*. The lateral vessels in the body lie below the level of the lateral nerves as a rule. In *Malacobdella* the vessels give off branches, especially in the head and posteriorly into the sucker. The blood spaces are filled with a liquid containing, in some cases at least, corpuscles, which are oval and red with haemoglobin in *Drepanophorus*. The existence of nephridia has not been demonstrated in *Cephalothrix* and some other Nemerteans. They are present, however, in many, probably in all. They are two in number, one on each side, placed anteriorly. Each organ

<sup>1</sup> Salensky regards it from its mode of development as the homologue of the proboscis of some Turbellaria, which is really the invaginated apex of the body. See papers on *Pilidium* and *Monopora*, cited p. 641.

consists in *Carinella* of a tube lying close to the blood-vessel, into which it opens in front and behind, and of a spongy (?) gland lying in the wall of the blood-vessel and connected from place to place with the tube. The nephridial tube of *Carinoma* has three connections to the blood-vessel. It is itself lined by glandular cells. In other Nemerteans it is wholly independent of the blood-spaces, though it may lie in the lacuna at the side of the oesophagus in *Schizonemertea*. It is branched to a greater or less degree in the *Hoplonemertea*. The nephridial cells are ciliated in *Carinoma*, *Valencinia*, and possibly in others. There is a single duct to each organ in *Carinella*, *Carinoma*, *Cerebratulus*, *Langia*, most *Hoplonemertea*; a large number in *Polia*, *Valencinia*, *Lineus*, *Amphiporus lactiflorus*. The duct, whether single or multiple, opens above the level of the lateral nerve.

The sexes are separate in nearly all instances. *Geonemertes palaensis*, *Tetrastemma* (= *Borlasia*) *hermaphroditica*, *T.* (= *B.*) *Kefersteinii* are hermaphrodite. The sexual glands are placed in a series on each side of the intestine, one in each set of dorso-ventral muscles. They have at first no external opening, but during the evolution of the genital products approach the surface and finally open by a dorsally directed pore. *Monopora vivipara*, *Prosorhochmus Claparèdii*, *Tetrastemma obscurum*, are viviparous forms. The ova are contained in capsules and laid in mucus in some *Schizonemertea*. Development is direct in *Cephalothrix*, viviparous forms, and *Hoplonemertea*; or in *Schizonemertea* accompanied by a metamorphosis. The genus *Lineus* has a creeping ciliated larva, the larva of *Desor*: others have a ciliated pelagic helmet-shaped larva, the *Pilidium*<sup>1</sup>.

The majority of Nemertea are marine. Many are capable of swimming. *Pelagonemertes* is pelagic. Two or three fresh-water forms are known, e.g. *Tetrastemma aquarum dulcium* from N. America; and four terrestrial, *Tetrastemma agricola* (Bermudas); *T. Rodericanum* (Rodriguez Is.); *Geo-*

<sup>1</sup> The larva of *Desor* is probably not so primitive a form as the *Pilidium*. The latter, according to Salensky, has an apical groove in which the ectoderm cells are thickened, probably representing the apical thickening of the Trochosphere. It has a provisional nervous system along the ciliated edges of the side lappets, besides various muscles. It has an oesophagus and stomach. In *Desor's* larva and the *Pilidium* alike, the larval epiblast is discarded after it has given origin to the ectoderm of the adult. As to the origin of the principal organs, the nervous is of ectodermic origin (Salensky), of mesodermic (Hubrecht). The ciliated cavities of the brain are derived from invaginations of the primary epiblast, which close and afterwards acquire an opening. The two oesophageal outgrowths which were supposed to give origin to the ciliated cavities, probably form the nephridia (Hubrecht). The proboscis is formed by an ingrowth at first solid (*Monopora*), or an invagination of the secondary (Salensky) or primary (Hubrecht) epiblast. Its muscular walls and sheath are formed from the same mesoblastic rudiment; the proboscis cavity by a split in the rudiment (Salensky); or the cavity represents a part of the archicoele (note, p. 636), and the muscular walls and sheath have separate mesoblastic rudiments (Hubrecht). The oesophagus of the adult is the first part of the tract in the larva; the intestine as far as the anus its second part, the two being separate (?) parts of the archenteron in the larva of *Desor*. The generative organs are perhaps derived from the epiblast.

*nemertes chalicophora* (? Australia); *G. palaensis*, Pelew Is. *Nemertes carcinophila*, and *Cephalothrix Galathea* live on crabs, *Malacobdella* in the pallial cavity of various marine Lamellibranchiata; they are usually considered to be parasitic. The larger Nemerteans feed on fixed tubicolous Chaetopoda. All are probably carnivorous. Most members of the class have the power of breaking themselves into fragments if irritated. The *Schizonemertea* when thus self-mutilated or otherwise injured are able to reproduce the head, or to develop a head in connection with a fragment.

The Nemertea are classified by Hubrecht as follows—

1. *Palaeonemertea*: no deep lateral fissure on the side of the head. No stylet in the proboscis. Mouth behind the ganglia. *Cephalothrix*, *Carinella*, *Carinoma*, *Polia*, *Valencinia*.

2. *Schizonemertea*: a deep longitudinal lateral fissure on each side of the head, from the bottom of which a ciliated duct leads into the posterior lobe of the ganglion. Lateral nerves between the longitudinal and inner circular muscular coat of the body-wall. Nervous tissue deeply tinged with haemoglobin. Mouth behind the ganglia. *Lineus*, *Borlasia*, *Cerebratulus*, *Langia*.

3. *Hoploneemertea*: one or more stylets in the proboscis. Mouth generally situated before the ganglia. Lateral nerves inside the muscular coats of the body-wall. No deep longitudinal fissures on each side of the head. *Amphiporus*, *Akrostromum*, *Drepanophorus*, *Tetrastemma*, *Oerstedtia*, *Nemertes*, *Geonemertes*, *Proso-rhochmus*, *Malacobdella*.

*Nemertines*, Hubrecht, Encyclopaedia Brit. (ed. ix.) xvii. Id. *Revision of genera*, Notes from Leyden Museum, i. 1879; ii. 1880. *Monograph of British Annelids*, pt. i., *Nemerteans*, McIntosh (Ray Soc.), 2 vols. 1873-74.

*Carinoma*, Oudemans, Q. J. M. xxv. 1885 (Suppl.), p. 7. *Malacobdella*, von Kennel, Arb. Zool. Zoot. Inst. Wurzburg, iv. 1877-78. *Monopora* (= *Borlasia*) *vivipara*, Salensky, Archives de Biol. v. 1884. *Pelagonemertes*, Moseley, A. N. H. (4), xv. and xvi. 1875.

*Freshwater genera*. *Tetrastemma aquarum dulcium*, &c., Silliman, Z. W. Z. xli. 1885, p. 70.

*Terrestrial genera*. *Geonemertes chalicophora*, Graff, M. J. v. 1879; *G. palaensis*, von Kennel, op. cit. *supra*. *Tetrastemma Agricola*, von Willemoes-Suhm, A. N. H. (4), xiii. 1874. *T. rodericanum*, Gulliver, Ph. Tr. 168, 1879.

*Anatomy and physiology*, Hubrecht, Niederländ. Archiv f. Zool. ii. 1874; cf. Q. J. M. xv. 1875; Id. Z. A. ii. 1879; Dewoletzky, Z. A. iii. 1880. *Nervous system, ciliated grooves and canals*, Hubrecht, Q. J. M. xx. 1880. *Circulatory and excretory systems*, Oudemans, Q. J. M. xxv. 1885, Suppl. (with lit.). Cf. *Ancestral Form of Chordata*, Hubrecht, Q. J. M. xxiii. 1883.

*Development of Lineus obscurus* (= Desor's larva), Hubrecht, Q. J. M. xxvi. 1886. *Structure and metamorphosis of Piliidium*, Salensky, Z. W. Z. xliii. 1886. Id. *Monopora*, *supra*.

Hubrecht is stated to be preparing a monograph of the Class in 'The Fauna and Flora of the Gulf of Naples.'

## CLASS TREMATODA.

*Unisegmental Vermes, with a flattish leaflike or more or less cylindrical body provided with organs of adhesion in the shape of suckers, and sometimes of chitinous hooks. The cuticle so-called appears to be a metamorphosed layer of cells. There is a well-developed nervous system, the ganglia of which are entirely supra-pharyngeal, i.e. dorsal. There is a mouth, and an alimentary canal which is usually forked, but no anus. The excretory system has the form of more or less branching tubes commencing with flame-cells, and either ending in a contractile vesicle, or opening by two independent orifices. Hermaphrodite. Self-impregnation occurs, as well as reciprocal impregnation. The embryo either develops direct into the sexual form—monogenetic Trematoda, or gives origin to a series of intermediate non-sexual dimorphic forms—digenetic Trematoda. Parasitic.*

The monogenetic Trematoda are either roundish or elongated in shape. Two small oral suckers are often present, one on either side the mouth, while the posterior end of the body is either provided with a single sucker, usually large and sometimes armed with chitinous hooks, or it is expanded and furnished with suckers, or hooks, or with both hooks and suckers or claspers. The digenetic Trematoda are usually elongate, and either flattish or rounded. They have an oral sucker, and there is, except in *Monostomidae*, a second, usually ventral, sometimes posterior as in *Amphistomum*, but anterior in *Gasterostomum* where the mouth is sub-median and ventral. A large number of suckers is rare. The suckers themselves are usually cup-shaped, sometimes compartmented as in the large ventral sucker of *Tristomum* and in *Aspidogaster*. They are either sessile or stalked. When numerous they may be set close together in a series of rows on the ventral aspect, e.g. *Gastrodiscus* from the horse; in three dorsal (?ventral) rows as in *Notocotyle* (= *Monostomum verrucosum*) from the duck, coot, &c.; in a single ventral row as in *Stichocotyle Nephropis* found encysted in the Crustacean *Nephrops*, or in a row on the margins of the body as in some monogenetic Trematoda. The chitinous hooks of the group just named are very generally situated on the suckers. The monogenetic family *Gyrodactylidae* is remarkable for possessing either 2-4 retractile adoral processes, or an incomplete circum-oral lobe (*Calceostoma*) as well as one or two posterior terminal discs armed with hooks (= retinacula). The claspers found in some *Polystomeae* are provided with two muscular valves supported by chitinous bars: one valve is fixed, the other free: and the free valve has a snapping action. These last named structures have been accurately investigated only in *Axine* and *Microcotyle*.

There is a cuticle, variable in thickness, sometimes perforated by pores,



and sometimes spiniferous. The spines are occasionally very conspicuous, e. g. on the body of *Fasciola hepatica*, on the oral extremity of some species of *Distomum*, and especially on the body and round the oral sucker of *Echinostomum*. The cuticle is prolonged inwards at the apertures of the different organs opening externally, and it is said in various instances to be underlain either by a layer of cells, by a granular layer, a layer of elastic fibres, or by the circular layer of body muscles<sup>1</sup>. Unicellular cutaneous glands are said to be present in some instances, e. g. on the posterior sucker of *Tristomum*, on the surface of the body in *Polystomum integerrimum* and *Aspidogaster*, &c. Glands open on the adoral processes of *Gyrodactylus*, and on the lateral lobes of *Holostomum*, and probably secrete an adhesive material. The musculature of the body consists typically of an external layer of circular fibres, followed by a layer of longitudinal fibres, and this in turn by diagonal fibres, crossing from right to left and *vice versa*. But there are variations from this typical arrangement. Bundles of dorso-ventral fibres pass vertically from the dorsal to the ventral surface, and their ends are attached to internal prominences of the cuticle. Special bundles of muscles are sometimes present in connection with the oral sucker, and the terminations of the genital organs. Cells disposed in groups or in a layer, are often present internally to the muscular layers. Their significance is not known. The suckers are limited internally by a distinct membrane, and are composed of muscular fibres, arranged equatorially, meridionally, and radially, the last-named constituting the bulk of the organ. The substance of the body is made up of a tissue variable in character; either simply cellular; or composed of a cell-network in which the cells are more or less distinct with other cells of a rounded aspect contained in their meshes; or consisting of a matrix imbedding distinct or feebly indicated cells and fibres. Spaces between the cells or in the matrix have been held to represent the coelome.

The nervous system consists of a pair of ganglia placed anteriorly, and connected by a transverse commissure dorsal to the pharynx. A subpharyngeal ganglion, connected by two commissures with the supra-pharyngeal ganglia, has been described in *Fasciola hepatica* (Sommer), and a pair of sub-oesophageal nervous commissures in *Distomum isostomum* (Gaffron). Two pairs of nerves usually pass forwards from the ganglia,

<sup>1</sup> Kerbert found in *Distomum Westermanni* (1) a delicate cuticle, (2) a layer of cells, (3) a basement membrane to which the spines were attached. (1) and (2) were sometimes missing. Hence he concludes that the Trematode cuticle = a basement membrane, A. N. A. xix. 1881, p. 531. But Ziegler is convinced (Z. W. Z. xxxix. 1883, pp. 542-7) that the cuticle is a metamorphosed layer of cells. Nuclei are to be found in it in *Bucephalus*, according to him. So too in *Sporocysts* and *Cercariae*, according to Biehringer (Arb. Zool. Zoot. Inst. Wurzburg, vii. 1885, p. 4). Schwarze agrees in the same view (Z. W. Z. xliiii. 1886), and, according to him, the cuticle of the oesophagus, excretory vesicles, and main excretory canals are similarly derived. The walls of the oviduct in some *Distomidae* are cellular.

two or three pairs backwards. Of the latter, one pair is dorsal and submedian, and extends in length to a variable degree, sometimes anastomosing posteriorly (*D. isostomum*). A second pair is perhaps best described as ventral or ventro-lateral, and the third, present e.g. in *Tristomum Molae*, *D. isostomum*, *D. palliatum*, may be termed lateral. The two ventro-lateral nerves may unite posteriorly. In *Tristomum Molae* *D. isostomum*, *D. clavatum* circular commissures connect these longitudinal nerves from place to place. In some species of *Distomum* the ventral nerves possess a strong transverse commissure in front, and another behind the ventral sucker to which fibres pass from them. It is probable that the Trematoda in general will be found to conform to the type of nervous system described. Ganglion cells occur in the nerves as well as in the ganglia. Large cells furnished with processes are scattered among the bundles of muscular fibres. In *Tristomum* nerve-fibrils were traced by Lang into continuity with these cells, but Looss was unable to demonstrate a similar connection in *D. palliatum*, and regards them as connective tissue cells. Eyes are present in *Tristomum* and *Polystomum* among monogenetic Trematoda, four in number, situated dorsally and anteriorly upon or within the ganglia. In *T. Molae* they consist of a mass of pigment, a refractile body, and a nerve terminating (?) in a ganglion cell. No other organs of special sense occur.

The mouth is usually situated anteriorly, either terminally, or on the ventral aspect. In *Gasterostomum* it is median and ventral. It is surrounded by a sucker in most *Distomeae*, but in the *Tri-* and *Poly-stomeae* it leads either directly into the pharynx, or into a vestibule, which may be armed with a sucker on either side, e.g. *Axine*, *Microcotyle*. A pharynx with strong muscular walls is rarely absent, as e.g. in *Bilharzia*, *Distomum reticulatum*, and it is followed by a longer or shorter oesophagus<sup>1</sup>, the digestive tube up to this point being lined by a cuticle, a continuation inwards of the cuticle of the body. In *Amphistomum* and *Gasterodiscus*, the pharynx is not specialised, and the oesophagus has strong muscular walls, and is furnished with a right and left caecal pouch. The digestive tract itself is either a simple sac, as in *Aspidogaster* and *Gasterostomum*, or a forked tube, one limb of the fork running backwards close to each side of the body. The limbs of the tube may end blindly, or unite posteriorly as in *Monostomum*, the female *Bilharzia*, some *Tri-* and *Polystomeae*. The tubes themselves may be simple, or furnished with caeca, small as in *D. palliatum*, *D. Megnini*; short and wide as in many *Polystomeae*, long and branched as in *Fasciola*, *Tristomum*, *Pseudocotyle*.

<sup>1</sup> It is perhaps open to doubt whether the muscular structure at the commencement of the digestive tract in *Monostomum* and *Gasterostomum* is a pharynx or an oral sucker. Schwarze considers the pharynx, so-called, of *Rediae* as a sucker. The pharynx is sometimes protrusible, e.g. in *Udonella*, and the *Redia* of *F. hepatica* uses it to devour the liver of its host (Thomas).

They are connected in *Polystomum integerrimum* by three transverse anastomoses, also beset with caeca. The tract is lined by cells the shape, size, and other characters of which appear to vary, not only in different Trematoda, but according to the state of the digestive cavity whether full or empty. Two muscular coats, an internal circular, and an external longitudinal, more or less well-developed, surround the digestive part of the tract. There is no anus. Unicellular salivary glands open into the pharynx in *Polystomum integerrimum*.

The excretory system consists in the digenetic Trematoda of a terminal or contractile vesicle, a system of canals, with terminal canalicules and ciliated funnels or flame-cells (see p. 581). The last-named have been recognised in a number of Trematoda, and they are without doubt universally present. The canalicules leading from the funnels have been seen to open in bundles near to one another into the system of canals. Close to their apertures they are said to anastomose. The canals are variously disposed, and their several sections, large or small, have a proper calibre throughout. Two at least, and sometimes more main canals are as a rule connected with the terminal vesicle. When there are two, they correspond one to either side of the body. The branches they give off either remain independent or anastomose in various ways. A net-work of vessels may be thus established as in *D. reticulatum* or *F. hepatica*. The terminal or contractile vesicle opens at or near the posterior extremity of the body, sometimes somewhat dorsally. It may be cylindrical or T-shaped, and a short narrow tube usually connects it to its pore. Small vessels occasionally originate from it, and in *F. hepatica* the vesicle itself appears to be drawn out into a long median dorsal canal giving origin to numerous branching vessels which form a reticulum over the posterior two-thirds of the body. The walls of the canalicules, canals and pulsatile vesicle are formed by a delicate structureless membrane or cuticle. It is possible that this membrane may represent a layer of metamorphosed cells<sup>1</sup>. The contents of the system is a liquid, sometimes coloured, and containing a variable number of large or small granules in suspension. The latter appear to be calcareous in nature. In *Diplostomum volvens* and *rhachiaeum*, the main canals and their branches give origin to short and either simple or dichotomously branched tubes, which terminate in small bulbs. Every bulb contains a calcareous body very similar to the structure so-named in Cestoda.

<sup>1</sup> Cells forming the walls of the pulsatile vesicle have been observed by Schwarze and Fraipont; the latter also observed them in the main canals of *D. squamula*; so too Looss in *D. reticulatum*. Cilia were seen by Cunningham in the canals of *Stichocotyle*, and have been described in other instances, e. g. by Zeller in *Polystomum integerrimum*; by Lorenz in *Axine* and *Microcotyle*; by Looss in *D. reticulatum*, &c. See authorities cited by Fraipont, Arch. de Biologie, i. 1880, p. 417 18.

Ciliated funnels have been detected in several monogenetic Trematoda, e. g. *Polystomum integerrimum*. There is generally a system of canals corresponding to the two sides of the body which branch and anastomose. In *Aspidogaster* and *Stichocotyle* there is a posterior terminal pore, from which two contractile (?) vessels originate. But in *Tristomum*, *Pseudocotyle*, *Epibdella*, &c., each main lateral canal terminates in a small vesicle, and the two vesicles open on the ventral aspect of the body anteriorly, one on either side of the pharynx. The two apertures are said to be dorsal in *Polystomum integerrimum* and *Axine*, but in *Onchocotyle* they are posterior, and situated respectively at the ends of the two contractile processes of the body. In most *Polystomeae* the excretory system is imperfectly known <sup>1</sup>.

The Trematoda are hermaphrodite with the exception of *Bilharzia* <sup>2</sup>. The male organs consist of the testes and efferent canals. The former usually lie near the centre of the body, and just behind the ovary. There is but one testis in *Udonella Caligorum*, *Octobothrium lanceolatum* and *Calceostoma elegans*. In other instances there are two, one somewhat in front of the other. They are generally more or less globular, sometimes lobed. In most of the monogenetic Trematoda the lobes are well marked, and the testes are frequently broken up into independent follicles, e. g. *Tristomum*, *Polystomum*. The digenetic genus *Fasciola* alone has branched tubular testes. The vas deferens is formed by the union of two or more efferent vessels according to the number of testes or testicular follicles. It is dilated more or less, for the first part of its course forming a vesicula seminalis; and in some *Distomidae* the part of the canal following the vesicula has cellular walls, and is surrounded by a number of unicellular glands which open into it, thus constituting a prostatic region. Similar unicellular glands are present in some monogenetic Trematoda, e. g. *Polystomum*. The terminal portion of the canal is generally more or less evaginable, and is surrounded by a muscular cirrus-sac, sometimes absent, e. g. *D. clavatum*, which may in some *Distomidae* include only the prostatic region, or the vesicula seminalis also, together with the terminal portion. The sac appears to be composed of external longitudinal and internal circular muscular fibres. Among monogenetic Trematoda the genera *Calicotyle* and *Pseudocotyle* have the vas deferens terminating in a perforated chitinous piece: while *Axine*, *Microcotyle*, *Polystomum*, *Gyrodactylus*, &c., have a cirlet of hooks (?) surrounding its aperture. The female organs consist of a germarium, vitellarium, their ducts, a shell-gland, and oviduct. The germarium is always single, usually globular or elongate, and even folded on itself, e. g. *Octobothrium*, sometimes lobed,

<sup>1</sup> Calcareous bodies are stated by Cunningham to occur in the two main canals of *Stichocotyle*.

<sup>2</sup> It is possible that *D. filicollis* (= *Köllikeria* of Cobbold, *D. Okeni* of Kölliker) is another example. See P. J. van Beneden, C. R. Suppl. ii. 1861, p. 186.

e.g. in *Tristomum*, the lobes being extremely well-developed in some instances, e.g. in the genus *Onchocotyle*. This gland gives origin solely to the germ by the segmentation of which the embryo is formed. The vitellarium is a symmetrical gland right and left. It consists very commonly of a number, generally very great indeed, of grape-like follicles connected to ducts which unite, and finally open into two longitudinal canals, one right, the other left, connected by a cross canal, usually situated just in front of the germarium. At the centre point of this canal a single duct which, as a rule, commences with a dilatation serving as a yolk reservoir, leads to the duct of the germarium. Instead of grape-like follicles, the gland may consist of two tubes provided with short caeca, e.g. *Calceostoma*, some *Distomidae*; or of two sacs as in *D. ventricosum*; or of several saccules arranged in a star-like fashion as in *D. rufo-viride*, *D. globosum*; or even of a net-work as in *Monostomum mutabile*, and *M. reticulare* (P. J. van Beneden). A canal, the Laurer-Stieda canal or vagina, which is double in *Polystomum*, *Calicotyle*, *Pseudocotyle*, single in all other instances where it has been recognised, opens externally in various positions, dorsally in *Distomidae* and *Microcotyle*, laterally in *Epibdella*, *Axine*, and *Polystomum*, ventrally in *Pseudocotyle* and *Calicotyle*, and near the uterine aperture in *Tristomum*. Internally it opens, when single, into the vitello-duct, or germ-duct, somewhere near the union of these ducts; when double into the lateral vitello-ducts in *Polystomum*, the united vitello- and germ-ducts in *Pseudocotyle* and *Calicotyle*. The canal itself is sometimes dilated, or there is a dilatation near its inner extremity in which spermatozoa are usually found<sup>1</sup>. Its function is doubtful. It has been supposed (1) to serve for copulatory purposes; (2) to act as a safety-tube for the escape of over-abundant or altered vitelline products and spermatozoa. Copulation has been actually observed to take place by its means in *Polystomum* (Zeller); and its structure in *Axine* and *Microcotyle* appears to favour that view. On the other hand its calibre is said to be too small to admit of copulation in some *Distomidae* (Poirier) and in *Calicotyle*. Both vitelline cells as well as spermatozoa and even germs have been observed in it in the former. The united vitello- and germ-ducts are surrounded where they merge into the oviduct by a set of unicellular glands which secrete the shell. In the monogenetic Trematoda the portion of the oviduct into which the shell-glands open is dilated, variously shaped, and endowed with peristaltic movement. To this portion the name 'Ootype' was given by P. J. van

<sup>1</sup> A receptaculum seminis (=inner vesicula seminalis auctt) may be present as (1) a dilatation of the Laurer-Stieda canal (*Tristomum*, *D. clavatum*); (2) a pear-shaped vesicle near the inner end of the same (*D. palliatum*, &c.); (3) a dilatation of the germ-duct (*Onchocotyle appendiculata*). In many *Distomidae* the sperm is aggregated at the spot where the shell-glands open. The term 'outer vesicula seminalis' is often applied to the dilated region of the vas deferens.

Beneden, or 'uterus' by Taschenberg. A germ, a certain quantity of vitelline cells and spermatozoa are moulded together in it into an egg, and provided with a shell. The ovum is then passed on. A number of ova may accumulate in the terminal portion of the oviduct which is then dilated, or each ovum is laid singly as soon as formed, e.g. in *Epibdella*, *Calceostoma*. The ootype is not represented in the digenetic Trematoda with perhaps the exception of *Gasterostomum*, but the oviduct is dilated, thrown into convolutions which occupy a greater or less extent of the body, and retain a large number of ova. In some *Distomidae*, e.g. *D. clavatum*, the terminal part of the oviduct is surrounded by unicellular glands. The oviducal aperture may in some monogenetic Trematoda, e.g. *Axine*, *Microcotyle*, be surrounded by chitinous hooks. The male and female apertures are always close together. They are usually placed anteriorly on the ventral surface a little to one side, e.g. *Tristomum*, or medianly, and in the *Distomidae* as a rule in front of the ventral sucker. They are, however, sometimes placed posteriorly to it, e.g. *D. ocreatum*, &c., or even on the posterior margin of the body as in *D. macrostomum*, *Opisthotrema*, *Holostomum*; rarely on the lateral margin as in *D. clavigerum* from the frog and the Tristomidan *Epibdella*. In many *Distomidae* the two orifices are surrounded by a sexual cloaca, and the male orifice may be situated on a projecting muscular papilla which bears in some instances the female aperture as well<sup>1</sup>.

Self-impregnation appears to occur as well as reciprocal impregnation<sup>2</sup>. The ovum has a shell at first clear, then becoming coloured,

<sup>1</sup> The prematurely sexual form of *Polystomum integerrimum* has sexual organs simplified as compared with those of the usual form. The testis is single, globular; and the vas deferens without prostatic glands. The germarium is long, coiled; the vitellarium of restricted extent; the two Laurer-Stieda canals absent; the oviduct devoid of a terminal coiled and dilated portion. Each ovum is laid as soon as formed. The animal is probably self-fertilising. Zeller, Z. W. Z. xxvii. 1876.

<sup>2</sup> Reciprocal impregnation has been observed by Zeller in *P. integerrimum*, by Looss in *D. clavigerum* (Z. W. Z. xli. 1885, p. 426), by Cobbold in *Campula* (= *D. campula*). The presence of hooks round the female apertures of some monogenetic Trematoda points in the same direction. In *Bilharzia*, where the sexes are separate, the male is so curled as to form a 'gynaecophoric' canal for the female.

Self-impregnation occurs beyond a doubt in some instances. A single *P. integerrimum* has been found in a Frog's bladder with sperm in the female passages. Von Linstow met with in *Gammarus Pulex* a Distome (*D. agamos*) encysted, a single Distome in each cyst. Some individuals were sexless; others had mature male organs; others again mature female organs. Developing ova were present in the oviduct. In this instance the male aperture is behind, the female in front of the ventral sucker. Sometimes the structure of the apertures makes self-impregnation more than probable. See Poirier, A. Z. Expt. (2), iii. 1885, pp. 582-85. Zaddach has actually observed the act in *D. cirrigerum* (Z. A. iv. 1881, p. 427), encysted in *Astacus*. The ova of this animal are laid in the cyst; the parent dies; the cyst decays, and the ova are then scattered. Leuckart states that he has noticed sexual maturity attained in cases of prolonged encystation in a host, e.g. in *Ephemeræ* larvae (Parasiten, ed. 2, i. note, p. 98). For a discussion of the whole subject, see Looss, Z. W. Z. xli. pp. 420-27.

A canal has often been described as connecting the testis to the germ-duct, e.g. by Zeller in *P.*

furnished at one end, except in *Bilharzia*, with a cover or operculum which the mature embryo thrusts open when it escapes. It is usually oval and smooth in the digenetic Trematoda. But in the monogenetic its shape varies, and is determined by that of the 'ootype,' and it is generally provided with a long process at one pole, or with two at opposite poles, and it is often fixed. In the monogenetic Trematoda it is always laid ; in the digenetic it may, or may not commence its development in the oviduct. If development begins, it may be completed before oviposition as in *Monostomum mutabile*, or only the first stages of fission may be passed through. The germ-cell usually lies near the pole, closed by the operculum, entirely or partially immersed among the vitelline cells. Fission is regular or irregular, but complete, and during its progress the vitelline cells degenerate and become used up more or less completely by the developing germ-cell. It has been found in those cases which have been thoroughly investigated that two layers of cells are successively differentiated from the surface of the embryonic mass (Schauinsland). The outermost layer is formed as follows. A cell at the upper, i. e. opercular pole of the embryonic mass becomes flattened, divides, and the two cells then grow round the mass ; other cells appear by division or by differentiation from the mass itself. Eventually an enveloping membrane is formed which lines the shell. A second superficial layer of flattened cells is next differentiated, which becomes a ciliated coat, or when cilia are not developed, a structureless cuticle as in *D. tereticolle*. The embryo of the monogenetic Trematoda appears to be non-ciliated as a rule. However, that of *Diplozoon* (= *Diporpa*) is ciliated laterally, of *Polystomum integerrimum* provided with five transverse ciliated bands, three anterior, incomplete dorsally, two posterior, incomplete ventrally. Among the digenetic genera some are, and some are not ciliated, and the cilia may cover the embryo but partially, e. g. they are present only on the anterior region of *D. lanceolatum*. The ciliated coat or its representative, is subsequently lost, but an underlying layer of flattened cells, afterwards transformed into the cuticle, covers the embryo. A caecal digestive tract is formed anteriorly, and the pharynx is sometimes to be detected. Flame-cells are also present, e. g. as a single pair in the embryo of *Fasciola hepatica*. One or two black eye-specks with or without a lens-like body may be developed. And the embryo may be furnished at its anterior extremity, either with chitinous plates or spines as in *D. tereticolle*, or an extensile boring process as in *F. hepatica*. When it quits the egg-shell it bursts the enveloping membrane, and then thrusts open the operculum. It may at

*integerrimum*. Its existence has been repeatedly denied. Ijima has recently maintained that Zeller's canal also exists in *P. ocellatum*, in *Diplozoon*, and an *Octobothrium* (sp. ?), but that it communicates with the alimentary canal in which he has observed germs in *P. integerrimum*. See Z. A. vii. 1883, p. 635.

the same moment moult its ciliated coat (*D. cylindraceum*, (?) *D. mentulatum*), but this coat is not usually lost until the embryo enters its first host.

The monogenetic Trematoda frequent a single host and are ectoparasitic, i. e. do not as a rule inhabit the internal organs of this host. The exceptions are *Calicotyle*, which has been found in the cloaca of Rays; *Aspidogaster conchicola*, which inhabits the nephridia of the Lamellibranch *Anodonta*, and *A. limacoides* from the intestines of the Teleosteans, *Leuciscus idus* and *L. dobula*; *Cotylaspis* from the American *Anodonta*; *Polystomum integerrimum* from the bladder of *Rana temporaria*, *R. esculenta* and *Bufo viridis*, and *P. ocellatum* from the pharynx of the Chelonian *Emys europaea*. The other genera are found for the most part attached to the gills of various fishes, or on the surface of their bodies, e. g. *Tristomum Molae*. *Udonella Caligorum* lives on the various species of the Crustacean *Caligus*. The majority are marine. *P. integerrimum*, *Diplozoon*, and *Gyrodactylus* are severally peculiar. The first-named attaches itself as an embryo to the internal gills of frog-tadpoles. When the gills atrophy at the time that the tadpole changes into a frog, the young parasite migrates through the digestive tract into the bladder, where it becomes sexually mature in three years, but does not attain its full size for five or six years. But if the embryo attaches itself to the gills of a very young tadpole, it undergoes a premature sexual development, does not migrate, and dies when the tadpole undergoes metamorphosis (cf. note 1, p. 648). *Diplozoon paradoxum* consists of two individuals fused together. The embryo known as *Diporpa* is at first free-swimming; it soon loses its cilia, and settles on the gills of a Minnow; loses its eyes, but lives in a single condition for weeks or months; but finally one individual attaches itself by its ventral sucker to a conical eminence on the back of a second individual, which thereupon so twists itself as to fix the first individual in the same manner. The cones and suckers fuse completely; in other respects, however, the two *Diporpae* which make up a single *Diplozoon* are independent of one another. *Gyrodactylus elegans*, found on the gills and fins of various freshwater fish, is viviparous, but the embryo before it is extruded, itself contains an embryo, and this in turn another, so that three generations of embryos are represented simultaneously.

The digenetic Trematoda have at least one intermediate generation, but as a rule very many before the sexual organism reappears. The embryo, whether it is or is not ciliated, enters first a host which is very rarely some Fish, but usually a Mollusc, either a Gastropod or Lamellibranch, but not necessarily always the same Mollusc for the same species of fluke<sup>1</sup>. The egg-shell with the embryo may be swallowed by a snail and the embryo set free in the alimentary canal, a mode by which land

<sup>1</sup> *Sporocysts* are occasionally met with in Fish. A free swimming *Sporocyst* has been observed by Ramsay Wright (American Naturalist, xix. 1885, p. 57).



Molluscs especially may be liable to infection. After its entry it becomes in some instances a *Sporocyst*, in others a *Redia*, which must be regarded as dimorphic forms, and are sometimes spoken of as 'nurses.' Both possess a cuticle, a delicate layer of circular and longitudinal muscle fibres, and a layer of cells covering the latter internally and bounding a cavity sometimes crossed by trabeculae of connective tissue in which lie developing germs in all stages<sup>1</sup>. Flame-cells have been detected in the body-walls. A *Redia* also possesses a digestive tract, i. e. a muscular pharynx (? = oral sucker<sup>2</sup>) and a caecal intestine, as well as a special opening for the birth of the germs rarely present in *Sporocysts*. It has also two short processes, one on either side of the posterior extremity of the body, as well as a projecting ring near its anterior extremity<sup>3</sup>. The *Sporocyst* possesses the power, at least in some instances, of multiplying either by transverse fission, as e. g. in *F. hepatica*, and the *Cercariaeum Limacis* not uncommon in the slug *Arion ater*; or by gemmation, producing branched structures, as in the genera known as *Bucephalus* (= *Gasterostomum*) inhabiting *Anodonta* and the Oyster, and *Leucochloridium* (= *D. macrostomum*) inhabiting the Gastropod *Succinea amphibia*. The germs to which a *Sporocyst* gives origin may develop in some instances into *Sporocysts*, in others into *Rediae* or into *Cercariae*; those which originate from a *Redia* may develop into either *Rediae* or into *Cercariae*. And it does not seem certain that there is any limit to the possible number of successive generations of *Rediae*. Both *Cercariae* and *Rediae* may occur side by side in the same nurse. The last term in the series is, however, invariably a *Cercaria*. The germs which give origin to these various generations arise from two sources: the first, cells which occupy the central region of the young *Sporocyst* or *Redia*; the second, the epithelium lining the body-walls, single cells of which enlarge, divide, form morulae, and drop into the cavity of the body to undergo further development<sup>4</sup>. An invagination without a lumen to form a digestive canal has been observed in the germs of *F. hepatica*; and a delicate pellicle has been seen surrounding the germ and young *Cercaria*.

<sup>1</sup> The *Sporocyst* may become enveloped in an adventitious epithelial coat or 'paletot,' formed from the blood corpuscles of its host (Biehringer).

<sup>2</sup> A rudimentary oral sucker is present in some *Sporocysts* (Biehringer).

<sup>3</sup> For the structure of this ring and the mistakes that older observers have fallen into respecting it, see Thomas, Q. J. M. xxiii. pp. 121-2, and note.

<sup>4</sup> Leuckart restricts (A. N. 48, 1, 1832, p. 95, p. 100) the origin of germs to cells with large nuclei (germinal cells) occupying the central region of the 'nurse.' The cells in question have no share in the growth of the nurse itself. His view appears to be adopted by Schwarze. But as Biehringer points out (1) there are great differences of size in the developing germs within the same 'nurse,' too great to be explained by a temporary arrest of development of some of them; and (2) it is scarcely possible to extend the view to such cases as the branched *Sporocyst* of *Bucephalus*, and he might have added, to *Leucochloridium* and such *Sporocysts* as multiply by repeated fission, e. g. *Cercariaeum Limacis*. The origin of germs from the epithelium lining the body-cavity has been established beyond doubt by Biehringer himself in the *Sporocysts* of *Cercaria macrocerca* from the gills of *Cyclas*, and by Thomas in the 'nurse' forms of *F. hepatica*.

It is probably derived from the surface of the germ, as in the case of the embryo (*ante*, p. 649).

The *Cercaria* has a body shaped like that of a sexual Trematode, though its proportions may undergo change in subsequent growth. It possesses the rudiments of suckers, digestive tract, and the excretory system, and is furnished with a tail, or in *Bucephalus* with two tails, attached to the body posteriorly, by means of which it swims when it is set free from its parent and its parent's host. The tail is sometimes of great length, and may be bifid at its extremity. It is in some marine forms armed with spines set in rings or tufts. Occasionally it is nearly obsolete, or even quite so, as in *Leucochloridium*, and then the *Cercaria* is probably always quiescent and only passes into its final host when the latter happens to devour its parent, as e.g. in the case named. The *Cercaria* is sometimes armed (except it is said when derived from *Rediae*) with a boring spine, close to which glands open on either side. The glands have been supposed to secrete either a poison or a cystogenous substance. The free *Cercaria* becomes after a time quiescent, and either encysts itself in the same host that contains its parent, in another intermediate host, usually non-Vertebrate, sometimes Vertebrate, e. g. the tadpole of frogs<sup>1</sup>, or on some foreign object, e. g. on stems of grass, &c., in the case of *Fasciola hepatica*<sup>2</sup>. Encysted *Cercariae* have been found in very various aquatic non-Vertebrates. The cyst is formed by the *Cercaria* itself, and its material is derived from the secretion of gland-cells. In some forms, e. g. *F. hepatica*, the gland-cells in question contain rods. These rods may be found afterwards in the walls of the cyst. The tail is cast off during the process of encystment<sup>3</sup>. The *Cercaria* now grows in size and becomes a sexually immature fluke. A period of rest for this purpose seems necessary, and then as soon as the encysted fluke is swallowed by its final host, a Vertebrate, it attains a sexual condition in the intestine of the latter. It is very rare for it to do so in the encysted condition and to produce ova, as do *D. cirrigerum* from *Astacus* and *D. agamos* from *Gammarus pulex*. It has been stated that the same *Cercaria* may give origin to different sexual forms in different hosts

<sup>1</sup> The non-sexual forms (= *Diplostomum*; *Tetracotyle*) of *Holostomum* are frequently met with in various Vertebrata.

<sup>2</sup> *D. nodulosum* is found in the sexual form in the intestines of various fresh-water fishes, e. g. of the Pope, *Aerina cernua*. Its *Cercaria* sometimes occurs encysted on the outer surface of the intestine of this fish. It probably enters it at an immature stage in this case, i. e. before undergoing encystation in the *Paludina*, which is the first host. See von Linstow, A. N. H. (4), xii. 1873.

<sup>3</sup> It has been stated by several authorities, as by Pagenstecher and Ercolani, that the tail of a *Cercaria* may in some instances become a *Sporocyst* and produce germs. The structure of the tail does not favour this supposition. According to Schwarze, it consists of a 'contractile substance occupying the axis and periphery with large vesicular cells between.' Compare Ziegler on the tail of *Bucephalus*, Z. W. Z. xxxix. 1883, pp. 558-562. For instances to the point, see the work of Ercolani, Dell' adattamento, &c. cited below.

(Ercolani), but as yet these statements have not been confirmed. A difference in size between specimens of *D. macrostomum* from the intestines of Songsters and Water-rails has been noted.

The genus *Holostomum*, usually classed with the digenetic Trematoda, has perhaps a direct development. The sexual worm inhabits the digestive tract of various carnivorous birds. The organisms known as *Diplostomum* and *Tetracotyle*, which occur encysted in various Vertebrata, are believed by Von Linstow and others to be the non-sexual states of this genus. The ova are large. The larva of *H. cornucopiae* is ciliated, except anteriorly, and has two eye-specks.

Digenetic Trematoda are found entoparasitic in members of all classes of Chordata. They usually inhabit various parts of the digestive tract. Man may be infested by *Fasciola hepatica* (ramifications of bile ducts); by *Distoma lanceolatum* (gall-bladder and bile ducts); by *D. crassum* (duodenum) in India and China: by *D. Ringeri* in the lungs, causing the endemic haemoptysis of Formosa; and by several *Distomata* of rare occurrence, together with the formidable *Bilharzia haematobia*, which lives in the blood-vessels of the urinary bladder, mesentery and portal system, and is widely distributed over the African continent. The ova of the last-named escape with the urine. Ruminants are principally infested by *Fasciola hepatica* and by *D. lanceolatum*, which cause great and widespread destruction. The former is the source of the disease known in this country as rot or liver-rot. Its embryo enters the small amphibious Pulmonate, *Limnaeus truncatulus*, in which it becomes a *Sporocyst*. The latter in turn gives origin to several generations of *Rediae*. The *Cercaria* is set free and encysts itself on some foreign object,—the stems of water-plants and grass, which are eventually devoured by sheep, cows, &c. A very large number of species of digenetic Trematoda are known which can be arranged under relatively few genera.

The Class Trematoda may be divided as follows—

1. Monogenetic Trematoda; development direct.

(a) *Tristomeae*: body roundish or elongate; posterior extremity of body never specially developed. Two adoral suckers often present; a large ventral sucker often armed with chitinoid structures. Sexual apertures on the left side or admedian. Laurer-Stieda canal single or double. Ova with a filament at one pole only.

Three sub-families: *Tristomidae*, with the single genus *Tristomum*; *Monocotylidae*, with *Calicotyle*, *Pseudocotyle*, and *Monocotyle*; *Udonellidae*, with the single genus *Udonella*.

(b) *Polystomeae*: body elongate, pointed and narrow anteriorly; broad behind, and generally provided with special organs of adhesion in the shape of suckers or chitinoid hooks, of suckers or claspers with chitinoid structures. Two adoral suckers in some instances. Sexual apertures median. Laurer-Stieda canal

single or double. Male sexual aperture often armed with chitinous hooks. Ova frequently provided with two long appendages.

Four sub-families: *Octobothriidae*, with *Octobothrium*, *Diplozoon*, &c.; *Polystomidae*, with *Polystomum*, *Onchocotyle*, &c.; *Microcotylidae*, with *Axine*, *Microcotyle*, &c.; *Aspidogaster*, *Cotylaspis*; *Gyrodactylidae*, with *Gyrodactylus*, *Dactylogyrus*, *Calceostoma*, &c.

2. Digenetic Trematoda; one or more non-sexual and dimorphic forms intervene between two successive sexual forms.

(a) *Monostomidae*: elongate, oval, or rounded in shape; an oral sucker. *Monostomum*.

(b) *Distomidae*: body flattish, more or less leaf-like, or elongate; an oral and a ventral sub-median or posterior sucker. *Distomum*, *Fasciola*, *Bilharzia*, *Echinostomum*, *Amphistomum*, *Gastrodiscus* (?).

(c) *Gasterostomidae*: oral sucker sub-median and ventral; an anterior sucker as well. *Gasterostomum*, with the larval form *Bucephalus*.

(d) *Holostomidae*: body flattened, and divided into an anterior and posterior part, the former bearing an oral and ventral sucker. Two adoral lobes with glands in connection, or a circumoral fold with lobes, *Holostomum*, with the larval forms *Tetracotyle* and *Diplostomum*; fold incomplete, *Hemistomum*.

There are two remarkable genera of uncertain position, *Didymozoon* and *Nematobothrium*. The first-named occurs encysted in various fish; two individuals in one cyst, and sometimes fused posteriorly; see von Linstow, A. N. 52, 1, 1879. *Nematobothrium filarina* attains a length of one metre, and is found encysted beneath the skin of the branchial cavity of *Sciaena Aquila*. See P. J. Van Beneden, C. R. Suppl. ii. 1861, p. 107. Its embryo has a cephalic disc armed with spines; E. Van Beneden, Q. J. M. x. 1870.

*Vers Intestinaux*, P. J. van Beneden, Paris, 1858 (C. R. Suppl. ii. 1861). *Parasites*, Cobbold, 1879. *Trematodes*, Leuckart, 'Parasiten des Menschen,' i. (ed. 1.) 1863, p. 448 et seqq.

*List of Parasites and Hosts*, von Linstow, Compendium der Helminthologie, Hannover, 1878.

*Tristomeae and Polystomeae: Genera, &c.*, Taschenberg, Zeitschrift f. ges. Naturwissenschaften (Giebel), 51, 1878; 52, 1879. *Marine Trematoda*, P. J. van Beneden and Hesse, Mém. de l'Acad. Roy. Belgique, xxxiv. 1864, p. 60. *Tristomum*, Taschenberg, Abhandl. Natf. Gesellschaft zu Halle, xiv. 1877-79. *Pseudocotyle*, Id. Festschrift of same, 1879. *Calicotyle*, Wierzejski, Z. W. Z. xxix. 1877. *Diplozoon and Diporpa*, Zeller, Z. W. Z. xxii. 1872; Paulson, Mem. Acad. Imp. Sci. St. Petersburg (7), iv. 1862. *Polystomum*, Zeller, Z. W. Z. xxii. 1872; xxvii. 1876. *Onchocotyle*, Taschenberg, Festschrift (*supra*). *Axine and Microcotyle*, Lorenz, Arb. Zool. Inst. Wien, 1, 1878. *Aspidogaster*, cf. Huxley, 'Anatomy of Invertebrated Animals,' 1877, p. 194. *Gyrodactylus*, Wagener, Arch. Anat. and Physiol. 1860. *Stichocotyle*, Cunningham, Tr. Roy. Soc. Edinburgh, xxxii. pt. 2, Session 1883-84.

*Digenetic Trematoda: Synopsis of*, Cobbold, J. L. S. v. 1861; Diesing, Systema Helminthum, i. 1850; cf. Id. SB. Akad. Wien, xv. 1855; xxxi. and xxxii. 1858; xxxv. 1859. *Anatomy*, Looss, Beiträge, &c., Z. W. Z. xli. 1885; Poirier, Contributions, &c., A. Z. Expt. (2), iii. 1885. *Dist. cirrigerum and D. isostomum*, Zaddach, Z. A. iv. 1881. *D. Westermanni*, Kerbert, A. M. A. xix. 1881. *D. crassum*,

Cobbold, J. L. S. xii. 1876. *D. Ringeri*, Manson, On the *Filaria sanguinis hominis*, &c., Lewis, London, 1883, cap. vii. p. 134. *Fasciola hepatica*, Macé, 'Recherches anat. sur la grande douve du foie,' Paris, 1882; Sommer, Z. W. Z. xxxiv. 1880. *Bilharzia*, Fritsch, Z. A. viii. 1885, and Leuckart, op. cit. *supra*, p. 617. *Gastrodiscus*, Lejtényi, Abhandl. Senck. Gesellschaft, xii. 1881. *Amphistomum*, Blumberg, Inaug. diss. Dorpat, 1871. *Opisthotrema*, Fischer, Z. W. Z. xl. 1884. *Gasterostomum* and *Bucephalus*, Ziegler, Z. W. Z. xxxix. 1883. *Holostomum* with *Diplostomum* and *Tetracotyle*, von Linstow, A. N. 43 (1), 1877, p. 187 et seqq.

*Typical Life-history with anatomy*, Thomas, 'On the Liver Fluke,' Q. J. M. xxiii. 1883; cf. Id. Royal Agricultural Soc. Journal (2), 17, 1881; 18, 1882; 19, 1883; Nature, xxvi. 1882; Leuckart, Z. A. iv. 1881; v. 1882; A. N. 48, 1882; W. H. Jackson, Z. A. vi. 1883. *Life-histories and non-sexual forms*, P. J. van Beneden, *supra*; Ercolani, Dell' adattamento delle specie all' ambiente, Mem. Accad. Sci. Istit. Lomb. Bologna (4), ii. 1882; iii. 1883 (cf. Arch. Ital. de Biologie, i. 1882, for abstract with plate); Moulinié, De la Reproduction chez les Trématodes endoparasites, Mém. de l'Institut National Genevois, iii. 1855; de' Filippi, Mem. Accad. Torino (2), xv. 1855; xvi. 1857; xviii. 1859 (cf. A. Sc. N. (4), ii. 1854; iii. 1855; vi. 1856).

*Formation of embryo*, Schauinsland, J. Z. xvi. 1883; *embryo of Bilharzia*, Chatin, A. Sc. N. (6), xi. 1881. *Synoptic tables of larvae*, von Willemoes-Suhm, Z. W. Z. xxiii. 1873, p. 341-3. *Anatomy of Sporocyst*, Biehringer, Arb. Zool. Zoot. Inst. Wurzburg, vii. 1885; *of Redia*, Thomas, *supra*. *Leucochloridium* (= *Macrostomum*), Zeller, Z. W. Z. xxiv. 1874. *Bucephalus* (sporocyst) = *Gasterostomum*, de Lacaze-Duthiers, A. Sc. N. (4), i. 1854; McCrady, Proc. Boston Soc. xvi. 1874; cf. Ziegler, Z. W. Z. xxxix. 1883, pp. 539-40. *Cercaria: Postembryonal development of Trematoda*, Schwarze, Z. W. Z. xliii. 1886. *Cercariae with spines and bifid tails*, see Villot, 'Marine Endoparasitic Trematodes,' A. Sc. N. (6), viii. 1879; Fewkes, American Journal of Science (3), xxiii. 1882. *Rod-containing cells of Cercaria*, Thomas, Q. J. M. xxiii. p. 127; Sonsino, Archives Ital. Biol. vi. 1885.

*Summary of views on nature of cuticle*, Looss, Z. W. Z. xli. p. 391 et seqq.; Ziegler, *ibid.* xxxix. p. 543 et seqq.; see also Biehringer and Schwarze, *supra*.

*Nervous system*: Gaffron, on *Dist. isostomum*, Schneider's Zool. Beiträge, i. pt. 2, 1884; Lang on *Tristomum*, &c., Mitth. Zool. Stat. Naples, ii. 1881; and Poirier, op. cit. *supra*.

*Excretory system*, Fraipont, Archives de Biologie, i. 1880; ii. 1881; and Looss, op. cit. *supra*.

*Fertilisation*, cf. note 2, p. 648, *ante*.

## CLASS CESTODA.

*Unisegmental or spuriously (?) segmented Vermes, devoid of organs of special sense and of a digestive tract. There are organs of adhesion in the shape of chitinoid hooks, suckers or grooves. The nervous system is well-developed, and has the form of two or more lateral cords with anterior ganglia. The coelome is represented by irregular channels, the excretory system*

by longitudinal canals, or by a network of vessels both alike furnished with terminal ciliated funnels, and opening externally by one or more pores or a pulsatile vesicle. Hermaphrodite. Male and female genital organs are rarely present in a single set, but are usually repeated many times. Endo-parasitic.

The sexual worm inhabits the digestive tract of some Vertebrate host, with the exception of *Archigetes*, which becomes sexual in the coelome of *Tubifex rivulorum* (*Oligochaeta*). It possesses but one set of male and female genital organs, and is therefore obviously unisegmental in *Archigetes*, *Caryophyllaeus* and *Amphilinidae*. In other instances it has many sets of genitalia metamerically disposed, and the body of the worm is then usually segmented to correspond. This segmentation, however, is scarcely indicated in some instances (*Triaenophorus*, *Ligula*), and it is generally well marked in the anterior region, where the rudiments of sexual organs are not to be traced, and it may even appear without their development. It commences anteriorly behind the head and neck or scolex (*infra*), and the segments increase in size, &c., the further they are from this spot. The terms 'joint' or 'proglottis' are applied to the segments which are by many authorities regarded as zooids produced by serial gemmation from the scolex and the sexual worm or 'strobila,' therefore, as a compound or colonial organism. These views are probably incorrect (see pp. 231-2), and it is possible that every Cestode possesses a certain fixed limit of size and growth<sup>1</sup>.

The non-sexual worm rarely occurs in the digestive tract, as e.g. of *Lophius*, but as a rule in the flesh, or one of the viscera (liver, brain, &c.) of a Vertebrate. It has been found also in the coelome or tissues of some Mollusca, Arthropoda, and Vermes. It is generally considered to consist of two generations united together: (1) the proscœlex, produced by the growth of the embryo, and (2) the scolex, developed from a disc of cells in the body-walls of the proscœlex. The proscœlex varies much in size: it is usually globular but sometimes oval or band-like, and may be either solid or, as in most *Taeniadae*, hollow. The scolex consists of a head with its various organs of adhesion and a longer or shorter neck. It is attached to the proscœlex, and generally invaginated into it, the position in which it is nearly invariably developed. The scolex may acquire a set of generative organs, and remain permanently in connection with the proscœlex, as in *Archigetes*; it may be set free and lead a wandering life, or enter an intermediate host, as in some species of *Tetrarhynchus*; and when it is trans-

<sup>1</sup> The scolex of *Anthobothrium Musteli* and *Phyllobothrium Lactuca* appears to increase 4-6 times in size after it enters its second host. The detached joints may similarly increase immensely, e.g. the strobila of *Calliobothrium Eschrichti* is 4-5 mm. in length, the free joint 8-9 mm., and the ovum, including its filaments, measures 6-7 mm. *Phyllobothrium thridax*, *Anthobothrium cornucopia*, and *Tetrarhynchus minutus* may also be instanced, but the contrast between the strobila and the joint is not so extreme.

ferred to the alimentary canal of its final host, either the region of the neck may lengthen, sets of generative organs appear, as well as a more or less distinct division into joints, and with the liberation of the first formed joints the prosclex may also be set free, as in *Ligula* and fish tapeworms, &c. ; or else, as most commonly occurs, the prosclex is digested in the stomach of the host and the scolex, passing on into its intestine, affixes itself, the neck lengthens, generative organs and joints appear. The view that prosclex and scolex are parts merely of a non-sexual worm which becomes sexual on transference to a new host is more probable than that there is an Alternation of Generations, including either three individuals, the non-sexual (1) prosclex and (2) scolex, with (3) the sexual joints ; or two, (1) the non-sexual prosclex, and (2) the scolex, which becomes sexual in the second host ; see pp. 232-3<sup>1</sup>.

The scolex is rarely devoid of all organs of adhesion, as in *Caryophyllaeus*, *Leuckartia*, and *Abothrium Gadi*. Suckers are usually present. There is a single terminal sucker resembling the oral sucker of a Distome in the *Amphilinidae* ; there are two lateral cephalic grooves in all *Pseudophyllidea* which are produced in *Solenophorus* and *Duthiersia* into cornucopia-like structures with basal perforations. *Echinobothrium* has two flattened suckers, but in other Cestoda there are four, cup-like in *Taeniadae* and *Tetrarhynchus* ; large, extremely mobile, and crisped marginally in some Phyllobothriums, e. g. *Phyllobothrium lactuca* ; areolate as in *Calliobothrium*, or pedunculate as in *Anthobothrium* ; whilst *Polycephalus*, from the intestines of an East Indian *Rhinobatis*, has the anterior extremity surrounded by sixteen hollow (?) muscular tentacles, as well as armed with two or four suckers. Chitinoid hooks are present in some *Taeniadae*, in *Tetrarhynchidae*, *Phyllacanthinae*, *Echinobothrium*, and *Triaenophorus*. They are disposed in one or more circles round the base of a rostellum or central projection from the head in *Taeniadae* ; in numbers upon four contractile proboscides, with which the head is furnished in the *Tetrarhynchidae* ; and on the upper part of the suckers in the Phyllacanthians and *Echinobothrium*. The last-named is remarkable for also possessing three longitudinal series of hooks on each surface of the neck. The hooks are curved, e. g. *Taeniadae* ; forked, e. g. *Acanthobothrium* ; straight, *Echinobothrium* ; implanted by large and forked roots in the *Taeniadae*, and moved by special muscles<sup>2</sup>.

The neck and body of the worm are more or less flattened. One sur-

<sup>1</sup> The life history of the non-segmented genus *Caryophyllaeus* is not known. It may be noted that it has recently been asserted that *Taenia serrata* may undergo its development within the intestines of one and the same host ; but the evidence is not conclusive, and such an occurrence is not probable.

<sup>2</sup> *Taenia echinobothrida* (Megnin) from the Fowl and tame Pigeons has the four suckers covered with minute hooks. According to the same authority, hooks, suckers, and even the scolex may atrophy when sexual maturity is attained. See on both points, Journal de l'Anat. et Physiol. xvii. 1881.

face, that beneath which the testes lie, is, judging from the analogy of the Trematoda, considered to be dorsal; the other, to which the vagina is approximated, and on which the genital apertures are sometimes situated, as ventral.

There is a cuticle, with a subjacent layer of transverse elastic (? muscular) fibres, a layer of vertical fusiform cells, and a more or less granular matrix, which forms the bulk of the substance of the body. This matrix imbeds cells of various kinds, nuclei, and the muscles of the body. It is traversed by irregular lacunae, generally held to represent the coelome. The muscles form one or more longitudinal layers, and an inner circular layer, inclosing a core of matrix in which lie the main nerves, excretory vessels and genitalia. There are also dorso-ventral fibres; see pp. 225-6. The whole worm is endowed with an extraordinary power of contraction and extensibility. For the calcareous bodies which are absent in the prosclex, see p. 227.

The nervous system of the *Taeniadae*, so far as is known, conforms more or less closely to that of *T. serrata* (p. 226). It is always situated in the anterior part of the head. It consists in *Bothriocephalus latus*, in another species of the genus parasitic in the dog, and in *Ligula* of a transverse commissure, containing ganglion cells in the former, and of two inconsiderable lateral ganglia from which a stout lateral nerve passes backwards on each side. In *B. latus* each lateral nerve gives origin to eight nerves which accompany it, four on either side. The principal nerves give filaments to the layer of subcuticular cells. Isolated ganglion cells have been said to occur in the lateral nerves; so too ganglionic swellings in each joint (p. 226). There are no organs of special sense. The pigment specks seen on the head of the scolices of certain species of *Tetrarhynchus* or on the neck of *Echinobothrium*, do not appear to be degenerate visual organs<sup>1</sup>.

The excretory system has been found, wherever it has been accurately investigated, to consist of ciliated funnels appended to delicate canaliculi, of main longitudinal canals with or without an intermediate network of finer canals. Ciliated funnels (p. 581) are found in all parts of the body, but most plentifully in a zone superficial to the central core of matrix, or in *T. lineata* within the layer of circular muscles. The canalicules may unite *inter se*, and open either conjointly or separately into a superficial network of fine canals, e. g. in *Tetrarhynchus*, *Bothriocephalus*, *Caryophyllaeus*, or directly.

<sup>1</sup> The ganglia of *Solenophorus* appear to be differently arranged to what they are in other Cestoda. See Griesbach, A. M. A. xxii. 1883. The 'plasmatic canals' of Sommer, found by him in *T. solium* and *T. medioanellata*, are perhaps to be identified with the lateral nerves. See note, p. 515, Z. W. Z. xxiv. 1874. The nerves from the ganglia of *T. plicata* are said by Rhemberg to end in the cuticula as delicate threads, terminated each by a slight swelling (Arch. f. Thierheilkunde, iii. 1877, p. 43). Sensory nerve endings and motor nerve endings have been described by Schiefferdecker (J. Z. viii. 1874, pp. 475-480). But the results of these two observers have not been as yet confirmed by others.



into one of the main longitudinal canals, e. g. *Scolex Trygonis pastinacae*. These canals take a longitudinal course. They number four—two on each side, one dorsal, the other ventral—in the *Taeniadae*, *Tetrarhynchidae*, and *Tetraphyllidae*. As to the first-named, the dorsal canals have a tendency to atrophy, and may even disappear, and this is especially the case with the large tapeworms that infest man<sup>1</sup>. The four canals are connected in the head by a simple or plexiform ring; at the posterior margin of each joint by a circular vessel, or when the ventral main canals alone persist by a cross vessel. In some instances the anastomoses are more complicated (Riehm). A valve, formed by two opposing folds of the walls of the canal, guards the aperture at either end of the cross vessel. The *Pseudophyllidea*, however, and *Caryophyllaeus* possess as a rule a larger number of main canals, 10–24, or even more, according to the genus or species; and Fraipont has drawn a distinction between ascending and descending canals. The former have a smaller calibre, contents rather granular, and are non-contractile; the latter are larger, with clear contents, and distinctly contractile. The two sets of vessels are connected by a network of vessels intermediate in size between them and the canalicules (*supra*). And it must be carefully noted that the different systems of vessels, i. e. main canals, intermediate network, and canalicules, invariably retain their own proper calibre and never graduate the one into the other. Their walls are formed by a delicate membrane. Those of the main canals are surrounded, according to Pintner, by an epithelium, the cells of which contain yellow droplets. In *Solenophorus* similar cells occur in the matrix in the neighbourhood of the canals, but not in contact with their walls (Griesbach); whilst in *Taenia lineata* flattened granular epithelioid cells immediately invest them (Hamann). The point is one requiring further investigation. The excretory system opens externally by a posteriorly placed pulsatile vesicle, with which the main canals are connected, e. g. in *Caryophyllaeus*, some species of *Bothriocephalus*, &c.; and when joints have been detached either by a shortened cross vessel, as in *Taeniadae* according to Leuckart, or by separate openings, one for each of the main canals, apparently the more usual mode. The pulsatile vesicle is always present, according to Pintner, at the end of the body of the scolex. The main canals have also been observed to open externally at the margins of the body by short tubes; on the head, e. g. in *Tetrarhynchus*; on the neck as well, e. g. *Scolex Trygonis pastinacae*, some *Taeniae* and also on the joints, e. g. *Bothriocephalus punctatus*, *Triaenophorus*, *Taenia osculata*. Two such openings in every

<sup>1</sup> According to Moniez ('Les Cestodes,' p. 185 et seqq.) the ventral vessel in *Taeniae* belonging to the type of *T. serrata* becomes lacunar; the dorsal appears to vary much. The cross anastomosis mentioned later on connects only the ventral vessels. But in the abortive joints of *T. crassicollis* and in *Tetrarhynchus claviger* both vessels have their cross anastomoses, which may fuse medianly; and in the first-named there is evidence for a connection between the ventral and dorsal vessels, establishing thus a circular communication.

joint, one on each side, have been observed in the immature *Schistocephalus* (Riehm<sup>1</sup>). These 'foramina secundaria' are probably more common than is usually supposed. The excretory vessels of the scolex are continuous with those of the proscölex. The latter appear to form a network, and open posteriorly by a pulsatile vesicle. The contents of the excretory canals, when extruded from the pulsatile vesicle or the foramina secundaria, appear to be immiscible with water. The granules suspended in the liquid are sometimes calcareous in nature (see p. 227).

All Cestoda are hermaphrodite. The male organs consist of a large number of vesicular testes, of delicate efferent canals, of a vas deferens which receives the latter and terminates in an evaginable portion or 'cirrus' surrounded by a muscular envelope or 'cirrus sac.' The testes are more or less globular, numerous, i. e. several hundreds in each joint of a large tapeworm, but in the tapeworms of Birds especially only 2-3, scattered, and usually confined to one aspect of the body—hence termed dorsal (*supra*). The vasa efferentia are extremely fine tubules, difficult to see unless naturally injected with sperm. They unite *inter se*, but eventually open by a larger or smaller number of canals into the vas deferens. This organ may be single, or, as in *Schistocephalus* and *Ligula*, double. It becomes as sperm collects, disposed in loops or coils, and at the same time dilated, especially towards its termination. In *Bothriocephalus latus*, *Schistocephalus*, and *Ligula* the dilatation or vesicula seminalis is surrounded by an envelope of chiefly longitudinal muscle-fibres and forms a globular or ovoid body. The termination itself of the duct is single, usually slightly coiled and is evaginable; the evaginated portion constitutes the cirrus or penis. The outer surface of the cirrus (the inner before evagination) is in some instances armed with spines, e. g. in *Echeneibothrium*. The female organs consist of two ovaries or germaria, of vitellaria, or the homologous 'albumen gland,' a shell gland, uterus, vagina, and spermatheca. The germarium is rarely single, as in *Caryophyllaeus* and *Ligula*. It consists either of branching anastomosing tubes, as in the larger *Taeniae*, *Bothriocephalus*, *Schistocephalus*, and *Ligula*, or of a small number of vesicles attached to a slender duct, as in *Taeniae*, with narrow joints, e. g. *T. perfoliata*; or it may be vesicular, and either lobed, e. g. *T. lineata*, or simple as in *Caryophyllaeus*. The vitellarium has much the same structure as the germaria in most *Taeniae*, e. g. *T. solium*, *T. mediocanellata*, and is a single gland placed near the posterior margin of the joints<sup>2</sup>. In other *Taeniae* it is vesicular, e. g. *T. echinococcus*, and may be double, e. g. *T. lineata*. It may have the form of a series of vesicles ranged along either side of each joint, each series with its own duct (=vitello-duct), the

<sup>1</sup> Quoted by Kiessling, A. N. 48, (1), 1882, note, p. 264.

<sup>2</sup> According to Moniez ('Les Cestodes,' p. 194 et seq.), this organ in the *Taeniae* named and their allies, e. g. *T. serrata*, is an ovary or germarium.

two ducts uniting, as is the case in many tape-worms inhabiting fish, e. g. *Tetrarhynchidae*, *Tetraphyllidae*, *Caryophyllaeus*. Or, as in *Bothriocephalus* and *Ligula*, etc. it consists of a large number of vesicles, lying close under the subcuticula, and scattered over the sides of both aspects of the joints in *Bothriocephalus*, over the dorsal aspect and the sides of the ventral aspect in *Schistocephalus* and *Ligula*. The vesicles are connected by a network of ductules from which a number of ducts proceed and unite into a common vitello-duct<sup>1</sup>. The shell gland or 'Mehlis' gland' usually consists of a large number of unicellular glands surrounding at one point and opening into, the duct leading to the uterus. In *T. lineata* however it consists of an inner layer of radial columnar cells and an outer of cells more or less flattened. The uterus, apparently absent in *Caryophyllaeus*, is a tube disposed in *Taeniae* with narrow joints, e. g. *T. perfoliata*, cross-wise, but in other instances lengthwise, in the joints. It is convoluted and opens externally by a separate aperture of its own in the *Pseudophyllidea*, but in all other Cestoda it is closed, and as the ova accumulate, it increases in size and may develop lateral offsets, especially in the larger *Taeniae*, or it may become divided into several portions<sup>2</sup>. The vagina is a narrow tube, of variable length, sometimes convoluted, often provided with internal hooks or spines, and in most instances dilated at its inner end to form a receptaculum seminis or spermatheca. In *Schistocephalus* and *Ligula*, however, there appears to be no special dilatation, but sperm collects at various points in the course of the tube. The innermost extremity of the vagina generally ends in a tube which receives (1) the ducts of the germaria, (2) the vitello-duct, and (3) the shell-gland, close to the commencement of the uterus. Certain *Taeniae*, sometimes termed generically *Dipylidium*, e. g. *T. elliptica* of the dog, have in every joint a right and left set of genital organs. But the uterus is common to the two sets and has the form of a network with marginal caeca, and the germarial ducts also enter the receptaculum seminis. The external apertures of the cirrus and vagina are placed close together, usually in a depression surrounded by a more or less prominent margin. The depression or sinus genitalis has a single external pore. It is placed commonly on one of the margins of the joints, frequently alternating from one side to the other in successive joints. Or it is placed on the ventral aspect of the joints as in some *Taeniae*<sup>3</sup>, and in the *Pseudo-*

<sup>1</sup> In *Ligula* successive germaria are connected, according to Moniez. In both *Schistocephalus* and *Ligula* the vitellarian follicles and testes do not appear, according to Kiessling, to be delimited from one another in adjoining proglottides; the vitellarian ductules are continuous throughout the body; A. N. 48, (1), 1882, p. 276.

<sup>2</sup> In *T. lineata* the ova accumulate finally in the cavity of the exhausted shell-gland which marks the commencement of the uterus. A resistant calcareous shell is then formed round them.

<sup>3</sup> *T. lineata* is an example. Hamann proposes the generic name *Ptychophysa* for these *Taeniae*. *Pt. lineata* has (1) the aperture of the sinus on the surface of the joints; (2) the vagina opening

*phyllidea* except *Triaenophorus*. The aperture of the cirrus into the sinus genitalis usually lies in front of, or anteriorly to, that of the vagina, but in some of the *Taeniae* with narrow joints the two apertures are side by side, e.g. in *T. perfoliata*<sup>1</sup>. In *Schistocephalus* and *Ligula* the male and female apertures are ventral, but there is no sinus; the uterus opens near to them and all three apertures are in the adult disposed in a straight line crosswise, but not always in the same order from right to left. The uterus of *Bothriocephalus* opens posteriorly to the genital sinus, of *Triaenophorus* anteriorly, and, unlike its genital ducts, on the surface of the joints.

Self-impregnation appears to be common if not universal; indeed, there does not appear to be the slightest evidence for the fertilisation of one joint by another; and if such an occurrence happens, it must take place by the accidental contact of individuals inhabiting side by side the same host<sup>2</sup>. The egg is composed of two sets of elements—the germ-cell derived from the germarium, and the vitellogenous cells or the secretion derived from the vitellarium. The germ-cell is nucleated and hyaline as a rule. In *Leuckartia* and *Abothrium* it is said to absorb the vitelline granules set free by degeneration of the vitellogenous cells, but in other instances the latter appear either to retain their integrity or else break down as in the *Taeniae* into a more or less granular albumen. The germ is impregnated, and together with the vitelline cells or secretion enters the uterus where it is surrounded by a shell, the material of which appears to be derived from Mehlis' gland (*supra*), inasmuch as the latter reaches its greatest development at the time when germs enter the uterus. The shell is delicate in the *Taeniae* and where the embryo is formed during the sojourn of the ova in utero, but resistant and furnished with an operculum where as in some species of *Bothriocephalus*, in *Schistocephalus*, *Triaenophorus*, and *Ligula*, it lies in water for a shorter or longer period. The shell is sometimes furnished with processes, e.g. in *Calliobothrium Eschrichti*, which however appear in *Taeniae* to be accidental formations. The ova of certain fish tapeworms turn green or black on exposure even for a few moments to light. The embryo is formed by the fission of the germ-

anteriorly to the cirrus; (3) the uterus at a certain period convoluted; (4) a peculiar shell-gland (*supra*); egg-shell hyaline, ovate as in *Pseudophyllidea*. In all four points it differs from a typical *Taenia*. Cf. Zschokke on sexual organs of *T. litterata* from the Fox, Z. A. viii. 1885.

<sup>1</sup> Van Beneden in his *Vers Cestoides* sometimes figures the cirrus of fish tapeworms as posterior to the vagina. Leuckart states that this is an error so far, at least, as concerns the genus *Tetrarhynchus*.

<sup>2</sup> The cirrus has been observed in the vagina of the same joint in *Taenia Echinococcus* by Leuckart; in *Phyllobothrium Lactuca* by P. J. van Beneden, who witnessed the emission of sperm. 'Depuis,' adds the latter, 'j'ai vu ce phénomène se reproduire dans d'autres espèces' (*Vers Cestoides*, p. 64). Sommer states that in *T. mediocanellata* the sperm passes into the sinus genitalis, and regurgitates into the vagina owing to the closure of the pore. The protrusion of the cirrus hinders impregnation in this case (Z. W. Z. xxiv. 1874, pp. 520-21). See also Moniez on *T. Giardi*, C. R. lxxxviii. 1879.

cell alone. It has been found in those instances which have been accurately investigated, that the superficial cells of the embryo give origin successively to two envelopes—(1) an outer, which is very delicate in *Ligula* and other *Pseudophyllidea*, but in *Taeniae* constitutes an albuminogenous layer; (2) an inner, which loses its cellular character and is ciliated in *Ligula*, *Triaenophorus*, *Schistocephalus*, and some species of *Bothriocephalus*, but is non-ciliated and capable of creeping movements in other species and in certain *Taeniae* inhabiting water birds and fresh-water fish; whilst in most other *Taeniae* it constitutes the chitinogenous layer and is transformed into a firm chitinoid embryonic shell (cf. p. 227–8 *ante*). When the shell is non-resistant it increases in size during the evolution of the embryo and eventually disappears.

The chitinoid shell is lost when the Taenian embryo enters the stomach of its first host. The soft ciliated or non-ciliated coat of the *Pseudophyllidea*, &c. is stripped off after a time, a gap previously appearing between it and the contained embryo; it is possible, however, that this occurrence takes place normally only after the entry of the embryo into its first host. The embryo itself is cellular, and provided as a rule with six hooks arranged in pairs close together at one pole. The number of hooks may be increased<sup>1</sup>. The muscles which move these hooks are sometimes visible as delicate lines. The embryo itself is composed of cells, among which a superficial set may be distinguished from a more central, the former appearing to grow round the latter<sup>2</sup>. It is possible that the former may represent an epiblast, the latter a hypoblast. After its entry into the first host (p. 656) the embryo or proscoplex grows and its tissues become differentiated. The account given of *T. serrata* p. 230 may be considered as typical. The adventitious connective tissue cyst formed by the metamorphosed lymph cells of the host is not (?) present when the first host is a non-vertebrate. The size attained by the proscoplex varies much. When its central cells liquefy, as in many *Taeniae*, and it is large, it is more or less globular in shape; when they do not liquefy and it is large, it assumes an elongated shape, e.g. in *Tetrarhynchus*. It sometimes grows into an irregular or branched form, due apparently to the influence of the tissues surrounding, e.g. the racemose form of *Cysticercus cellulosae* from the base of the human brain. It may multiply asexually as in the formation of brood capsules or daughter vesicles in *Echinococcus*, in *Staphylocystis* and *Urocystis* which inhabit the Myriapod *Glomeris limbatus*. It gives origin to a head and neck=scolex, except in *Echinococcus*, in which the scolices originate from brood-capsules only, or the proscoplex and its daughter-

<sup>1</sup> Cf. Leuckart, Parasiten (ed. 2), pp. 417–18; Hamann, Z. W. Z. xlii. p. 728. The entire absence of hooks in some cases, asserted by J. P. van Beneden (Vers Intestinaux, p. 237), is extremely doubtful, and in certain instances, e.g. *Ligula*, *Bothriocephalus*, is known to be incorrect.

<sup>2</sup> Cf. E. van Beneden, Archives de Biol. ii. p. 198; Hamann, Z. W. Z. xlii. p. 728.

vesicles sometimes grow and multiply without giving origin to scolices at all. The scolex develops from a small mass of cells: see p. 230. The majority of non-sexual Cestoda have the *Cysticercus*-form, i. e. a single scolex in connection with each proscœlex. The *Coenurus*-form, i. e. many scolices in connection with a single proscœlex, occurs in *T. Coenurus*<sup>1</sup>, and perhaps in *Triaenophorus*. Brood-capsules which give origin to several scolices are distinctive of *T. Echinococcus*; or to one scolex, of an Echinococcoid inhabiting the Earthworm<sup>2</sup>.

The scolex of *Ligula* and *Schistocephalus* develops joints and immature sexual organs while still within the first host, a Stickleback; that of *T. crassicollis* (= *Cysticercus fasciolaris* of the Mouse) develops non-sexual joints under similar conditions which however are digested when transferred to the stomach of the Cat, in this instance the final host. But in other Cestoda joints and sexual organs appear only when the scolex reaches its last resting-place.

Though many Cestoda are known, the life histories of relatively few have been traced. The most important tapeworms inhabiting Man are—*T. solium*, the *Cysticercus cellulosae* of the Pig, &c. and man himself; *T. mediocanellata*, the *Cysticercus Bovis* of the Ox; *Bothriocephalus latus*, the non-sexual state of which inhabits the Pike and Burbot (*Lota vulgaris*), perhaps however only as intermediate hosts; and *T. Echinococcus*, but in the non-sexual state only. The chief forms found in the Dog are given

<sup>1</sup> It is possible that there is more than one species of *Coenurus*. The identity of the two forms occurring in the Sheep and Rabbit has not been established, and there are others known.

<sup>2</sup> Villot has proposed to classify the cystic forms of *Taeniae* as follows:—

I. Cystic forms properly so-called. 'The caudal vesicle originates from the *Proscœlex* by simple growth and structural modification, without the production, strictly speaking, of any new part.' *Cysticercus*, *Coenurus*, *Echinococcus*.

II. Cystic forms 'in which the caudal vesicle originates from the *Proscœlex* by budding, i. e. by the addition of a new part' = Cysticercoid forms. There is a head, the future *Scolex*; a body and caudal vesicle, or cystic portion; and a blastogen = *Proscœlex*, 'which preserves its autonomy and embryonic characters.' There are two subdivisions.

A. The caudal vesicle is formed by endogenous budding. *Polycercus*, the blastogen gives origin to a number of individuals which are contained within it; *P. Lumbrici*, the Echinococcoid form from the Earthworm mentioned in the text. *Monocercus*, a single individual is formed and contained within the blastogen; *M. Arionis* (= *Cysticercus Arionis*) where Villot considers what is usually held to be an adventitious cyst as the blastogen; *M. Glomeridis*, from *Glomeris limbatus*; and perhaps some others.

B. The caudal vesicle is formed by exogenous budding. *Cercocystis*, a single individual is produced by the blastogen and remains in connection with it; *C. Tenebrionis* (Stein, Z. W. Z. iv. 1853, p. 205); *Staphylocystis*, the blastogen produces a colony which remain in connection; *St. bilarius* & *St. micracanthus*, both from *Glomeris limbatus*. *Urocystis*, the blastogen produces a series of individuals which are detached; *U. prolifera* from *Glomeris limbatus*. *Cryptocystis*, the blastogen forms a single individual which is detached; *C. Trichodectis* (= *Cysticercus T. ellipticae*), the strobila of which is *T. elliptica* of the Dog (Melnikow, A. N. 35, 1, 1869, p. 62). See Villot, A. Sc. N. (6), xv. 1883.

Braun has proposed to divide the non-sexual forms of Cestoda into (1) *Cysticerci* with a vesicle containing much liquid; (2) *Cysticercoides* with little fluid in the vesicle; (3) *Plerocerci*, forms with a small but solid *Proscœlex*; (4) *Plerocercoides*, forms with a solid elongated *Proscœlex*.

on p. 225. The Cat gives shelter to *T. crassicollis* (*supra*) and *T. elliptica* (p. 225).

The duration of a Cestode's life is unknown. It probably varies. The proscolices of *Echinococcus* (= hydatids, acephalocysts) have been known to persist for thirty years, and the strobila of *T. mediocanellata* five, six, seven, nine, or even eleven years. A *Cysticercus cellulosae* (= *T. solium*) has been observed in the eye for twenty years.

*Archigetes Sieboldi*, which occurs in a sexual scolex stage in the coelome of *Tubifex rivulorum*, an Oligochaete, is about 3 mm. long. It consists of an oval body, the scolex, about 1-1.3 mm. long, and a cylindrical tail, the prosclex, which is attached to a pit at the end of the body, and bears at its other end three pairs of hooks. Both parts are capable of motion. The scolex has two grooves, one on either side the head. There are eight longitudinal excretory vessels, and a vesicle opening at the insertion of the tail. The testes are placed anteriorly; the vitellaria, one on each side of the body. The genital aperture is ventral, and is the common exit of the vas deferens, a vagina or oviduct, and a uterus separate from the latter. Leuckart, Z. W. Z. xxx. 1878, Suppl.; Gruber, Z. A. iv. 1881.

The family *Amphilinidae* contains two genera, *Amphilina* from the coelome of the Sturgeon, *Amphiptyches* from the intestine of *Chimaera*. The body is flat, and like that of a Distome, with a sucker at its anterior pole. In *Amphilina* a number of unicellular glands open into the sucker<sup>1</sup>, and are surrounded by the retractor muscles of that structure. Its nervous system consists of two anterior swellings connected by a transverse commissure, and two lateral nerves, which unite posteriorly and give off branches. The testes are vesicular; the vas deferens opens posteriorly; the germarium is single, the vitellaria double, one on each side, and structurally resembling the same organs in a Trematode; the vagina opens near the vas deferens, the uterus anteriorly. The embryo is ciliated anteriorly, and has ten hooks. The family has been supposed to connect the Cestoda and Trematoda. Cf. Lang, Mitth. Zool. Stat. Naples, ii. 1881, p. 394; Salensky, Z. W. Z. xxiv. 1874; Grimm, Z. W. Z. xxv. 1875. *Amphiptyches*, Wagener, Archiv f. Anat. und Physiol. 1852; cf. Id. A. N. 24, 1, 1858.

The Class is divisible into the following groups, the value of which is uncertain, but they are generally regarded as families.

1. *Taeniadae*: head provided with four suckers, and sometimes with a single or double circlet of hooks. Proglottides well-defined and cast off. No uterine aperture. *Taenia*, *Ptychophysa*?, *Dipylidium*?

2. *Tetraphyllidae*: head with four very mobile and distinct suckers. Proglottides well-defined and cast off; inhabit Selachians. Subdivisible into (a) *Phyllobothridae*, e. g. *Echineibothrium*, *Phyllobothrium*; and (b) *Phyllacanthinae*, with two to four hooks to each sucker, e. g. *Calliobothrium*.

3. *Tetrarhynchidae* (= *Phyllorhynchidae*): head provided with four suckers and four protractile proboscides armed with hooks. Non-sexual form occurs chiefly in Teleostean fishes, the sexual in *Elasmobranchii*. *Tetrarhynchus*.

4. *Diphyllidae*: the neck and two suckers armed with hooks. *Echinobothrium*, in the Ray.

<sup>1</sup> Traces of this sucker are found together with glands in some *Tetrarhynchidae*. See Lang, cited below.

5. *Pseudophyllidea*: head provided with two sucking grooves. Proglottides not always well defined. A uterine aperture. Embryo, so far as known, ciliated, and egg-shell provided with an operculum. *Bothriocephalus*, *Triaenophorus* (= *Tricuspidaria*), *Solenophorus*, *Schistocephalus*, *Ligula*. The genus *Duthiersia* appears to belong here.

6. *Caryophyllaeidae*: no proglottides. Head end expanded and mobile. ? development. *Caryophyllaeus*, from the intestines of Cyprinoid fishes.

7. *Amphilinidae*: *supra*, p. 665.

The position of the genus *Leuckartia* of Moniez, and P. J. van Beneden's *Abothrium*, is uncertain.

For lit. see pp. 228, 238.

*Duthiersia* (from *Varanus*), Perrier, A. Z. Expt. ii. 1873. *Leuckartia* (from Salmon), Moniez, 'Les Cestodes,' Travaux Zool. Inst. Lille, iii. pt. 2. *Abothrium* (from Cod), Id. *ibid.* *Polyocephalus* (from *Rhinobatis*), Braun, Arb. Zool. Zoot. Inst. Wurzburg, iv. 1877-78. *Echinocoid from the Earthworm*, Leuckart, 'Parasiten,' i. (ed. 2) p. 464.

*Origin of Cestodes*, Schneider, in his Zool. Beiträge, i. 1885.

*Head of Tetrarhynchus*, Pintner, Arb. Zool. Inst. Wien, iii. 1881.

*Nervous system of Tetrarhynchus*, Lang, Mitth. Zool. Stat. Naples, ii. 1881; of *Ligula*, *Schistocephalus*, and *Bothriocephalus*, Niemiec, Arb. Zool. Inst. Wien, vii. (1), 1886.

*Genital organs of T. litterata*, Zschokke, Z. A. viii. 1885; of *T. elliptica* and *Triaenophorus*, Steudener, Abhandl. Natf. Ges. zu Halle, xiii. 1877.

*Direct development of T. serrata* (!), Mégnin, A. N. H. (5) xi. 1883. *Cysticercus racemosus* (a form of *C. cellulosa*), Zenker, Beiträge zur Anat. &c. als Festgabe zu Jacob Henle, Bonn, 1882. *Cystic forms of Taeniae*, Villot, A. Sc. N. (6), xv. 1883. *Scolex of Tetrarhynchus*, Hoek, Nederland. Archiv f. Zoologie, v. 1879. *Embryonic development of Bothriocephalidae* (= *Pseudophyllidea*) Schauinsland, J. Z. xix. 1885. *Host of Bothriocephalus latus*, Braun, Zur Entwicklungsgeschichte des breiten Bandwurmes, Studer, Wurzburg, 1883; cf. Z. A. iv., v., vi. *Life history of Ligula*, Donnadieu, Journal de l'Anat. et Physiol. xiii. 1877.

## CLASS TURBELLARIA.

*Unisegmental Vermes*<sup>1</sup> with a ciliated ectoderm in which are found rhabdites, pseudo-rhabdites, or nematocysts; with two cerebral ganglia connected transversely, each of which is continued backwards into a long nerve, with a mouth and muscular pharynx, but no anus; with an excretory system of tubes ending in flame-cells, and a coelome formed by spaces between the parenchyma and viscera when it is present at all. Respiratory and circula-

<sup>1</sup> The marine Triclad, *Gunda segmentata*, is divided (but not externally) into 25 segments by septa formed chiefly by the dorso-ventral muscles. There are 25 simple and paired lateral branches to the intestine; a pair of ovaries with 24 pairs of vitellaria, and 25 pairs of testes. The genital organs correspond to the septa. The excretory canals open dorsally and probably by segmentally arranged pores. A similar segmentation is indicated, but much less markedly, in other *Tricladida*.



tory organs wanting. *Hermaphrodites with rare exceptions and the ovary commonly divided into a germarium and vitellarium.*

The small Turbellaria are mostly cylindrical, or the ventral surface is flat, the dorsal convex: the larger Turbellaria are usually broad and thin, with the exception of those inhabiting damp earth which are long, narrow, and thick bodied. The anterior extremity is usually wider than the posterior, but it may be narrow and pointed, and partially or wholly retractile, forming the proboscis of the Rhabdocoele *Proboscida* and some few genera. It is occasionally provided with tentacles as in the Rhabdocoele genus *Vorticeros* and in many *Polycladida*. These tentacles are either *nuchal*, and then solid, contractile, sometimes retractile into pits and placed one on either side the nerve ganglia (*Planoceridae*), or *marginal* and anterior, and then either lobes (*Pseudoceridae*) or pointed processes (*Euryleptidae*) into which branches of the intestine pass. The ectoderm consists of a single layer of ciliated cells sometimes covered by a delicate cuticle. Pigment rarely occurs in them, but the majority contain rhabdites—clear homogeneous smooth rods pointed at each end and formed probably as a secretion either in the superficial cells themselves (*Polycladida*), or also in cells of the ectoderm imbedded in the parenchyma (most *Tricladida*, all *Rhabdocoelida*). Pseudorhabdites occur in *Alloiocoela*: they are rod-like, but granular and with an uneven surface. True nematocysts are rarely found, e.g. in *Microstoma lineare*<sup>1</sup>. Some of the ectoderm cells are glandular, but unicellular glands occur also in the parenchyma with ducts leading up to the surface. Adhesive cells with processes and a sticky secretion are commonly found on the ventral aspect at the posterior end of the body, but not in the adult *Polycladida* (?), though sometimes present in the larva. Tactile cells with bundles of immobile but bendable hairs are met with in all *Polycladida* and in some other Turbellaria. Beneath the ectoderm is a basement membrane, the thickness of which varies much. It is stout and contains richly branched cells in *Polycladida*. The musculature of the body forms a continuous investment. In the *Rhabdocoelida* it consists of an outer circular, and inner longitudinal layer of fibres which are reversed in position in *Microstoma lineare*, and in many instances have interposed between them a diagonal layer. The layers are more complicated in *Polycladida*, but consist generally speaking of an outer and inner longitudinal layer, the latter absent on the dorsal surface, inclosing between them a layer of circular, and two layers of diagonal, fibres. The layers vary in *Tricladida*, but the outer layer is circular. Many *Polycladida*

<sup>1</sup> Still more rare are the structures known as sagittocysts, i.e. capsules similar to those of nematocysts, but inclosing a needle-like rod, which is expelled on irritation of the animal. It is very rare to find a Rhabdocoele without any of the structures named, e.g. the parasitic *Graffilla*, or *Prorhynchus stagnalis*. There is some doubt as to whether the rhabdites are expelled, as is usually supposed. They may serve as a skeleton. See Iijima, Z. W. Z. xl. pp. 372-74.

possess a muscular sucker situated near the centre of the body: others (*Leptoplanidae*) have a sucker between the male and female generative openings. A system of dorso-ventral fibres traverses the parenchyma. Its fibres branch at each end, and are attached to the basement membrane. The parenchyma consists in *Acoela* of a soft granular protoplasmic mass into which the food passes, a digestive tract not being differentiated. In *Rhabdocoela* and *Alloicoela* it consists of delicate connective tissue-fibres with nuclei which form a reticulum, and connective tissue cells. The coelome is formed by the spaces between these elements and the viscera. The degree to which it is developed varies much, and the fluid which fills it is usually colourless. On the contrary the parenchyma of *Polycladida* is composed apparently of nucleated cells, containing vacuoles, and filling up the whole space between the viscera. A coelome is consequently wanting. Pigment is scattered in the parenchyma, in *Rhabdocoelida* in special cells<sup>1</sup>. *Convoluta paradoxa* possess peculiar yellow cells, containing plates of diatomin (?); *Vortex viridis*, *Convoluta Schultzii*, &c., cells containing chlorophyl and starch granules. These coloured cells usually lie near the integument and are perhaps symbiotic algae (see pp. 242-4).

A nervous system does not exist in *Acoela*<sup>2</sup>. In other *Turbellaria* there are a couple of ganglionic swellings usually placed anteriorly, sometimes, as in *Polycladida*, more posteriorly, in front of or above the pharynx. The two ganglia are usually more or less closely united, and each of them gives origin, except in *Polycladida*, to a nerve which runs backwards ventral to the digestive system. These cords are rarely united by a transverse commissure in *Rhabdocoela*, but in the *Tricladida* they possess many such commissures. The *Polycladida* have several stout nerves radiating from the ganglia, as well as others from the longitudinal cords. Numerous commissures unite them one with another. The branches given off by the lateral nerves ultimately form a sub-muscular plexus. In addition to the tactile ectodermic cells which are chiefly grouped about the anterior region of the body, or in *Polycladida* on the dorsal papillae and tentacles, both eyes and auditory organs are found. As to the former, pigment spots without a lens lie in the ectoderm of *Acoela* and the *Microstomidae* (*Rhabdocoela*). But in all other *Turbellaria* the eyes when present lie in the parenchyma. In the *Rhabdocoelida* they sometimes lie in the ganglia themselves. There are usually two or four in this group, and in

<sup>1</sup> The fore-part of the body in *Derostomum(-a) Benedeni* is coloured red with haemoglobin (Francotte).

<sup>2</sup> But *Convoluta Schultzii* is stated by Delage (A. Z. Expt. (2), iv. 1886) to have a ganglionic mass surrounding the otolith, with two other and smaller masses connected *inter se* and to it. Six parallel longitudinal nerve-fibres extend backwards. They lie apparently on the dorsal aspect, are connected by transverse commissures, and unite posteriorly in a plexus. There is a peculiar frontal sensory organ. Lang mentions (p. 672, *Polycladen*) an Acoelan with well developed nervous system.

the *Tricladida*, but in the latter they are sometimes more numerous, and in a terrestrial form from Brazil extend along the lateral margins. They are generally numerous in *Polycladida*, two groups lying constantly above the ganglia, others upon the tentacles, or where these are absent on the anterior and lateral margins of the body. The most complex eye consists of a pigmented cup into which project visual rods with retinal cells at their outer ends. These cells are continuous with the optic nerves. Such eyes are found in *Tricladida* and all *Polycladida*. In the latter group they increase by division, whereas in some fresh-water *Tricladida*, e. g. *Polycelis nigra*, the eyes which are simple in structure have been observed to fuse. Otolithic vesicles are very rare in *Dendrocoelida*, and when present in the *Rhabdocoelida* there is usually only one. It lies anteriorly and consists of a vesicle with fluid contents and suspended calcareous otoliths. A pair of ciliated grooves, one on each side, lie close to the ganglia in many *Rhabdocoela*. In fresh-water *Tricladida* and the *Polycladida* a ciliated groove extends along the anterior margin of the body, and backwards laterally on the dorsal aspect. These structures appear to be sensory.

The mouth varies much in position: it may be anterior, median, or posterior. It leads, as a rule, into a muscular pharyngeal sac, within which lies a muscular pharynx. The pharynx can be extended from the mouth, and is an organ for the prehension of food. It assumes various forms. In the *Acoela* the mouth leads into a short tube which ends in the parenchyma, into which the food passes. In other Turbellaria there is an intestine, simple and saccular in *Rhabdocoela*, lobed or irregular in *Alloicoela*, branched in *Dendrocoelida*. In the last-named group it consists, in *Tricladida* of three chief branches, one extending forwards above the ganglia, and one backwards on each side, all beset with secondary branches; in *Polycladida* of a main intestine, which usually sends a branch forwards above the ganglia, and gives off a variable number of paired lateral branches, never, however, less than four. These branches divide in their turn, and the points of division are often constricted. In some instances the ultimate divisions form an anastomosing network. The epithelium of the main intestine of *Polycladida* is ciliated; that of its branches, like the intestinal epithelium of other Turbellaria, emits pseudopodial processes which absorb nutriment. Digestion is therefore parenchymatous. The cells often contain vacuoles, concretions, and coloured granules. The main intestine of *Polycladida* possesses a well developed musculature, while the constrictions of the lateral branches are provided with both constrictor and dilator muscles. The branches of the intestine in three genera of *Polycladida* open externally through the ectoderm<sup>1</sup>. A nervous commissure generally surrounds the branch of the intestine extending forwards above the ganglia.

<sup>1</sup> *Yungia* with dorsal, *Cycloporus* with marginal apertures. *Oligocladius* has a doubtfully present pore situated dorsally and posteriorly.

A nephridial or excretory system is absent in *Acoela*. In other *Rhabdocoelida* it may consist of a single median trunk opening posteriorly, or of two lateral trunks which either unite and open posteriorly, or remain independent, and then open ventrally or posteriorly, or, as is most usual, into the pharyngeal cavity. It is rare for them to open near the centre of the ventral surface, and to be connected anteriorly by a cross branch, from which a canal passes backwards on each side parallel to the main trunk. With these main trunks finer vessels are connected, which form a more or less distinct network. Canalicules terminating in flame cells open into this network, or into the blind terminations of its branches in *Mesostoma Ehrenbergi* and a number of other Rhabdocoelids (*Vortex*, *Prostomum*, *Monocoelis*, &c.). Cilia may occur in the main or in the secondary canals. In the *Tricladida*, *Polycoelis nigra* possesses both on the ventral and dorsal aspects a network of canals in which there is an undulating membrane. Straight vessels lead to the surface of the body, and probably open upon it; and short canalicules ending in flame-cells are connected to the network. In other cases there appears to be a pair of dorsal, or as in *Gunda*, of dorsal and ventral, lateral canals, which anastomose anteriorly. These canals open by more or fewer dorsal pores, which in *Gunda* are segmentally arranged. There is a system of finer branching canals which end in flame-cells. The excretory system of *Polycladida* is scarcely known. In *Thyrsanozoon*, Lang detected large undulated canals which anastomose, and are provided with stout lateral branches which approach the ectoderm, and probably open externally. Fine branched canals are connected to the main vessels, and end in flame-cells, and small cells with large cilia occur in the course of the canals. It is certain that in some instances, and it is probable that in all, the excretory canals are really intra-cellular<sup>1</sup>.

All *Turbellaria* are hermaphrodite except the Rhabdocoelae genera, *Microstoma* and *Stenostoma*. But the male organs tend to ripen before the female (= successive hermaphroditism) in *Acoela*, in *Polycladida*, and perhaps in others. The glands are paired with the exception of the germarium in some *Rhabdocoela*. The testes in *Rhabdocoela* are two large compact glands, in all other Turbellaria scattered and numerous globular follicles. Specialised ducts are not developed in *Acoela*, *Alloiocoela*, and some *Rhabdocoela*. The two vasa deferentia when present receive the sperm from finer vessels, and either open together or separately into the

<sup>1</sup> The structures called by Geddes *Pulsatella Convolutae*, and found in the Acoelan *Convoluta Schultzii*, are perhaps not parasitic organisms, but indications of an excretory system. They occur in very young specimens indeed. See Delage, A. Z. Expt. (2), iv. p. 150. According to Francotte, the cross anastomosis of the lateral canals in front of the mouth has in *Derostomum Benedeni* an external opening. As to *Gunda*, Lang states that the dorsal and lateral vessels are connected in the septa of the body in which they are convoluted; the efferent branches and pores are similarly situated. He also observed in the same animal that some of the flame-cells were connected by basal processes to the cells of the intestinal epithelium, and that others were actually situated among them.

copulatory organ<sup>1</sup>. They are often dilated into seminal reservoirs, or in some instances a vesicula seminalis is formed from or attached to the penis. One or more accessory glands are usually present, and their secretion is mixed with the sperm. The penis is either a protrusible or an evaginable organ, and is often contained within a sheath and armed with chitinous spines, especially in *Rhabdocoela*. In the Polyclad *Anonymus* there are 2-15 copulatory organs on each side the body, and 2-4 occur in three other instances in the same group. The ovaries are two and simple (*Acoela*, *Rhabdocoele Macrostromidae*); they are numerous and simple in *Polycladida*. In some *Rhabdocoela*, e.g. *Prorhynchus*, the two glands, though simple externally, are functionally divisible each into a germarium and vitellarium, and this division becomes marked externally, and the two parts have their separate ducts in other *Rhabdocoela*; whilst in *Tricladida* there is on each side of the body a single anterior ovary connected to a long oviduct, which is beset on its outer side by follicular or branching vitellaria<sup>2</sup>. Many *Acoela* and *Alloicoela* have no specialised ducts, but the ova like the sperm pass into spaces in the parenchyma. A network of ciliated tubules connects the ovaries of *Polycladida*. They unite into a canal on each side of the body. Each canal is dilated into a uterus, to which accessory glands are attached. The two uteri unite into a common canal, which is dilated and receives a number of shell-glands. Its termination is often muscular, forming a female copulatory organ. The male and female ducts open into a genital atrium in all *Tricladida* and most *Rhabdocoelida*. To this atrium is commonly appended a uterus, and in some *Rhabdocoela* a bursa copulatrix and receptaculum seminis<sup>3</sup>. Or in other *Rhabdocoelida*, and in *Polycladida* with the exception of two genera, the two ducts open separately, the male usually in front of the female, and both behind the pharynx. In *Prorhynchus* (*Rhabdocoele*) and *Stylostomum* (Polyclad) the penis opens into the mouth; and in many *Rhabdocoela* the penis with its chitinous hooks is employed to catch and

<sup>1</sup> Iijima denies this connection between the testes and the vasa deferentia in the fresh-water *Tricladida* which he examined. He thinks that the sperm is set free into the spaces of the parenchyma, and is taken up thence by lateral openings in the walls of the vasa deferentia. But as the latter do not extend far forwards, the sperm of the anteriorly placed testes never reaches them at all. See Z. W. Z. xl. pp. 405-408. When ducts are absent, as in *Acoela*, the sperm traverses the parenchyma.

<sup>2</sup> Iijima states that the vitellaria do not communicate directly with the oviducts in the fresh-water *Tricladida* which he examined. The ducts have openings into the spaces of the parenchyma, and in these spaces the vitelline cells accumulate just as do the spermatozoa. The openings in question are closed each by a peculiar large cell before the vitellaria ripen (Z. W. Z. xl. pp. 415-16).

<sup>3</sup> The uterus of the fresh-water *Tricladida* does not serve as a store-house of ova as do the uteri of the *Polycladida*. It is single, and is probably a gland secreting the material for the cocoon. Albumen glands usually open into its duct (= so-called vagina) or into the oviducts. A structure called 'muscular glandular organ' opens into the atrium genitale, but it appears to be variably present. Its walls are stout and muscular, and Iijima believes that it receives the ducts of various glands. See Z. W. Z. xl. pp. 419-26.

retain the prey. *Macrorhynchus helgolandicus* has a poison dart in connection with the atrium genitale.

The form of the spermatozoon is very variable, especially in *Rhabdocoelida*. There is a reciprocal copulation, but self-fertilisation occurs in the case of the summer ova of many *Rhabdocoela*. The ovum is contained in a shell, or a number of ova within a common shell or cocoon, as in *Tricladida*, some *Rhabdocoelida*, and some *Polycladida*. The last-named usually lay their ova in rows united by a cement. In some *Rhabdocoela* (certain fresh-water *Mesostomidae*) there are thin-shelled summer and thick-shelled winter ova. The egg shell, or cocoon, is formed either by the atrium genitale, by the uterus, or by special glands. In those forms where there are vitellaria, it contains vitelline-cells in addition to the germ-cell. The vitelline-cells retain their integrity, and are devoured by the young Turbellarian at a certain stage of growth. Segmentation is total but unequal, and there is a gastrula formed either by invagination or overgrowth. Development takes place within the parent in the case of summer ova (*supra*). There is a metamorphosis in many *Polycladida*, the larva having a praeoral ciliated ring, which is produced first into four (= Götte's larva) then into eight ciliated processes (= Müller's larva), subsequently absorbed. A few viviparous species are known<sup>1</sup>.

Asexual reproduction by posterior gemmation occurs in the Rhabdocoele family *Microstomidae*; chains of sixteen individuals may be thus formed in *Microstoma lineare*. Transverse fission has been observed in the Triclads *Planaria subtentaculata*, *Planaria* (sp.?), and *Polycoelis cornuta*.

The Turbellaria are carnivorous. They inhabit fresh brackish and salt water, and damp earth. A few Rhabdocoeles are parasitic, the genera *Graffilla* and *Anoplodium* entirely so, the former in marine Mollusca, the latter in or on Holothurians; so too the Triclad *Bdelloura* on *Limulus*.

Two curious Polyclads have recently been described with certain Ctenophore-like characters. These are the *Coeloplana* of Kowalewsky (Z. A. iii. 1880, p. 140) and the *Ctenoplana* of Korotneff (Z. W. Z. xliii. 1886). They resemble Polyclads in the flattened aspect of the body, the general ciliation of the ectoderm, the branched digestive system with ventral mouth. *Ctenoplana* has an outer longitudinal layer of muscles, an inner transverse, as well as dorso-ventral bundles. Both resemble *Ctenophora* in the presence of two solid retractile tentacles, one on each side, at right angles to the plane of the stomach. There is an aborally placed otolith-mass. In *Ctenoplana* this lies, supported by the ends of stiff hairs, in an open depression, at the sides of which the nervous system is situated (?), and there are eight short dorsal rows of ctenophoral plates, arranged as in *Ctenophora*, and lodged in grooves which can be depressed by special muscles. Two branches arise

<sup>1</sup> See Silliman, Z. W. Z. xli. 1885, pp. 59-63. *Mesostoma viviparum* and *Planaria gracilis* from the fresh waters; *Vortex Warrenii*, marine; all N. American.

from the stomach in *Coeloplana*, and pass aborally but end blindly. A right and left opening near the plane of the tentacles is found in the same animal, but what they lead to is uncertain. Both genera appear not to have, unlike both Polyclads and Ctenophores, anything homologous with the ectodermal pharyngeal pouch of the former or stomach of the latter.

It cannot be denied that there is a general resemblance in the symmetry and in the position of the chief planes of the body in the *Polycladida* and *Ctenophora*; in the existence of an oral and aboral pole in some Polyclads and all Ctenophores; both groups are hermaphrodite, and the genital organs are in relation to the digestive system, but there are genital ducts and a coitus in Polyclads, which do not exist in Ctenophores. Certain resemblances are to be found in the mode of segmentation of the ovum, and the persistence of the Gastrula-mouth. But the nervous system of Polyclads can hardly be compared with that of *Ctenophora*, i. e. with the sensory aboral plate and ctenophoral rows of cilia and sub-ectodermic plexus; there is no trace of anything which can pass for an excretory system in *Ctenophora*; the Polyclads possess a true mesoblast, whereas in *Ctenophora* the muscle-cells are either ectodermal, or cells lodged in the supporting jelly into which they are said by most authorities to wander from the ectoderm. Metschnikoff has quite recently described (Z. W. Z. xlii. 1885) the formation in some Ctenophores of a small mass of cells from the primitive endoderm cells close to the Gastrula-mouth, which mass is carried inwards through the central axis to the aboral pole, where it gives rise, so he says, to the musculature of the tentacles and to the wandering cells of the jelly. It is doubtful whether the cells in question can be strictly considered as mesoblast. They form a small aboral group, but extend no further round the body, and the mode in which they shift their place is at least remarkable. For a full discussion of the relationship of *Polycladida* to *Ctenophora*, see Lang, Polycladen, Fauna des Golfes von Neapel, xi. Monograph, pp. 645-667. He regards the Polyclads as the primitive group of Turbellaria.

The Turbellaria are classified as follows—

1. *Rhabdocoelida*: small in size, body cylindrical or depressed.

(a) *Acoela*: no distinct intestine or excretory apparatus; testes follicular; two ovaries; an otocyst; all marine.

(b) *Rhabdocoela*: a straight intestine and complicated pharynx; testes compact; an ovary, or a germarium and vitellarium; otocysts rare; freshwater, marine, or in damp earth (*Prorhynchus sphyrocephalus*; *Pr. stagnalis* sometimes).

(c) *Alloicoela*: intestine lobed or irregular; a pharynx; testes follicular; otocysts in the *Monotidae*: marine except *Plagiostoma Lemani* from the deep water of Swiss lakes.

2. *Dendrocoelida*: large; intestine branched; testes follicular; otocysts very rare.

(a) *Tricladida*: body elongate; intestine with three main branches; a compact germarium, follicular vitellarium; an atrium genitale. *Gunda* marine; *Planaria*, *Dendrocoelum*, *Polycelis*, freshwater; and various Land Planarians, e. g. *Rhynchodemus*, *Geodesmus*, *Bipalium*.

(b) *Polycladida*: body leaf-like, broad; a central stomach; testes and ovaries follicular; with or without a ventral sucker (*Cotylea*, *Acotylea*); marine.

'Planarians,' von Graff, *Encyclopaedia Britannica* (ed. ix.) xix. 1885.

*Rhabdocoelida*, von Graff, *Monographie der Turbellarien*, Leipzig, 1882; cf. Moseley, *Nature*, xxvii. *Convoluta*, Yves Delage, *Études, &c.*, A. Z. Expt. (2), iv. 1886. *Mesostomum*, Jaworoski, Z. A. ix. 1886. *Derostomum Benedeni*, Francotte, *Bull. Ac. Roy. Belg.* (3), vi. 1883. *Graffilla*, Böhmig, Z. W. Z. xliiii. 1886. *Excretory system of Microstoma*, Zacharias, Z. A. viii. 1885. *Development of Acoela*, Pereyaslawzew and Repiachoff, Z. A. viii. 1885.

*Tricladida*: *Gunda segmentata*, Lang, *Mitth. Zool. Stat. Naples*, iii. 1882; of *freshwaters*, Iijima, Z. W. Z. xl. 1884; of *N. American freshwaters*, Silliman, Z. W. Z. xli. 1885. *Land Planarians*, Moseley, Ph. Tr. 164, 1874; Id. Q. J. M. xvii. 1877; Kennel, *Arb. Zool. Zoot. Inst. Wurzburg*, v. 1879. *Transverse fission*, Zacharias, Z. W. Z. xliiii. 1886, p. 271. *Nervous system*, Lang, op. cit. (*supra*).

*Excretory system of Rhabdocoela and Dendrocoelida* (Triclads), Francotte, *Archives de Biologie*, ii. 1881.

*Polycladida*, Lang, *Fauna und Flora des Golfes von Neapel*, xi. Leipzig, 1884.

For *Rhodope Veranii* = *Sidonia elegans*, which appears to be a Turbellarian, but was formerly referred to the non-palliate *Gastropoda*, see von Graff, M. J. viii. 1882; Bergh, Z. A. v. 1882.

#### CLASS CHAETOGNATHA.

This class of Vermes contains two genera, *Sagitta* and *Spadella*; pelagic with the exception of *Sp. cephaloptera*, which is littoral. They occur in all seas. The organism is divided by two septa into three regions, a head, body, and tail. The head has a slit-like mouth on its ventral aspect, is guarded by a hood-like integumental fold on each side, and bears one or two rows of stout spines, and a single row of sickle-shaped setae, or jaws. The body and the tail carry one (*Spadella*) or two (*Sagitta*) pairs of lateral fins, and the tail always terminates with a caudal fin. The body is covered by a many-layered squamous ectoderm with an underlying delicate supporting lamina. The fins contain a gelatinous skeletal lamella, on each surface of which lie fine rods extending outwards from the body beneath the ectoderm. The muscles are striated, broken up into special bundles in the head, but in the body and trunk arranged in four bands, two dorsal and two ventral.

The nervous system consists of a supra-oesophageal ganglion in the head, connected by long commissures to an infra-oesophageal ganglion which lies near the centre of the body. They give off various nerves; the latter especially a very large number, which eventually break up into a fine plexus with nodal ganglion cells. These parts lie in the ectoderm. But two pairs of small ganglia are connected with the supra-oesophageal ganglion, and lie in the mesoderm supplying the muscles of the head. The organs of special sense are: a pair of eyes lying in the ectoderm connected with nerves arising from the supra-oesophageal ganglion; a



band of ciliated epithelium behind the eyes which is disposed in a ring varying in shape in different species, and perhaps olfactory in function; a variable number of tactile organs scattered over the body, tail, and fins, formed of a central row of cells bearing sense-hairs, surrounded by supporting cells.

The alimentary canal consists of a stomodaeum, or pharynx, lined by a single layer of epithelium, and provided with a thin layer of striated muscle fibres running dorso-ventrally, followed by an intestine (archenteron) lined by a single layer of ciliated epithelial cells, some of which appear to be glandular. The anus is ventral, and placed where the body and tail join. The intestine is suspended by dorsal and ventral mesenteric bands which are fenestrated, and divide the coelome of the body into a right and left half. The coelome is roomy, and lined by a layer of epithelium not visible in all places. The tail also contains a coelome, similarly divided by a vertical partition, which appears to originate in a backward extension of the archenteron at the period when its original cavity is obliterated, and before it has acquired its permanent cavity (Hertwig).

The Chaetognatha are hermaphrodite. There are two ovaries lying one in each half of the coelome of the body. Each ovary has a duct in which sperm is often found. It opens laterally on the dorsal side of the lateral fin, where the body and tail join. Two testes, solid cellular ridges, lie, one in each half of the coelome in the tail on its outer wall. Masses of cells are set free into the coelome, and there differentiate into spermatozoa. The cell masses are in constant motion owing to the presence of cilia on the coelomic epithelium. The spermatozoa are filamentous, transversely striated in *Spadella cephaloptera*. They escape on each side by a narrow ciliated canal, which has an internal ciliated funnel, and ends in a dilated vesicula seminalis. The latter has an external aperture in the posterior third of the tail.

The ova are enclosed in a membrane, are transparent, and float on the surface of the water, except in the case of *Sp. cephaloptera*, which attaches them by a gelatinous peduncle to algae. Segmentation is total. There is an invaginate gastrula, and the coelome is formed as a right and left enterocoele. The permanent mouth is formed at the opposite pole to the gastropore, which is closed. There is a stomodaeum; the mode of formation of the anus is unknown. The sexual glands are derived from two cells of the archenteron, which differentiate early, and divide each into two, an ovarian and testicular cell or rudiment.

*Spadella Marioni*, Gourret, An. Mus. Nat. Hist. Marseille, ii. 1884-5.

*Die Chaetognathen*, O. Hertwig, J. Z. xiv. 1880; cf. *Die Wurmfauna von Madeira*, Langerhans, Z. W. Z. xxxiv. 1880. *I Chaetognathi*, Grassi, Monograph v, Fauna und Flora des Golfes von Neapel, 1883.

## CLASS NEMATODA.

*Unisegmental Vermes, with a narrow elongated body of more or less cylindrical shape and tapering to each end. There is a well-developed cuticula, derived from a subcuticula or hypodermis; a peripharyngeal nerve-ring from which six nerves pass forwards and six backwards; a digestive tract divided into three sections, oesophagus, mesenteron, and rectum, and two excretory tubes opening by a common anterior and ventral pore. The sexes are separate; the male usually possesses special copulatory organs in the shape of spicules and of a bursa. Ciliated epithelium is universally absent. Free-living or parasitic. An Alternation of Generations occurs among some of the parasitic genera.*

The body is of a very uniform shape. The anterior portion is filamentous, the posterior thicker in the genus *Trichocephalus*; so too in the female *Trichosoma*, though to a less degree. The head is dilated in *Ichthyonema globiceps*. Cuticular spines may be present, and folds as well, extending down each side of the body, to a greater distance in the female than in the male. The bursal membranes of the latter (*infra*, p. 681-2) must be carefully distinguished from these folds. The male is usually smaller than the female, and its tail is differently conformed, either strongly curved at the apex, or provided with a bursa, and invariably beset with a number of sensory papillae. It is sometimes forked, e. g. in *Pseudalius* (= *Prosthecosacter*) from the lungs of the Porpoise. The free-living genera are all small. Among the parasitic the female *Dracunculus* (*Filaria*) *medinensis* may attain a length of six feet and the female *Eustrongylus gigas*, which inhabits the kidneys of various mammals, that of three feet or more. The greatest number of parasitic Nematoda infest in the sexual state the various classes of Vertebrata.

There is a chitinoid cuticle, which is thin and delicate in the smaller Nematoda, but in the larger becomes much thickened. It then consists of an outer thin and more resistant layer, prolonged inwards to a greater or less distance at the external apertures of the various organs, and an inner thick layer, said to be subdivisible into secondary laminae. The outer layer is frequently marked by transverse lines which give the body a ringed appearance more or less pronounced. The inner layer is fibrous, and the fibres of the different laminae decussate with one another. Cuticular processes occur in the shape of circumoral fringes, of papillae or spines, and lateral membrane-like expansions, variable in breadth and extent. A subcuticula or hypodermis lies beneath the cuticle as a more or less granular layer with sparse nuclei, most numerous posteriorly; but in larger species, such as *Ascaris megaloccephala* from the Horse, *A. lumbricoides* from Man, the subcuticula and its longitudinal thickenings contain numerous fibres which take a more or less circular direction, and have

been supposed to be muscular in nature, and continuous, in part at least, with the extremities of the muscle-cells. These fibres are especially well developed in the rectum. The subcuticula is thickened internally, as a rule in four longitudinal lines,—a median dorsal, a median ventral, and two lateral, one on either side. The latter are especially prominent, and are generally known as the ‘lateral areae.’ The dorsal and ventral lines are probably always present, the lateral except in *Trichocephalus*, and perhaps some others. Cutaneous glands are absent<sup>1</sup>. The muscles of the body-wall consist of a single layer of longitudinally disposed muscle-cells. In these cells the contractile substance is fibrillate, and forms a superficial stratum on the basal part of the cell, which is applied to the subcuticula in the *Meromyarii* of Schneider (e. g. *Oxyuris*, *Strongylus*), or on the base, the sides, and ends of the cells, as in other Nematoda. The body of the muscle-cells consists of a feebly granular protoplasm or medulla in which a nucleus may be found. This medulla projects freely on the inner or coelomic aspect of the cell to a variable degree, and over a variable extent of that aspect. The projection is greatest in the *Coelomyarii* of Schneider (e. g. *Ascaris*, *Filaria*), in which protoplasmic bands connect it to the median ventral or dorsal lines, to the lateral areae, or to both. The ends of the muscle-cells are said to break up into processes, which are traceable into the fibres of the subcuticula. The number of cells visible in a transverse section is usually very great, but in the Meromyarian Nematoda there are only eight, two lying in each of the four quadrants limited by the median lines and lateral areae<sup>2</sup>. In addition to the body-muscles there are certain others; the exsertors and protractors of the male spicules; a paired ventral muscle which is the cause of the curvature in the tail. The radial muscles which are connected to the mesenteron and are of all, those most obviously prolonged into the fibres of the subcuticula; the dorso-ventral and latero-ventral muscles which cross the body behind the anus; the bursal muscles which pass in a similar direction, and are present only in the male; have a different structure. They are nucleated, but their medulla and contractile fibrillae are intermixed.

The nervous system, said to be absent in some of the free-living genera, consists of a fibrous ring surrounding the oesophagus, at a little distance from the anterior extremity. Six nerves originate from this ring both anteriorly and posteriorly. Of the anterior nerves one corre-

<sup>1</sup> Long pear-shaped glands, open by a common duct on the ventral aspect, and near the tip of the tail in the free-living marine genus *Enoplus*. They secrete a tenacious substance, by which the animal anchors itself. They are perhaps present in some fresh-water forms.

<sup>2</sup> Schneider supposed that in certain Nematoda, e. g. *Trichina*, *Trichocephalus*, the muscles of the body-wall were ‘either not divided, or only divided in a longitudinal direction,’ i. e. by the lateral areae and median lines. Such Nematoda he classed as *Holomyarii*. There are, however, numerous muscle-cells in all so-called Holomyarian genera which have been carefully re-examined, e. g. in those named above and in *Mermis*. See Bütschli, ‘Giebt es *Holomyarii*?’ Z. W. Z. xxiii. 1873.

sponds to each lateral area, two are submedian and dorsal, two submedian and ventral; of the posterior, one corresponds to each of the two median lines, the dorsal and ventral, whilst two on each side are sublateral, i. e. submedian, and are imbedded in the subcuticula. The dorsal median nerve extends to the tip of the tail; the ventral divides just in front of the anus, and its two branches pass to the sides of the rectum, in the female backwards to the lateral areae, supplying the two sensory papillae, whereas in the male the chief part of the fibres turn forwards in the lateral areae, and supply the bursal muscles. Subcutaneous, transverse, and paired fibres connect the dorsal and ventral median nerves, especially in the head and tail. The median and ventral nerve arises by two short roots; but in *Plectus* (sp.?) there are two ventral nerves fused only posteriorly, and connected from place to place by transverse commissures. Two similar ventral nerves have been also met with in the young *Ascaris* (Joseph). Ganglion cells are found in the oesophageal ring, chiefly at the origins of the nerves; in the circumoral plexus into which the anterior nerves pass, in the anterior lateral nerves, in the ventral median nerve, and in the bursal nerves of the male. In the larger *Ascarides* at least (*A. megaloccephala*, *A. lumbricoides*), there is a well-marked ganglion at the spot where the ventral nerve bifurcates, and in the male a circumanal ganglionic ring (Rohde). Organs of special sense are represented by sensory cutaneous papillae, and by eyes. The former are widely distributed, and occur as oral papillae placed on the lips, or on the cuticle round the mouth, on the neck, at the sides of the anus, and on the ventral aspect of the tail in the male. These papillae project in part, and are in part imbedded in the cuticle. A single nerve-fibre has been traced into a papilla, and the granular mass which occupies its centre is probably a sensory nerve-bulb. Eyes are confined entirely to the free-living genera, and are situated anteriorly in the region of the nerve-ring. They consist, so far as is known, of a mass of pigment, black, brown, or blue, which may or may not inclose lens-like bodies.

There is a coelome, which in most cases does not form a large cavity; but whatever space there may be, it is largest round the oesophagus and in the tail. It is traversed by fibres which may be muscular in nature, and appear to be in connection with the fibres of the subcuticula. The coelomic fluid is clear and coagulable, but it is doubtful whether or no it contains any corpuscles. It is often reddish in colour, but this occurs only when the worm feeds on blood, e. g. *Syngamus trachealis*. The red colour is due to discharged oxy-haemoglobin, and gradually disappears if the animal is isolated and starved.

The digestive tract appears to undergo regressive changes in *Sphaerularia*, and its several parts are said not to communicate in *Mermis*. The mouth is either anterior and terminal, or else it opens, as in *Strongylus*, *Dochmius*, *Sclerostomum*, &c., into a more or less spheroidal cavity, which

may be smooth-walled, or covered with small pointed teeth variable in number and size. When terminal it is usually surrounded by small projecting lips formed by the cuticula and sub-cuticula, in number two, three, four, or six, but most commonly three. There are no muscles to these lips, but the hold of the animal is maintained by suction through the oesophagus. In *Sclerostomum*, and, according to Luckart, also in *Dochmius*, two long glands, probably poisonous in nature, open into the oral capsule. The digestive tract itself is divisible into three sections: an oesophagus with muscular walls lined by a cuticle which is shed with the cuticle of the body, a mesenteron, and a rectum, the later lined by a cuticle shed in the same manner as that of the oesophagus. The oesophageal walls have an external cuticle, with radial muscles passing from it to the internal lining cuticle. Granular remnants of the original cells with nuclei are to be found here and there between the muscle-fibres, most plentifully in the young. Longitudinal muscle-fibres may also be present. The oesophagus sometimes retains very clearly its cellular origin. This is especially the case in *Trichina* and *Trichocephalus*. In *Mermis* muscular elements are entirely wanting. The cavity of the oesophagus is usually triangular in cross section, and may even be reduced to a three-legged slit. Its hinderpart is dilated into a muscular bulb or gizzard, frequently armed with teeth in *Heterakis*, in *Oxyuris* and its allies. There are often two such bulbs in the *Anguillulidae*. A solid oesophageal spine is present in *Tylenchus Tritici* (= *Anguillula scandens*) and the embryo *Mermis*; a hollow tubular spine in the free-living *Dorylaimus*. The mesenteron is composed of a single layer of columnar or flattish cells, covered both internally and externally by chitinous membranes, which may be resolved into small plates, adapted to the ends of the individual cells, the internal plates being usually perforated by vertical pores. In *Trichina spiralis* it consists of a single row of cells, one behind the other, perforated by a canal; so, too, the larval *Tylenchus Tritici*. It consists in *Leptodera*, *Pelodera*, and *Pseudalius inflexus* (?), of two rows of cells alternating from side to side, whilst the genus *Strongylus* constitutes a transition to the usual structure, in which there are many rows of cells in a transverse section of its walls. A muscular coat is, as a rule, absent; but in a few instances, e.g. *Oxyuris vermicularis*, the hinder region is covered by a network of circular fibres; and there is sometimes a strong sphincter-muscle developed at the junction of the mesenteron with the rectum. These muscles, as well as the mesenterial or radial bands, which support the mesenteron *in situ* in some forms, e.g. *Eustrongylus*, are probably connected, like the muscular coat of the rectum, with the subcuticular fibres. The mesenteron is, properly speaking, cylindrical, or flattened dorso-ventrally, but it becomes deformed by the pressure of the generative organs as they mature. The rectum is usually short, but it is of great proportional length in *Trichina*; and it is said not

to communicate with the mesenteron in *Ichthyonema globiceps*. It consists of an internal cuticle, a well-developed subcuticula, and a circular muscular coat, the latter derived from the radial bands which originate from the body-walls, and act as divaricators. The anus is a more or less transverse slit, usually opening on the ventral aspect of the tail. It is, however, sometimes terminal or sub-terminal, e. g. *Trichina*, *Trichocephalus*, and the male *Strongylidae*, in which it is surrounded by a membranous umbrella-like expansion, or bursa. The anus is wanting in *Ichthyonema* and *Mermis*. Two or more unicellular glands are said to open on each side of it in some cases, e. g. in *Dochmius*.

An excretory system is probably always present, though it is not certainly known in all the small free-living species. The excretory pore is ventral and anterior near the head. A narrow canal, rarely ampullar as in *Oxyuris*, runs backwards from it, and opens into a transverse vessel at about the level of the posterior end of the oesophagus. The transverse vessel is continuous on either side with a longitudinal vessel which runs backwards, imbedded in the corresponding lateral area at its internal margin. A vessel is also sometimes prolonged forwards on each side towards the head, and is then either continuous with the corresponding posterior vessel, or unites with a separate cross canal which opens however at the same external pore. There are few variations from this typical structure. The vessels end blindly; their walls consist of a granular substance with nuclei, and an internal highly refractile layer; their fluid contents are clear, and somewhat reddish, at least in the larger forms. Two unicellular glands open in many instances, one on each side of the excretory pore<sup>1</sup>.

The Nematoda are of separate sexes with the exception of the genus *Angiostomum*, where one generation is composed of individuals which are, anatomically speaking, females, but in which spermatozoa are first of all formed, then ova, and the latter are thereupon impregnated. They are, therefore, physiologically hermaphrodite and self-impregnating. The genital organs are tubular. The testis is single; very rarely paired. It opens on the ventral aspect of the rectum close to the anus, and therefore the termination of the rectum is sometimes called cloaca. It stretches forwards on the dorsal aspect, or to one side of the alimentary canal, and may hook backwards anteriorly, or in the large Nematoda, even be disposed in several longitudinal coils. It is divisible according to peculiarities of structure, into the testis proper, which is terminal, vas deferens,

<sup>1</sup> Joseph states (Z. A. v. 1882, p. 605) that if the digestive tract of a living *Ascaris megalcephala* be injected with Carmine-albumen solution, and the worm be kept at the natural degree of warmth in a portion of a horse's small intestine, its body will be found on dissection to be traversed by a naturally injected system of fine branching canals, devoid of proper walls, and covering the surface of all the internal organs and muscle-cells. The coloured fluid passes by osmosis into the excretory vessels.

vesicula seminalis, and ductus ejaculatorius. The walls of the whole tube are composed of a delicate membrane, lined in the testis and vas deferens by protoplasm containing nuclei, and disposed in lines which are longitudinal, and in the testis parallel, in the vas deferens interlaced, whereas the vesicula seminalis and ductus ejaculatorius have a distinct epithelium very variable in character in different genera and species. In the vesicula each cell is in some of the larger species, e.g. *A. megalcephala*, provided with filamentous processes capable of changing their shape. The ductus ejaculatorius has a well-formed external layer of muscles, chiefly transverse. Properly speaking, the vesicula is only its upper and less muscular part. Two caeca of unknown function open into the male duct near its termination in *Heterakis* and *Pelodera*. The spermatozoa are peculiar. During their formation they are attached to a central, or in *Trichina*, *Trichocephalus*, and *Trichosomum* lateral, rhachis, which may become much divided, but they do not attain their characteristic shape until transferred to the female. In the male organ they are small truncate nucleated spheres. Four types of form and structure have been distinguished by E. van Beneden successively assumed in the uterus: (1) spheroidal—a layer of homogeneous substance covers one pole of the sphere; (2) pyriform—this substance assumes a conical shape; (3) campanuliform—the substance becomes a cornucopia-like figure, and is separated at its base from the protoplasm of the body of the spermatozoon by a limiting plate, from which a clearly defined line rises and traverses the cornucopia; (4) conoid—the cornucopia-figure is replaced by a cone, which consists of a superficial membrane, a layer of protoplasm, and an axial refractile rod. One of the forms 2, 3, or 4, may effect impregnation. The protoplasmic body of the spermatozoon is capable of amoeboid motion<sup>1</sup>. Copulatory organs take the form of spicules, and a 'bursa.' Spicules are wanting in *Sphaerularia*, *Trichina*, *Dermatoxys*. One is present in *Oxyuris*, *Trichocephalus*, and *Trichosoma*; two dissimilar in *Heterakis*, *Filaria*. &c.; two similar in all respects in the majority of genera<sup>2</sup>. The spiculum is chitinoid, pointed, often dark-coloured, and either homogeneous or containing a soft core. It is contained in a sheath, which is an evagination of the dorsal wall of the cloacal region of the rectum, and with which its base is continuous. The sheath has a smooth internal surface except in most species of *Trichocephalus*, and in *Trichosoma aerophilium*, where it is covered with spinules. It is provided with retractor and exsertor muscles, and may, as in *Trichocephalus*, be partially extrusible. A bursa is not always present. In its

<sup>1</sup> This motion has been actually observed, but not in Nematoda inhabiting warm-blooded Vertebrata. It is possible that in such cases the sperm is motile only at the natural temperature of the host. E. van Beneden draws attention to their great variability of outline in specimens preserved in Osmic acid.

<sup>2</sup> The two spicules are occasionally fused at their apices, and their bases supported by an extra piece, e.g. in *Angiostomum*.

least developed form it consists of a slight cuticular ridge on either side of the tail, which begins anteriorly to the anus. The ridges may become thin folds, which may or may not be connected in front of the anus, and sometimes stop short of the apex of the tail, or extend beyond it. These membranes are best developed in *Strongylus*, where they form an umbrella-like expansion. The ventral area inclosed by the bursa is provided with sensory papillae, sometimes with ridges, spines, a sucker, as in the genus *Heterakis*, or five suckers (?) on either side the anus, as in *Nematoxys ornatus*<sup>1</sup>.

The female aperture is usually on the ventral aspect and near the middle of the body, but it may be close to the mouth, or just in front of the anus, as in some *Strongyli*. It is generally a cross slit with more or less prominent margins, and in *Trichocephalus* is supported by a spinulose papilla. The female sexual tube is divisible into vagina, uterus, oviduct (or tuba), and ovary. The vagina is always short, and in small Nematoda scarcely visible. It is an invagination of the cuticle and subcuticula. The remainder of the tube has a wall composed of a delicate membrane lined by an epithelium which has a characteristic shape in its different sections. In the uterus and lower part of the oviduct it consists of polyhedric plates, usually numerous, bearing papilliform projections, and separated by furrows. The papillae probably secrete a substance which cements the ova together while the furrows give shelter to the sperm. The epithelium of the ovary consists of nucleated protoplasmic bands; that of the upper part of the oviduct is a nucleated protoplasmic layer in *A. megalocéphala*. The lower part of the oviduct and the uterus have an external muscular layer of chiefly transverse fibres, whilst the vagina has fibres which radiate towards the lateral areae. The genital tube is of greatest length in the larger Nematoda, in which it is disposed in many longitudinal coils; it is short and simple in the smaller species. It may be single and directly prolonged from the vagina as in *Trichina*, &c.; double, and then one branch may run towards the head, the other towards the tail, the vagina being at right angles, e.g. *Oxyuris*, *Strongylus*, &c.; or the two branches may run either parallel or at an acute angle to one another. A greater number of branches than two is rare. The spermatozoa accumulate near the junction of the uterus and oviduct; hence this part is sometimes termed spermatheca. They become mixed with the descending ova, and those which do not effect impregnation appear to reascend to the spot named by means of the intra-epithelial furrows.

Remarkable peculiarities are the following:—In the impregnated female *Sphaerularia* which inhabits the coelome of the Humble Bee, the uterus undergoes prolapsus, and while the body of the Worm is only  $\frac{1}{30}$  in. long, the prolapsed uterus with the contained genitalia and a loop of

<sup>1</sup> See Schneider, Die Nematoden, p. 113, *sub sp.*



intestine grows to a length of one inch. A similar prolapsus appears to occur in the female *Simondsia* from the stomach of the Pig. The male *Trichodes crassicauda* passes bodily into the uterus, and the male *Syngamus trachealis* has been said, but probably erroneously, to undergo fusion with the female<sup>1</sup>.

The ova originate in the upper part of the ovary, and it is said from a syncytium disposed like the corresponding part in the male. In the small Nematoda there is a single row of ripening ova connected by a slender rhachis; in the larger a number which are grouped round a central simple rhachis. The ova gradually increase in size, and their protoplasm becomes more or less granular as they approach the oviduct, where they are set free. A vitelline membrane is sometimes formed before impregnation, sometimes after. There is in the latter case a micropyle, which E. van Beneden states is closed by the fusion to its margins of the membrane covering the conoid process (*ante*, p. 681) of the entering spermatozoon. There is an egg-shell which is thin where the embryo hatches *in utero*, and in some other instances. In other cases it is thick, and then often ornamented externally, and brownish in colour, and lined by one or two internal membranes<sup>2</sup>. The egg is usually oval in shape. The number formed varies, and the size of the worm does not necessarily regulate the size of the ovum. Segmentation may not begin until some time after the laying of the egg, e. g. in *Ascaris lumbricoides*; it takes place before laying, as in *Dochmius*—or the embryo may be already formed as in *Oxyuris*, or even escape from the shell *in utero*, e. g. *Ollulanus*, *Pseudalius*, *Trichina*, *Dracunculus*, *Filaria Bancrofti*. Segmentation is total, and the odd numbers are found among the blastomeres. The latter possess the power of amoeboid motion. In some cases where the embryos undergo development *in utero*, the rest of the maternal viscera are destroyed by their growth and movements, but the cuticle persists, and is turned into a moving sac of embryos, e. g. in the female form of *Angiostomum*<sup>3</sup>.

<sup>1</sup> The body of the female *Sphaerularia* was supposed by Sir J. Lubbock to be an adherent male. As to *Syngamus*, it is difficult to see how the ova escape, as they undoubtedly do escape, if fusion occurs.

<sup>2</sup> How the egg-shell and its contained membranes arise is a matter of dispute. According to E. van Beneden, the egg itself of *A. megalcephala* gives origin to a delicate vitelline membrane, and then successively to two peri-vitellar envelopes, its protoplasm retreating after each formation, and leaving a space filled by liquid. The shell proper is formed by the uterus. The same view is held by Leuckart. From Schneider's account, it seems that the thin egg-shell is a vitelline membrane; the thick, a vitelline membrane modified by subsequent growth, due to the fact that the protoplasm does not retreat from it; the two internal membranes are formed at a later period. If, he says, the impregnated egg of *A. megalcephala* is removed from the uterus and suffered to lie in water, the thick shell develops as usual, thus proving its non-uterine origin.

<sup>3</sup> The history of the embryonic development presents difficulties. Nusbaum speaks of an invaginate Gastrula in *Ascaris megalcephala* (Z. A. vi. 1883). Hallez observed an invagination in the same animal, and the derivation of both oesophagus and rectum from endoderm (C. R. 101. 1885). In *Cucullanus elegans*, Bütschli states that there is a plate formed of two layers of cells, epi-

Three stages accompanied by moults of the cuticle have been distinguished in the growth of a Nematode after hatching—the embryo, larva, and the adult worm. The first is very small; mouth, anus, and digestive tract may or may not be discernible; the oesophagus is proportionately longer, and the sexual gland is present as a uni- or multicellular rudiment. The tail is often singularly different to that of the adult, and the head may be provided with a boring spine, lost in the next stage, e. g. oral spine of *Cucullanus*, of *Mermis*, and ventral boring process of some Ascarid larvae. The larva has the various organs distinct; its tail resembles that of the adult female, and has acquired sensory papillae sometimes of great size; the genus and even species is discernible. Under the larval skin the characters of the adult are assumed, and after a moult the worm grows in size and matures genital products.

The mode of life in the Nematoda is very variable, and no less than thirteen distinct modifications of development are enumerated by von Linstow as follows<sup>1</sup>:—(1) The embryo develops directly into the sexual animal, and inhabits fresh, salt, or brackish water, earth, plants, putrefying substances, e. g. *Enoplus* and many other genera; (2) the larva lives in earth, the sexual form in plants, e. g. *Tylenchus Tritici* in the ear of wheat, *T. putrefaciens* in the Onion; (3) the larva lives in worms, is set free by their death and decomposition, and becomes sexual in the earth (*Rhabditis pellio*); (4) the sexual worms live in the earth; the fertilised female enters different species of Humble Bee (*Bombus*) and the Wasp, passes into the coelome, produces ova which hatch out, and the offspring bore their way into the intestine, and so escape (*Sphaerularia Bombi*); (5) the larva lives in earth; the sexual form in a Vertebrate (*Dochmius, Strongylus*); (6) the worm lives as a hermaphrodite in an animal, its progeny becomes sexual in earth, and the progeny of the sexual animals enter the animal again (*Angiostomum*, e. g. *A. nigrovenosum*, often called *Ascaris* or *Leptodera nigrovenosa*, from the lung of the Frog; *Rhabdonema strongyloides* from the intestine of Man); (7) a bisexual free form gives origin to a bisexual form parasitic in a Snail (*Leptodera appendiculata*); (8) the egg is laid and passes into earth, gives origin to an embryo which is transferred within the egg-shell to an animal,

and hypo-blast: that its edges fold over, fuse from behind forwards, leaving a pore—the future mouth (Z. W. Z. xxvi. 1876). A similar mode of closure of the blasto- (gastro-) pore has been noted in *A. megaloccephala* and *Angiostomum nigrovenosum*. Götte found an epibolic gastrula in the last-named worm; a stomodaeum but no proctodaeum (Entwickelungsgeschichte der Thiere, i. 1882). He also says that a proctodaeum has been observed by Ganin and Natanson in some Nematoda. Örley found both a stomo- and a procto-daeum in *Anguillula aceti*, s. *Tylenchus oxyphila* (Monographie der Anguilluliden, Buda-Pesth, 1880). In certain Oxyurids Galeb states that there is a delaminate Gastrula, and that the whole digestive tract is derived from two ectodermic invaginations (A. Z. Expt. vii. 1878, pp. 323, 368). Judging from structural anatomy alone, both oesophagus and rectum would be said to be respectively a stomo- and procto-daeum.

<sup>1</sup> Z. W. Z. xlii. 1885, pp. 715, 716. Von Linstow reckons a 14th-mode, that characteristic of *Gordius*; see p. 687. *post.* The heads are kept as given by Von Linstow, but instances have been added and a few slight changes introduced into the wording.

is hatched, and becomes sexual (*Oxyuris*, *Trichocephalus*<sup>1</sup>); (9) the larva lives in Insecta, the sexual animal in earth or water (*Mermis*); (10) the larva lives encysted in one animal and is transferred with it to a second animal (*Ollulanus*, from the Mouse to the Cat<sup>2</sup>; *Cucullanus elegans*, with *Cyclops* to the Perch; *Spiroptera obtusa*, with the Meal-worm to the Mouse; *Filaria rhytipleurites*, from the Cockroach to the Rat); (11) the sexual Worm lives in the intestines of a Vertebrate, the female produces young which penetrate its walls and encyst themselves in the muscles (*Trichina spiralis*); (12) the sexual worm lives in the tracheae of Birds, the ova containing embryos are coughed up, the embryo acquires the power of movement and is swallowed in food within the egg-shell, quits the shell in the oesophagus and stomach, wanders into the bronchia and air-sacs, and thence, when grown larger, into the trachea (*Syngamus trachealis*, the cause of Gapes); (13) there are two larval forms; the first lives in water, the second in the lung of an Amphibian, whence it wanders into the intestine and becomes sexually mature (*Nematoxys longicauda* in *Triton alpestris*, and more rarely in *T. cristatus*). It must be noted that in (6) and (7), *supra*, there is an Alternation of Generations.

The parasitic Nematoda most commonly infest the digestive tract, but they occur also in the lungs, kidney, and urinary bladder of Vertebrata, as well as encysted in various parts of the body. Haematozoa, or parasites living in the vascular system, also occur, e.g. *Filaria immitis* in the right cavities of the heart of the Dog; and *Strongylus armatus*, the palisade Worm, in an immature state, is a common cause of aneurism, especially abdominal aneurism, in the Horse and Ass. The species ordinarily inhabiting Man are the following:—*Ascaris lumbricoides*, the male of which is 4–6 inches long, the female 10–14, inhabits properly the upper and middle part of the small intestine, but may enter the stomach and escape through the mouth or perforate the intestine, and even the abdominal walls, where it may give rise to abscesses; *Oxyuris vermicularis*, the common round Worm, the embryos of which are set free in the stomach, pass through their stages of

<sup>1</sup> The *Oxyuris vermicularis* lays ova containing at the time of their escape ready formed embryos. Hence the great ease with which infection not only spreads, but is maintained in the case of this parasite. The embryos of *Ascaris megalcephala* are developed more quickly in damp air than in water. The embryos are set free from their shells if the latter are strewn on moist earth, and they continue to live if supplied with slices of pear, &c. The natural mode of development probably follows a similar course. See Hallez, C. R. 101, 1885. Von Linstow believes that *Julus guttulatus* is the intermediate host of *A. lumbricoides*; Z. A. ix, 1886.

<sup>2</sup> The embryo of *Ollulanus*, a viviparous genus, may wander from the intestines of the Cat to its lungs, sometimes with results fatal to the host. After encystation it undergoes fatty degeneration. This is an instance of a parasite going astray. See Stirling, Q. J. M. xvii. 1877.

It is probable that the life-histories of a very large number of parasitic Nematoda fall under this heading (10): among others, perhaps those of *Dracunculus medinensis* and *Filaria Bancrofti* s. *F. sanguinis hominis*. The larva of the former inhabits a *Cyclops*; of the latter a certain sp. (?) of Mosquito; but the mode in which both are introduced into the human subject is still unknown.

development in the small intestine, enter the caecum, their head-quarters, and are found throughout the whole large intestine; *Dochmius* (*Anchylostoma*) *duodenalis*, which inhabits the small intestine, and occurs in Europe, Egypt, Comoro Is., Brazil, and Cayenne, and is the cause of a pernicious anaemia; *Filaria Bancrofti* s. *F. sanguinis hominis*, found in Australia, China, India, Egypt, and Brazil, the sexual female of which inhabits the lymphatic glands, is the cause of elephantiasis, lymph scrotum, &c. and produces living embryos circulating with the blood, giving rise to chyluria and haematuria, and passing into a larval state within a mosquito; *Dracunculus* (*Filaria*) *medinensis*, the female only of which is known, attains a length of 1-6 ft., lives encysted under the skin of the lower leg or shoulder, produces living young which become larvae in a *Cyclops*, and is distributed over certain districts of Asia (Arabia Petraea, Persian Gulf, Caspian Sea, Ganges), of Africa (Upper Egypt, Abyssinia, Guinea), in several W. Indian Is., and formerly in Brazil; *Trichina spiralis*, rare in England, found in the Pig as well as Man, the sexual worm of which inhabits the intestines, is viviparous, and its progeny migrate through the tissues and encyst in the muscles, causing what is known as *Trichiniasis*; *Trichocephalus dispar*, not uncommon in England and Ireland and the Continent, infrequent in Scotland, which infests the caecum and upper part of the colon, and the young of which appear to enter the body with water or food; *Rhabdonema strongyloides* (= *Leptodera* s. *Anguillula stercoralis* and *intestinalis*), which occurs in Cochin China and Europe, and has been stated, but probably erroneously, to be the cause of a peculiar dysentery or diarrhoea, at least in Europe, the disease being really due to associated *Dochmius* (*Anchylostoma*) *duodenalis*<sup>1</sup>.

The classification of the Nematoda is not easy. The class was divided by Schneider into three sections: (1) *Polymyarii*, with many muscle-cells in each quadrant of the body, e.g. *Ascaris*; (2) *Meromyarii*, with the muscle-cells disposed in eight rows, two rows in each quadrant, e.g. *Oxyuris*; and (3) *Holomyarii*, with the musculature of the body either undivided or divided only by the longitudinal thickenings of the subcuticula, e.g. *Trichina*, *Mermis*. But this last section appears to be founded on error.

Örley has proposed to establish three sub-divisions: (1) *Nematentozoa*, (2) *Rhabditiformae*, and (3) *Anguillulidae*, for the characters of which see his paper in A. N. H. (5), ix. 1882, p. 301 et seqq.

Claus distinguishes eight families: (1) *Ascaridae* (*Ascaris*, *Heterakis*, *Oxyuris*); (2) *Strongylidae* (*Eustrongylus*, *Strongylus*, *Dochmius*, *Anchylostoma*, *Sclerostoma*, *Syngamus*, *Pseudalius*, *Olullanus*); (3) *Trichotrachelidae* (*Trichocephalus*, *Trichosoma*, *Trichina*); (4) *Filariidae* (*Filaria*, *Dracunculus*, *Ichthyonema*); (5) *Mermithidae* (*Mermis*, *Sphaerularia*); (6) *Gordiidae*, see *infra*; (7) *Anguillulidae*, free-living in fresh-water or earth or in plants (*Tylenchus*, *Anguillula*, *Angiostomum*, *Leptodera*, *Pelodera*); (8) *Enoplidae*, free-living and mostly marine.

<sup>1</sup> Cf. A. N. 51, 1, 1885, pp. 11-12.

The *Gordiidae* are regarded by recent writers as a group distinct from the Nematoda, and Vejdovsky has proposed the name *Nematomorpha* for them. The principal points of anatomy are the following: There is an ornamented cuticle, pierced by pores containing processes of the subcuticula or hypodermis, which consists of distinct cells in the anterior and posterior regions of the body, of a granular nucleated matrix in the middle region. The muscle-cells are numerous, longitudinal, and disposed in a single layer. The body-cavity is filled up to a certain period by cells with distinct walls, which, during the evolution of the genital products, are reduced to an epithelium lining the body-walls, covering the 'egg-' and 'sperm-sacs,' and forming epithelioid mesenteries, which apparently constitute the walls of the efferent genital ducts, &c. The nervous system is represented by a peripharyngeal ring, a ventral cord composed of ganglion cells and nerve-fibres, and a caudal ganglion. Papillae similar to those of Nematoda are the sole organs of special sense, and are especially well developed on the ventral aspect of the tail of the male. There is a digestive tract, with cellular walls; the mouth appears to be occluded in some species when they become free; the anus is ventral and posterior. A dorsal canal is regarded by Vejdovsky as excretory. The sexes are separate, the tail of the male deeply cleft. The female genitalia consist of paired metamericly-arranged ovaria; of two laterally-placed 'egg-sacs,' in which the ova ripen; of two median 'egg-receptacula,' which narrow posteriorly into the oviducts; of a large receptaculum seminis dorsal to the digestive tract, with two ducts leading one into each oviduct; of an atrium, which has glandular walls, opens posteriorly, and receives the two oviducts. As to the male organs, the true testes are not known (Vejdovsky); there are two vesiculae seminales, the homologues of the 'egg-sacs,' *supra*; and two vasa deferentia, continuous with the vesiculae and opening into the dilated termination of the digestive tract, which is capable of partial evagination. Villot's account differs from that of Vejdovsky, which has been followed here.

There are two larval forms, both annulated. The first has a distinct head, body, and tail. The head is in- and e-vaginable, armed at its base with three circles of spines, and at its apex with three stylets, the whole forming a boring apparatus. It is lost in the second larval form, which is more elongated than the first. The first form of *Gordius aquaticus* is stated by von Linstow to inhabit a Mollusc (*Limnaeus*), the second, the coelome of a carnivorous insect, e.g. *Dytiscus*, *Carabus*, *Mantis*. Villot believes that fish form the proper host, the first form occurring encysted in the mucous membrane of the intestine, the second free in the tissues. The first has been recorded from the Frog, various fish, aquatic Insectan larvae, and the Molluscan *Planorbis* and *Limnaeus*; the second from the Frog, various fish, a large number of adult Insecta, and some Spiders. The worm becomes free after a time, lives in water, and after copulation the female lays its eggs, which are cemented together by the secretion of the atrium.

The characters of the nervous, digestive, and generative system are markedly different from those typical of Nematoda. Vejdovsky has discussed the subject of affinities in detail at the end of his paper cited below.

*Nematoidea*, Beddard, Encyclopaedia Britannica (ed. ix.), xvii. 1884; Cobbold, 'Parasites,' London, 1879; Leuckart, 'Die Menschlichen Parasiten,' ii. 1876; Schneider, 'Monographie der Nematoden,' Berlin, 1876.

*Genera, &c.*, Diesing, Systema Helminthum, ii. 1851. *Revision*, Id. SB. Akad. Wien, xlii. 1860; von Drasche, Verh. z. b. Gesellsch. Wien, xxxii. 1882; xxxiii. 1883.

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## CLASS ACANTHOCEPHALA.

This small class of entoparasitic Vermes contains the single genus *Echinorhynchus* with many species very variable in size. The adult worm is found in the alimentary canal of some Vertebrate, the immature in the body of a Non-vertebrate; e. g. *Ech. Proteus* of the Pike and other fresh-water fish is found in the body cavity of the Amphipod Crustacean *Gammarus pulex*; *E. angustatus* of the Perch in the Isopod *Asellus aquaticus*.

The body is divisible into three regions, a proboscis, neck, and body proper, which is cylindrical, and when contracted, transversely wrinkled. The proboscis carries a variable number of chitinous recurved hooks, arranged in longitudinal rows, and is plunged into the tissues of the host. The body-walls consist of an external delicate cuticula, a striated subcuticula, a layer of circular and most internally of longitudinal muscle-cells. The subcuticula has an outer layer composed of a complicated tissue of circular and longitudinal fibres and an inner layer of radial fibres, amid which lies a system of canals. The subcuticula of the body proper, and consequently its canal system, are separated from the corresponding structures in the neck by a fold of cuticula. Two remarkable semilunar masses of subcuticula, the lemnisci, depend from the neck into the body cavity. They vary in length in different species. The canal system of the body proper consists of two longitudinal vessels, right and left in most instances, dorsal and ventral in *Ech. clavaiceps*, with lateral vessels which branch and anastomose. There is a circular canal at the base of the neck connected with an irregular network, but in the proboscis longitudinal vessels alone are found, one between each series of hooks, united laterally between each pair of hooks. The circular vessel, also sends into each lemniscus two principal vessels, each of which divides into two with a number of secondary branches. There is no opening into the system of canals. Their contents are a granular liquid. The granules appear to be of a fatty nature, and are orange coloured, or in the lemnisci of *Ech. Proteus* brownish-yellow. Nuclei of large size are also found in the canals as well as in the intervening fibres, and differ in shape, &c. In the body proper and the neck. The muscular layers of the body are continued into the neck, and the longitudinal layer forms a sheath for each lemniscus. A longitudinal muscle layer is absent in the proboscis. The muscular tissue is peculiar and somewhat like that of Nematoda, the striated fibrillar substance being developed only on the outer surface of the cell.

A double circular layer of muscular cells forms a proboscis sheath, which hangs down towards the coelome and is attached to the base of the proboscis. It contains four longitudinal retractor muscles for the proboscis, by means of which that structure can be invaginated. These retractors are

continued on (?) through the sheath into the coelome as two retractor muscles of the proboscis-sheath and are attached to the body-walls.

A mass of ganglion cells lies at the bottom of the proboscis-sheath. It sends two sets of nerves forwards and two nerves (posterior lateral) backwards. The latter pass to the sides of the body inclosed each within a muscle-cell, the retinaculum. In the male two ganglia, connected together, lie anteriorly upon the genital sheath, and not only supply the sexual apparatus, but are connected to the two nerves just mentioned. There are no organs of special sense. Mouth and alimentary tract are also absent. There is a coelome. An axial muscular sheath, the suspensory ligament, is attached to the base of the proboscis-sheath. It is tubular, and incloses the testes, the first part of their ducts, and the cement glands in the male; the ovaries in the female. The two testes are ovular, one placed in front of the other. The two vasa deferentia which unite into a single ejaculatory duct are furnished each with 3-4 vesiculae seminales. There are 6-8 cement glands. Their ducts eventually open into the ejaculatory duct, and are surrounded by a muscular genital sheath derived from the longitudinal body-muscles. There is a papilliform penis situated at the base of a copulatory bursa formed by the invagination of the posterior end of the body, but capable of eversion by a compressor muscle. The two ovaries are broken up at an early period into masses of egg-cells. These masses grow and multiply, eventually rupturing the suspensory ligament and filling the body cavity. The hind end of the ligament either passes into or is inserted (*Ech. clavaiceps*) round the edge of a 'bell.' This structure consists, as do the oviducts and uterus, of muscle cells with circularly disposed fibrillae. It opens and shuts rhythmically, and swallows the ova. The long oval ripe ova (really embryos in their envelopes) pass onwards through the two oviducts into the uterus, but the unripe ova, which are rounder, are rejected by a dorsal aperture at the base of the bell. A vagina opens at the posterior end of the body. Its walls are composed externally of two sphincter muscles, internally of four or eight peculiar hour-glass shaped cells.

The ovum is impregnated in the coelome, undergoes unequal segmentation, and surrounds itself with three envelopes. The larva has a tapering body and an anterior disc bearing a circle of spines. It has a delicate cuticle, an underlying semifluid syncytium inclosing three structures, a rudimentary pharynx (?), a muscle which depresses the centre of the disc, and a granular mass or 'embryonic nucleus' formed by the central cells of the ovum. The larva inclosed within its envelopes passes out of the Vertebrate, and is swallowed by the Non-vertebrate host. It breaks through its envelopes, and enters the coelome. The adult worm is formed entirely from the 'embryonic nucleus' (*supra*) with the exception of the cuticula, which is the only larval structure that persists. It only becomes sexually mature when transferred to the alimentary canal of its Vertebrate host.



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### BRACHIOPODA, VERMIFORMIA, POLYZOA, PTEROBRANCHIA.

The systematic position and relations of these four classes still remains, in spite of much research, a matter of complete uncertainty. They are often grouped together as *Molluscoidea*. The term is not used here because there does not appear to be any reason to approximate them to the Mollusca. If, however, recent views as to the resemblance between the larval *Loxosoma* and the Molluscan Trochosphere prove correct, the entoproctous *Polyzoa* will have to be separated in all probability from the other *Polyzoa*, as well as from the remaining classes, with the possible exception of *Pterobranchia*.

The nearly complete atrophy or the total absence of a praeoral region, the presence of a lophophore bearing ciliated tentacles, of a lip or epistome overhanging the mouth, and of a fixed mode of life are characteristic of this assemblage of forms. The *Brachiopoda* and *Vermiformia* are social, the *Polyzoa* and *Pterobranchia* form colonies by gemmation. The two first possess a coelome, which is an enterocoel, and at least one pair of nephridia, the *Pterobranchia* and ectoproctous *Polyzoa* a coelome, the entoproctous nephridia but no coelome. As to the lophophore it may be remarked that in *Brachiopoda*, *Vermiformia*, and apparently in ectoproctous *Polyzoa*, it is postoral, in entoproctous *Polyzoa* praeoral, in the *Pterobranchia* doubtful in position on account of the development being as yet completely unknown. The epistome of the entoproctous *Polyzoa* appears to be homologous with the foot of the Molluscan Trochosphere, and in *Pterobranchia* it is not only an organ of locomotion but also secretes, at least in *Rhabdopleura*, the tube in which the animal lives. In *Brachiopoda* and *Vermiformia*, certainly in the last, it is a remnant of an atrophied praeoral lobe. The position of the mouth within the lophophoral area, as in *Brachiopoda* and *Vermiformia*, would tend to the supposition that the epistome of the phylactolaematous *Polyzoa* is also a remnant of the same region. It is however often regarded as homologous with the foot of *Pterobranchia*. The peduncle of the *Vermiformia* is a ventral growth; there is no reason to suppose that the corresponding structure in *Brachiopoda* is anything of the kind; nor are the divisions of the coelome homologous in the two classes as has been supposed; nor again is the anus of *Brachiopoda* to be considered as dorsal in position as it is in *Vermiformia*.

There is some slight evidence in favour of considering *Brachiopoda* as primitively segmented animals, not on account of the segmentation of the

larva which does not affect the mesoderm, but owing to the presence of two pairs of nephridia in the genus *Rhynchonella*. It is not a necessary inference from the fact, inasmuch as there may be more than one pair of nephridia to a somite in some *Chaetopoda*; but the difference in position of the two pairs of organs rather lends weight to the view. The presence of a pair of otocysts in the larvae of the hingeless genera, of setae in the adult, but more especially of provisional setae in most of the larvae, are points which should also be noted in the anatomy of *Brachiopoda*. Setae are not necessarily characteristic of the Vermian *Chaetopoda*; e.g. they occur in *Chiton* among Mollusca, but provisional larval setae are not met with elsewhere. The presence of the structures named tends rather to the supposition, when coupled with other facts, that *Brachiopoda* are a group of simplified or degenerated organisms.

It is better under these circumstances of doubt to retain the four classes in question apart by themselves, but it must be carefully borne in mind at the same time that there is no evidence worth much to connect them one with another.

#### CLASS BRACHIOPODA.

*Coelomate Metazoa fixed to some foreign object usually by a peduncle, and provided with a bivalved calcareous shell. This shell is inequivalve, but each valve is equilateral (see p. 124). Its valves are either free from one another, or one, the dorsal, is hinged on the other, the ventral. They are lined by two mantle folds or extensions of the body-walls, the free margins of which are generally beset with chitinous setae. There is a lophophore which typically surrounds the mouth and bears ciliated tentacles or cirri, but is in some cases produced into spirally coiled 'arms.' The digestive tract is ciliated and furnished with glands, the liver so-called. The anus is either absent, or when present, is either posterior or lateral. There are one or two pairs of nephridia. The sexes are either separate or united (?). There is a metamorphosis. Exclusively marine.*

A difference of size between the two valves of the shell is well-marked in all Brachiopoda with the exception of the *Lingulidae* where it is but slight. The larger valve is termed ventral, or superior; the smaller, dorsal or inferior<sup>1</sup>. The outline of the valves varies in shape and is rounded, oval, or triangular, but the shell is usually narrowed towards the attachment of the peduncle or the line of the hinge, which may be pointed, curved, or straight. The shell may be convex, flattened, or concave,

<sup>1</sup> The terms 'dorsal' and 'ventral' are applied by Von Buch and Quenstedt to the larger and smaller valves respectively, i.e. conversely to what is usual in English Manuals. The larger valve appears to have been called ventral because the chief nerve ganglion corresponds to it. In the living animal it lies uppermost except where, as in *Crania*, it is fixed to some foreign object.

and the two valves may not be similar in this respect. They may be smooth, ribbed, or spinose<sup>1</sup>. One valve may have depressions or sinuses to which correspond elevations or juga on the other. In the hinged Brachiopoda or *Testicardines* the dorsal valve is furnished with a projecting cardinal process to which are attached the divaricator muscles. At the base of the cardinal process is a right and left socket into which fit the two teeth of the ventral valve. The latter is prolonged posteriorly into a more or less prominent beak which is generally deeply curved and grooved for the passage of the peduncle. The groove is usually converted into a foramen by a 'deltidium,' which consists of two calcareous pieces remaining separate ('d. discretum'), e.g. in *Terebratella*; fusing into either a single flat plate ('d. sectans'), e.g. in *Terebratula*, or one so curved as to embrace the orifice for the peduncle ('d. ampletens'), e.g. in *Rhynchonella*. In the *Spiriferidae*, &c. the groove of the beak is frequently closed by a simple calcareous plate or 'pseudo-deltidium' which grows towards the hinge line. The aperture for the peduncle consequently becomes closed, and the shell must then have been set free. The peduncular aperture is wanting in *Productus*, &c., and the shell is found either free, e.g. *Trimerellidae*, *Strophonemidae*, many *Productidae*, or attached to some foreign object by the beak of the ventral valve, by its surface, e.g. *Crania*, *Thecidium*, or by spines<sup>2</sup>. *Discina* among *Ecardines* has the ventral valve perforated centrally or excentrically for the peduncle.

As to the structure of the shell. A thin external periostracum or cuticula covers its external surface and is traceable into a groove at the margin of the mantle (at least in *Lingula pyramidata*) as well as over the peduncle. The bulk of the shell in *Lingulidae* and *Discinidae* consists of horny and structureless calcareous layers alternating one with another. A thin layer of horny matter extends to the mantle edge, and is said by Beyer to become continuous in *Lingula pyramidata* with the supporting substance of the mantle. In *Crania* the shell substance is almost entirely calcareous, but it is pierced by vertical canals which in the dorsal valve commence with wide apertures, bifurcate three times, and then divide near the surface into a number of minute branches, but in the ventral valve scarcely bifurcate, and are connected with an irregular network of canalicules. In the *Testicardines* a fine structureless calcareous layer underlies the cuticula<sup>3</sup>; it is followed by a layer of calcareous prisms united more or

<sup>1</sup> A living spinose *Rhynchonella* (*R. Döderleinii*) has been recently dredged off the coast of Japan. See Davidson, A. N. H. (5), xvii. 1886, who states that spines 'formerly prevailed among Palaeozoic *Productidae*, *Orthidae*, &c., and the Oolitic *Spiriferidae* and *Rhynchonellidae*,' and that 'no spinose Brachiopoda are known from the Cretaceous or Tertiary period.'

<sup>2</sup> The presence and extent of a flattened triangular 'Area' horizontally and vertically striated; and situated on the dorsal, i. e. inferior aspect of the beak of the ventral valve, and sometimes extending on to the dorsal valve too, is to be noted as a point of classificatory importance.

<sup>3</sup> Shipleigh states that in *Argiope* the calcareous matter of this layer increases and that the outer ends of the prisms become square and are packed together like bricks.

less distinctly into lamellae between which are delicate organic membranes. The axes of the prisms are oblique to the surface of the valves. It is rare for the systems of prisms to cross one another or to fuse. A second prismatic layer may be found in old specimens internal to the first. The substance of the valves is sometimes perforated, but not in *Rhynchonellidae*, by vertical canals occasionally branched, which widen at their outer extremities beneath the cuticula, e. g. in *Terebratula*, *Terebratella*, *Waldheimia*, *Spirifer*. The canals in question contain hollow or solid processes (van Bemmelen) of the mantle<sup>1</sup>. The superficial contour lines parallel to the margins of the valves probably represent periods of little or no growth. The calcareous matter is in the form of Calcite except in *Lingula*, where it consists chiefly of Calcium Phosphate.

The body of the Brachiopod lies at the base or peduncular end of the shell, more on the side of the dorsal valve than of the ventral, a position most marked in *Testicardines*. Two 'mantle' folds, one dorsal, the other ventral, line the corresponding valves. And the body is as a rule continued posteriorly into a peduncle, usually short, but in the *Lingulidae* of considerable length, which is attached at its apex to some foreign object. The arms, from which the class obtains its name, have their simplest form in *Argiope Kowalewskii* among *Testicardines*. In this animal the part of the body affixed to the dorsal valve carries a horse-shoe-shaped disc or lophophore, the two arms of the horseshoe being turned towards the free margin of the dorsal valve. The lophophore carries a single and continuous peripheral row of tubular cirri to the inner side of which is a 'brachial' groove bounded on its inner side by a prominent fold or lip. The mouth lies in the brachial groove at the centre of the convexity of the horseshoe, therefore within the area inclosed by the lophophore. In *A. decollata*, as in *Thecidium*, the lophophore forms four prominent processes instead of two, all turned, however, towards the free margin of the valve. The lophophore of the *Terebratulidae* is also horseshoe-shaped, but from the centre of the concavity of the horseshoe a process of the lophophoral area extends towards the free margin of the valve, is of great extent, and the edges of its apex are disposed in folds. The cirri, groove and lip follow the edges of the disc and process as in *Argiope*, and the mouth has the same relation to the groove and the convexity of the horseshoe. The cirri are, however, very numerous, and are arranged either in zigzag or in double file. The disposition of parts is somewhat different in the *Ecardines*, and in the *Rhynchonellidae* among *Testicardines*. The lophophore takes the shape of two long processes or arms which are coiled into a spiral of variable but sometimes of very

<sup>1</sup> The significance of the small globular bodies which occur beneath the cuticle and in the horny layers of the shell of *Lingula*, and in the processes of the mantle contained within the canals of the shell in *Testicardines*, is not known. Shipley considers them to be blood-corpuscles.

great length. The mouth occupies the same position relatively as in the two former types, and is lodged in a brachial groove bordered by a lip. Lip and groove extend to the tips of the arms, together with a row of cirri, viz. that which corresponds to the convex side of the horse-shoe of *Argiope*. The cirri are, however, numerous, and are arranged along the whole or part of the length of each arm in double file<sup>1</sup>. The apex of the spiral is turned towards the aperture of the shell in *Lingula*; towards the dorsal valve in *Rhynchonella* among living *Testicardines*, and in a few extinct, e.g. *Atrypa*. The spiral skeleton supporting the arms shows that in the extinct *Spiriferidae* the apex of each spiral was turned outwards laterally, in *Coelospira* (*Atrypidae*) inwards, towards its fellow, and in the *Koninckinidae* towards the ventral valve. The lophophore can be protruded in *Rhynchonella*, and to a slight extent in *Lingula* (Morse), but apparently not in other Brachiopoda. It is often supported by a calcareous skeleton, which takes the form of two ridges on the inner aspect of the dorsal valve in extinct *Productidae* (Neumayr); of two simple processes projecting freely, one from each side of the dorsal hinge plate, e.g. *Argiope*; of two rods or crura similarly placed, e.g. in *Rhynchonella*; of two crura prolonged towards the margin of the valve where they recurve upon themselves towards the ventral aspect, and are prolonged back again towards the base of the shell, where they are usually united by a transverse bar, e.g. *Waldheimia*, some *Terebratulae*; or finally, of a calcareous spiral attached to each of the crura as in the extinct *Spiriferidae*, &c. A cross bar usually unites the bases of the two spirals. There is much variety in the skeleton supporting the lophophore of *Terebratulidae*.

The free surfaces of the mantle-folds, body, lophophore and peduncle, are covered by a unilaminar ectoderm, the cells of which vary in different regions. They secrete an extremely thick laminated cuticle on the peduncle. The surface of the mantle-folds applied to the valves of the shell is also covered by a layer of ectoderm cells in *Lingula* and *Crania*, but in the *Testicardines* the place of the epithelium is taken by a thin membrane (?). The ectoderm of the inner and lateral aspects of the cirri, of the brachial groove, and the aspect of the lip turned towards the groove, and in *Crania* of the mantle, is ciliated. The edges of the mantle-folds are in most instances only free for a short distance, so that the valves of the shell can be opened but to a short extent. The free edges are produced into a fold so as to form a circumpallial groove at the bottom of

<sup>1</sup> The preceding description of the lophophore in the text is based on a comparison of recent memoirs and such specimens as were accessible with Hancock's figures and descriptions. Compare the following figures in his Memoir, Ph. Tr. 148, 1858; Pl. LV, fig. 1, *Waldheimia australis*; fig. 2, *Terebratula caput serpentis*; fig. 3, *Rhynchonella*; Pl. LVI, figs. 2 and 3, *Waldheimia australis*; Pl. LXV, figs. 6, 7, 8, *Lingula*.

which are implanted fine close-set chitinous setae, rarely wanting as in *Argiope* and *Thecidium*. They are developed from tubular invaginations of the ectoderm as are the setae of Chaetopoda. Calcareous spicules or plates are often found at the bases of the ectoderm cells, e. g. in *Lingula pyramidata* and many *Testicardines*, sometimes in great numbers<sup>1</sup>. The body-walls are supported by a cartilaginous connective tissue which varies somewhat in character in different Brachiopoda, and in different parts of the same Brachiopod. It may be structureless, and hyaline, or penetrated by cells which often form a reticulum, or be fibrillated. The coelomic aspect of this supporting substance is covered by a unilaminar epithelium which appears to be ciliated wholly, or in places, thus keeping the contained fluid or blood in motion. There are special muscles for opening as well as closing the valves, differing in arrangement in *Ecardines* and *Testicardines*. The muscles are composed of a number of separate parallel fibres each of which has a nucleus and a small remnant of protoplasm, and the fibres of the posterior occlusor muscles of the shell are transversely striated in some *Testicardines*. They are attached to the dorsal valve on thickenings of the supporting connective tissue; to the ventral valve by tendons which appear to be composed of the same substance. The points of attachments cause distinct impressions. The substance of the muscles is said to be reddish. Fine muscular cells occupy in part the cavity of each cirrus, organs which can be rolled up or extended. The fibres at the edges of the mantle, and those which occupy the centre of the peduncle when short and solid, as in *Testicardines* and *Discina* among *Ecardines*, or surround its central cavity when long and hollow, as in *Lingula*, are of a nature doubtfully muscular. They form, however, at the base of the peduncle distinct bundles (adjustor muscles of Hancock) which are inserted on the valves of the shell where they cause impressions.

The central nervous system consists of a peri-oesophageal ring of some size, its ventral part usually lying posterior to the cirri, its dorsal anterior to the lip. In *Lingula pyramidata* this ring contains five ganglionic enlargements, two dorso-lateral, or supra-oesophageal, two ventro-lateral, and a median ventral, or sub-oesophageal. The ganglia lie immediately beneath the ectoderm, which here consists of one or more layers of cells supported on their inner aspect by connective tissue. The ring of *Crania* is said to contain one dorsal, or supra-oesophageal, ganglion, and two sub-oesophageal. As to the *Testicardines*, Hancock has described in *Waldheimia australis* a ring similarly constituted to that of *Lingula* (*supra*), but van Bemmelen finds only a single supra- and a single sub-oesophageal ganglion connected by a commissure. So too in *Argiope Kowalewskii* according to Shipley, whereas Schulgin found in the same animal three

<sup>1</sup> They do not occur in *Lingula anatina*, *L. affinis*, *Waldheimia* or *Rhynchonella*.

sub-oesophageal ganglia, i. e. two ventro-lateral and a median. All the ganglia are in continuity with the ectoderm in *Argiope* (Shiple), but van Bemmelen found this to be the case only with the sub-oesophageal. Ganglion cells occur in the commissures, as well as in the nerves to the lophophore, or arms. Three nerves pass, according to van Bemmelen, along each arm, one from both the supra- and sub-oesophageal ganglion, the third from the commissure, and are connected, especially that from the supra-oesophageal ganglion, with a rich ganglionic plexus. The sub-oesophageal ganglion gives off nerves to both the dorsal and ventral mantle-folds, in which they branch as they pass towards their free margins, as well as to the muscles and viscera. The disposition of the nerves is similar in *Lingula* (Beyer). Special sense organs are usually said to be wanting in the adult. Rudimentary eyes are stated by Schulgin, citing Kowalewsky, to be found in *Megerlia* 'on the inferior,' i. e. posterior 'margin of the tentacular disc not far from the mouth.' In *Argiope Kowalewskii* two parallel bands of massed ectoderm cells lie, according to Schulgin, posterior to the lophophore not far from the mouth, the one nearest consisting of 'specific,' i. e. sensory cells, innervated from the sub-oesophageal ganglia. The same author states that rod-like bi-nucleate sense-cells, connected basally to a nerve-filament, are found among the pyramidal ectoderm cells of the margins of the mantle. Joubin has traced in *Crania* filaments from the brachial nerve plexus to pads of elongated ectodermic cells at the bases on the inner aspect, i. e. the one turned to the brachial groove, of each cirrus, and to a continuous band of similar cells on the outer aspect of the same structures.

The mouth opens into the brachial groove at a spot coinciding with the centre of the convexity of the horseshoe. It leads into an oesophagus which turns anteriorly and dorsally, and then curves back upon itself and passes into the stomach. The latter is enlarged, and receives the ducts of the so-called liver lobes, which vary in number in different Brachiopoda, e. g. two in *Argiope*, &c., five in *Lingula pyramidata*. The stomach is followed by the intestine, which turns towards the ventral valve in the *Testicardines*, and, sooner or later, ends blindly. The *Ecardines* have an anus. In *Lingula pyramidata* the intestine skirts along the right side of the body; but in *L. anatina* it forms two loops before it does so; in *Discina* the curvatures are more complex; in *Crania* more simple, consisting of a three-quarter circle to the left, and in both there is a terminal dilated rectum. This rectum in *Crania* lies in the middle line between the two posterior adductor muscles, and the anus opens into a sinus between the posterior ends of the two valves, where the hinge and peduncle should be<sup>1</sup>, and not into the pallial cavity between the two valves as in *Lingula* and *Discina*, where it lies on the right side but nearer to the ventral valve than

<sup>1</sup> See Joubin, A. Z. Expt. (2), iv. 1886, pp. 218-19, figs. 2, 3, and p. 233.

the dorsal. Whether the anus has or has not become aborted in the *Testicardines* is a difficult question. Probability is, of course, in favour of the former opinion. The walls of the digestive tract consist of an outer layer of supporting substance lined by ciliated epithelium<sup>1</sup>. A 'liver' lobe in *Argiope* consists of 6-7 simple elongated caeca opening by a simple common duct. The ducts are, however, usually ramified forming lobules. The caeca are lined by a non-ciliated glandular epithelium. The food of Brachiopoda consists of Diatoms, unicellular Algae, &c., collected by the ciliated epithelium probably of both the cirri and brachial groove. Processes of the outer, or supporting, tissue coat of the digestive tract serve to suspend it in the body cavity. Their general disposition is as follows. A median dorsal lamina connects it to the dorsal shell, while a ventral lamina unites the oesophagus, stomach, and intestine, and is in *Testicardines* attached also to the ventral end of the occlusor muscles, or in *Crania* among *Ecardines* to the ventral valve. These laminae constitute the 'mesentery' of Huxley. The commencement of the stomach is connected by two (*Lingula*) or three (some *Testicardines*) 'gastro-parietal' bands, absent in *Crania*, to the dorsal shell at the attachment of the posterior occlusor muscles, while a right and left 'ileo-parietal' band tie it to the side walls of the body behind the junction of the two mantle-folds. The perivisceral portion of the coelome is large, and is broken up by the viscera, muscles and supporting bands of the digestive tract. It is continued outwards into each lobe of the mantle as the pallial sinuses, which are usually two or four in number in each lobe. The sinuses branch, as a rule, in a manner characteristic of the genus or species, and in *Lingula anatina* those branches which run radially and side by side towards the free margins of the mantle lobes are close-set, thin-walled, and terminate in small ampullae.

A circumpallial sinus uniting the terminations of the pallial sinuses is figured by Joubin in *Discina*; and is said by Hancock, but with some doubt, to exist in *Waldheimia australis*, &c. Other extensions of the coelome are the sinuses at the sides of the oesophagus, which are connected to a canal coursing along the bases of the cirri in the lophophore of *Argiope*, or to two canals in the lophophoral arms of *Crania*, &c. The coelomic epithelium is ciliated partially or wholly.

The existence of a circulatory system has been denied by most modern authorities, but the recent investigations of Blochmann prove its existence, and, to a certain extent at least, as it was described by Hancock, in a large

<sup>1</sup> Beyer describes the wall of the tract in *Lingula pyramidata* as consisting of three layers: (1) a layer of supporting tissue; (2) one of granular small cells; (3) one of ciliated cells. Joubin figures the epithelium in *Crania* as consisting of extremely narrow and long ciliated cells with basal nuclei. It is possible that Beyer's second layer corresponds to the basal nuclei or to granules in the bases of the cells.



number of Brachiopoda. It appears to communicate with the coelome, but is not, as yet, known in its finer details. The heart is usually a contractile vesicle lying in the dorsal mesentery of the stomach: it is connected to a vessel (branchio-systemic vein of Hancock) which runs forwards along the oesophagus, and is only a split in the dorsal mesentery. It appears to be connected with the circum-oesophageal lacunae, and these in their turn with a vessel which runs in the sinus beneath the cirri of the lophophore and gives off a vessel to each cirrus. Genital arteries arising from the heart are also said to be present. Variations are the presence of two hearts in *Argiope decollata*, and of two large and several small dilatations at the posterior end of the branchio-systemic vein in *Crania anomala*. Blochmann agrees with van Bemmelen in the opinion that Hancock described as blood-spaces the nervous plexuses of the arms and the branched connective tissue cells of the arms and mantle<sup>1</sup>. The coelomic fluid contains corpuscles of various kinds in suspension. In *Lingula pyramidata* there are minute refractile globules seen also in the shell: striated spindle-shaped bodies (spermatophores): small round granular cells or young ova: and the blood corpuscles proper, rounded or oval bodies, homogeneous and nucleated. The blood corpuscles of *Argiope Kowalewskii* are brown, changing to red, according to Schulgin. There are no special respiratory organs, but the cirri and sinuses of the mantle must serve to aerate the coelomic fluid.

The nephridia serve the purposes of ovi- and spermi-ducts as well as of renal organs(?). They are two in number, except in the genus *Rhynchonella* which has four, and open internally into the coelome, and externally into the mantle cavity. The inner aperture is more or less expanded, trumpet-shaped and plicated longitudinally; it leads into a contracted tube. The lining epithelium of the tube is usually yellow in colour and is ciliated in *Argiope Kowalewskii*, and probably in other Brachiopoda also. The presence of coloured granules in the cells doubtless indicates a secretory function. The internal apertures are turned towards the dorsal valve. Those of the pair of organs always present are supported by the ileo-parietal bands. The ducts run in the lateral walls of the body, and they open below the convex or posterior edge of the lophophore by separate slit-like orifices. These orifices are situated in *Argiope*, each at the bottom of a brood-pouch or sac, invaginated from the lateral walls of the body in which the ova develop. *Thecidium* has a similar, but single and median brood-pouch. The second pair of nephridia present in *Rhynchonella* have their internal apertures supported by the

<sup>1</sup> Beyer describes in *L. pyramidata* two oblong tubular organs, one in each of the lateral oesophageal lacunae, filled with blood-corpuscles. The supporting tissue of the body-walls and mantle contain in the Brachiopod just named channels lined by coelomic epithelium, and containing blood corpuscles.

lateral gastro-parietal bands, and their external apertures are above, i. e. dorsal or anterior to the bases of the two arms.

The sexes are certainly separate in *Crania* among *Ecardines*, and in many *Testicardines*. Beyer, the most recent investigator of *Lingula* (*L. pyramidata*), has come, like his predecessors, to the conclusion that it is hermaphrodite; Schulgin and Shipley, who have investigated *Argiope*, have seen none but females. As to *Ecardines* the genital organs of *Discina* are attached in groups, some to the lower edge of the lateral gastro-parietal bands, others to the ileo-parietal bands at their origin from the stomach. In *Lingula anatina* and *L. affinis* there is a set of dorsal and of ventral glands suspended to the ileo-parietal bands. *L. pyramidata* however agrees with *Crania* and other *Brachiopoda* in which the glands, two dorsal and two ventral, are contained in the trunks and main branches of the pallial sinuses, but extend sometimes to a greater, sometimes to a less degree into the central portion of the coelome. They are usually attached to the outer aspect of the sinuses, more rarely to the inner, i. e. the side towards the shell as in *L. pyramidata* and *Argiope*. They consist essentially of a process of supporting substance which grows out into lamellae, very numerous in the case of the testis, excavated by cavities, and covered superficially by an epithelium. The supporting substance is continuous with that of the wall of the sinus, the epithelium with the coelomic epithelium lining it. From the epithelium are derived both sperm-cells and ova. The striated corpuscles found in the blood of *Lingula* are said to be spermatophores. Impregnation probably takes place after the escape of the ova. The latter during their growth (? in *L. pyramidata*) are surrounded by a layer of small cells, probably abortive ova.

The Brachiopoda are found in all seas. The greatest number live at moderate depths down to 100 fathoms; few range to 500 fathoms; but *Discina atlantica* occurs between 690–2400, and *Terebratula Wyvillii* between 1035 and 2900. Some species exist at very varying depths, e.g. *Terebratula vitrea* from 5 to 1456 fathoms. *Lingula* and *Glottidia* live at about half-tide marks, and extend down to seventy fathoms. They bury themselves in mud, and their peduncle agglutinates a sand tube. When the shell of the living *Lingula* is open, the mantle-folds are disposed so as to form an aperture on either side through which water enters, and a single central opening by which it escapes. These openings are converted into funnels by the prominent setae fringing the mantle edges. The majority of Brachiopoda attach themselves to rocky bottoms. The animals occur in great numbers wherever they are found.

Of living genera *Lingula* and *Discina* range from Cambrian strata to the present time, *Discinisca*, *Crania* (?) and *Rhynchonella* from the middle Silurian, *Crania* and *Terebratula* from Devonian, *Thecidium* and *Wald-*

*heimia* from the Trias, *Argiope*, *Terebratulina*, *Macandrewia*, *Terebratella* and *Megerlia* from Jurassic times. Other living species belong to the present epoch. There are a large number of extinct Palaeozoic forms, some of which extend into the Mesozoic period; and a relatively small number of peculiar Mesozoic genera.

A larval Brachiopod, supposed to be a *Crania*, has been described by F. Müller (Archiv f. Anat. und Physiol. 1860). It possesses an orbicular bivalve shell, the dorsal larger than the ventral valve: the latter furnished with four pairs of stout setae, the former with one pair, but also with a number of fine setae which bend round the ventral valve. The mouth is overhung by a dorsal process or lip with a singular resemblance to the epistome of Phylactolaematous Polyzoa, and is surrounded by eight ciliated cirri: it is mounted on a contractile stalk. A pair of eye-specks and of otocysts are situated, the latter dorsally, at the base of the peduncle. There is a stomach. In swimming the oral stalk is extended, and the cirri spread out; in creeping the ventral valve is moved from side to side, the fourth, a very long pair of ventral setae, together with the fine setae of the dorsal valve, serving as fulcra.

The larval *Lingula* is also free swimming. The two valves are at first orbicular. The tips of the cirri are protrusible from the shell. The mouth, overhung by a lip, lies in the centre of a circular lophophore turned towards the ventral aspect. New cirri are added on each side of a median dorsal, or anterior cirrus. The lophophore becomes gradually extended laterally. There is a pair of dorsal otocysts. The peduncle arises as a hollow process at a comparatively late period. The intestine is perhaps formed as an outgrowth of the stomach. The coelome grows out into each mantle lobe, as two hollow processes.

It is interesting to note (1) that in both these larvae the lophophore is free, and at first orbicular, as in *Argiope*, though the conformation of the arms in the adult is so different, and (2) that in *Lingula* the peduncle appears late.

As to the *Testicardines*, *Thecidium* appears to have a delaminate gastrula; *Argiope*, *Terebratula* and *Terebratulina* an invaginate. The coelome is formed by a right and left diverticulum of the archenteron. In *Argiope* and *Thecidium* the larva is affixed to the walls of the maternal brood-pouch by a filament attached to its head. *Argiope* becomes divided first into two segments, then into three. The most anterior acquires the shape of a ciliated umbrella with a short stalk, and a row of especially long cilia at its margins. The second segment develops a dorsal and ventral flap with ciliated edges, the future lobes of the mantle. The ventral lobe carries four bundles of provisional setae. The third, a ciliated segment or a small fourth (Shiple), becomes the future peduncle. Eye-specks four, rarely six in number, are borne upon the head. The mantle-lobes and setae are eminently mobile. The animal fixes itself by a secretion of the peduncular segment, and then the two mantle-flaps are reversed over the head, the provisional setae lost, the head segment becomes less and less prominent. The lophophore originates as a nearly orbicular ridge on the inner aspect of the dorsal mantle-flap, and appears to pass on the ventral side of the mouth, and the eye-specks lie near its ventral edge. Finally, the valves of the shell are formed on the reversed mantle-lobes. The larva of *Thecidium* is somewhat similar to that of *Argiope*. The head is not so

well marked off. The dorsal aspect of the middle segment is large. There is, at least in early stages, no ventral mantle-lobe, and consequently no provisional setae<sup>1</sup>. In *Terebratulina minor* the mantle-folds appear before the terminal segment, and there is no head nor eyes. The lophophore of *Terebratulina septentrionalis* (and *T. caput serpentis* ?) is at first orbicular. The former has no provisional setae, but has an apical tuft of cilia.

The *Testicardines* differ from the *Ecardines* in becoming fixed before the formation of the shell and in the relatively late appearance of the lophophore. The last fact, coupled with the early atrophy of the head, may perhaps explain the share taken by the dorsal mantle-fold in the formation of the lophophore. In the larvae of *Ecardines*, supposing F. Müller's larva to be rightly allocated to that sub-order, the lophophore is a disc with the mouth in its centre, free from the dorsal valves, and in Müller's larva protrusible. It may be noted (1) that the lophophoral circle of Brachiopoda always passes ventrally to the mouth; it is therefore post-oral; (2) that the segmentation of the body is not comparable to that, e. g. of *Chaetopoda*, and does not affect the mesoderm.

The Brachiopoda are divisible into two orders.

I. *Ecardines* (= *Pleuropygia*, *Tretenterata*): shell not composed of oblique calcareous prisms; no hinge; no calcareous support for the lophophore; an anus which is either lateral or, as in *Crania*, posterior.

The existing families are the *Lingulidae* with the two genera *Lingula* and *Glottidia*; *Discinidae* with *Discina*; and *Craniadae* with *Crania*; the extinct families are two, the *Obolidae* and *Trimerellidae*, almost exclusively Silurian.

II. *Testicardines* (= *Apygia*, *Clistenterata*): shell composed of oblique calcareous prisms; a hinge nearly always well developed; a cardinal process to the dorsal valve. The living genera have no anus.

(1) *Eleutherobranchia* (Neumayr): no (free) brachial support. *Orthidae* s. *Strophonemidae*, and *Productidae*, both extinct families, nearly confined to post-Cambrian Palaeozoic strata.

(2) *Pegmatobranchia* (Neumayr), with a (free) brachial support. The two living existing families are the *Rhynchonellidae*, with one living genus *Rhynchonella*, and many extinct, which are principally Palaeozoic; and the *Terebratulidae* with living genera *Argiope*, *Thecidium*, *Terebratulina*, *Terebratula*, *Waldheimia*, *Terebratella*, *Megerlea*, and a few others; together with extinct genera, partly Palaeozoic, partly Mesozoic. Wholly extinct families are the *Koninckinidae*, partly Palaeozoic, partly Mesozoic; the *Spiriferidae*, for the most part Palaeozoic, and the *Atrypidae* and *Stringocephalidae* wholly so.

*Recent Brachiopoda*, Davidson, Tr. L. S. (2), iv. pt. 1, 1886. *Lingula* (*Glottidia*) *pyramidata*, Beyer, Studies Biol. Laboratory, John's Hopkins University, iii. (5), 1886. *Crania with notes on Discina*, Joubin, 'Recherches sur l'Anat. des Brachiopodes Inarticulés,' A. Z. Expt. (2), iv. (2), 1886. *Argiope*, Schulgin, Z. W. Z. xli. 1854; Shipley, Mitth. Zool. Stat. Naples, iv. 1883. *Brachiopoda Testicardinia*, van Bemmelen, J. Z. xvi. 1883. Cf. Hancock, 'Organisation of Brachiopoda,' Ph. Tr. 148, 1858, and Bronn, Klass. und Ordn. der Thierreichs, iii. (1), 1862.

• *Classification, &c.*, Neumayr, 'Ueber Branchialleisten der Productiden,' Neues Jahrb. für Min. Geol., &c. ii. 1883.

<sup>1</sup> De Lacaze Duthiers assigns to the larva of this Brachiopod four segments. His first, however, is evidently the disc bearing the eyes, which is not reckoned by Kowalewsky as a segment.

*Fossil Brachiopoda*, Zittel, Handbuch der Palaeontologie, Abth. 1, Palaeozoologie, i. p. 641; Davidson, 'British Fossil Brachiopoda,' Palaeontographical Society, i-vi. 1853-1886; vol. vi. is a Bibliography. *Life-history of Spirifer levis*, Williams, Amer. Journal of Science, xx. 1880.

*Bathymetrical and Geographical Distribution*, Davidson, 'Report on Brachiopoda,' Challenger Reports, i. 1880.

*Extension of arms*, Morse, Amer. Journal of Science, xvii. 1879; *Habits of Lingula*, Id. *ibid.* xv. 1878.

*Circulatory system*, Blochmann, Z. A. viii. 1885.

*Development of Argiope*, Shipley, *op. cit. supra*; *of ditto with others*, Kowalewsky (abstract in French with a few figures), A. Z. Expt. (2), i. 1883. See also Balfour, *Comp. Embryology with authorities cited*, i. p. 257.

## VERMIFORMIA.

This group contains only a single marine genus, *Phoronis*, with several species. It occurs on our own coasts in societies of separate individuals. The animal inhabits a fixed leathery tube within which it can move. It has a long body or stem, really an out-growth of the ventral surface, the true dorsum being represented by a short line joining the mouth and anus. The latter lies in the centre of the concavity of a horseshoe-shaped disc or lophophore, which bears a series of ciliated tentacles supported by a mesoblastic skeleton, and surrounded at the base like that of Phylactolaematous Polyzoa by a calyx or thin membrane. The youngest tentacles are the two nearest the dorsal median line, in the concavity of the lophophore. The mouth is overhung by a valve or epistome, the remains of the larval praeoral lobe. The nervous system lies in the ectoderm. It is concentrated in two places; as a circumoral ring following the line of the tentacles, and as a cord which runs down the left side of the body. Two ciliated sensory pits lie one on either side the anus. The alimentary canal is ciliated and divisible into an oesophagus, a first stomach, a second stomach, which is a 'small strongly ciliated chamber at the spot where the canal bends on itself in the body,' and an intestine. The coelome, which is an archenteron, is divided into an anterior and posterior part by a septum which crosses the lophophore from one side to the other at the level of the nerve ring. The anterior part is therefore small. The posterior is subdivided into three longitudinal chambers, which communicate at the base of the body, by three mesenteries, one median connecting the outer aspect of the digestive tract in its whole extent to the body-wall, the other two extending laterally from the stomach only to the body-wall. There is a vascular system consisting of two longitudinal trunks, one of which divides in the median dorsal region, and forms a ring lying at the base of the tentacles into each of which a caecal vessel passes. An outer ring is connected to these same

vessels by valved inlets. It divides; the branches surround the oesophagus, and unite to form a second, the longitudinal ventral vessel, which runs towards the base of the body in the left ventral chamber of the coelome giving off many lateral caecal branches. There is a vascular sinus round the stomach. The vessels are all contractile and contain nucleated corpuscles tinted with haemoglobin (or haemerythrin?). A fatty tissue surrounds the lateral caecal vessels above named. In it are developed, but on opposite sides, the spermatozoa and ova. The latter are impregnated in the coelome, and pass out thence by two ciliated tubes or nephridia, which open internally into the single one of the three posterior chambers of the coelome, and externally near the anus. The ova adhere to the tentacles. Segmentation is total, but unequal. The larger cells are invaginated, and the blastopore persists as the mouth. The larva is known as *Actinotrocha*. It has a large praeoral hood-like lobe with strongly ciliated edges: an imperfect postoral circlet of ciliated larval tentacles: and a ring of large cilia round the anus which is a proctodaeum. The body is also ciliated. There is a supra-oesophageal ganglion in the praeoral lobe, a sense organ in some species, and in one, four eye-spots. At the metamorphosis the praeoral lobe, ganglion, and larval tentacles, are swallowed and digested after disruption along a line of vacuolated ectoderm cells (Caldwell). The body, at first developed as a ventral invagination, is suddenly evaginated, and a new set of tentacles is formed.

Caldwell, P. R. S. xxxiv. 1883; Ray Lankester, Encyclopaedia Britannica (éd. ix), xix. p. 433.

For *Actinotrocha*, see also Wilson, Q. J. M. xxi. 1881.

## CLASS POLYZOA.

### (*Bryozoa*).

*Coelomate Metazoa, small in size, and, with one exception, forming colonies, or zoaria, which are, as a rule, fixed. There is a cuticle, secreted by the ectoderm, usually thickened and rigid on the posterior part of the body, but flexible on the anterior part. The ectoderm is generally unilaminar. The nervous ganglion is single. The mouth and anus are approximated: both of them may lie within the lophophoral area (Entoprocta), or only the mouth does so (Ectoprocta). The digestive tract is U-shaped, its flexure ventral in Entoprocta, and, perhaps so, in Ectoprocta: it is always partially ciliated. The larva is free-swimming. Gemmation is universal.*

There are two sub-classes, the *Entoprocta* and *Ectoprocta*, which are better considered apart.

*Entoprocta*.—Two well-known genera, both marine, are comprised in

this sub-class, *Loxosoma* and *Pedicellina*<sup>1</sup>. The body is more or less cup-shaped, and affixed by its dorsal or convex surface to a contractile flexible stem, which, in *Loxosoma*, is attached in turn to some foreign object by an expanded foot, or sole, but, in *Pedicellina*, is continuous with a branched stolon. This stolon usually creeps over other Polyzoa or Hydrozoa. A diaphragm separates the body from the stalk in *Pedicellina*, and the body frequently breaks off and is replaced by a successor, produced by budding from the stem. The foot of *Loxosoma* contains a foot-gland perhaps homologous with the primitive shell-gland of Mollusca<sup>2</sup>. It is always present in the young organism, and is retained in many species by the adult. It appears to be represented in the larva of *Pedicellina*. The rim of the cup, or body, i.e. the lophophore, is contractile, and can be partially closed over the cavity of the cup or vestibule. Just within its border is inserted a bilaterally symmetrical and single series of tentacles, ciliated on their adoral surface, towards which they can be rolled up when the animal is irritated or alarmed. A small lobe, or epistome, which carries a tuft of cilia in the larva of *Pedicellina*, projects between mouth and anus, both of which lie within the vestibule. The nervous system consists of a single ganglion, placed transversely between the mouth and anus. It gives off nerves to each of the tentacles and, in *Loxosoma*, to a pair of sensory tubercles (= the dorsal organ described below?). The nerves terminate in bipolar ganglion cells, one branch of which goes to an ectodermic sense cell provided with a single sense-hair. In *Loxosoma* each tentacle-nerve has a ganglion at the base of the tentacle. Sense cells are found on the aboral surfaces of the tentacles and, in *Loxosoma*, numerous round the rim of the vestibule, more sparsely elsewhere, and rarely on the stem. The intestine is U-shaped, and consists of a stomodaeum and a mesenteron, the cells of which contain pigment. There is a proctodaeum in *Pedicellina*, but in *Loxosoma* it is possible that the blastopore persists as the anus. There is no body cavity, but a gelatinous matrix with connective tissue cells and muscle cells occupies the interval between the alimentary tract and body walls. There are two nephridia with ciliated tubes which open on the adoral side of the nerve ganglion, as in some Chaetopod Trochospheres (Harmer). Testes and ovaries are both present, but appear to ripen at

<sup>1</sup> To these add: *Ascopodaria*, a marine undescribed form dredged by the 'Challenger,' with an umbel of *Pedicellina*-like zooids borne upon a stalk (Lankester, 'Polyzoa,' Encyclopaedia Brit. xix); *Urnatella gracilis*, from the Schuykill river, U. S., a fresh-water form occurring in small colonies, consisting of a disc of attachment bearing one to six stems with urn-shaped joints and more or less branched, zooids like *Pedicellina*, dying at the end of the year, and stems persisting to bud the following year (Leidy, Journal Acad. Nat. Sc. Philadelphia (2), ix. pt. 1. 1884, and Proc. of same, 1884). *Barentsia*, with a chitin-covered creeping stolon, giving off stems with lateral zooids, is supposed by Hincks (A. N. H. (5), vi. 1880) to belong here. Its full description by Vigelius (Bijdrag tot de Dierkunde, xi. 1884) has been inaccessible to me.

<sup>2</sup> Or it may be a portion of the ciliated ring of the larva. See Harmer, Q. J. M. xxvii. (2); 1886, p. 250.

different times, and the generative pore lies aborally behind the epistome. Segmentation is total, and there is an invaginate gastrula. The larva has a circular ciliated ridge, a sucker or depression, in the centre of the convex aboral surface surrounded by sense-cells, and on the same surface near the oesophagus a so-called 'dorsal organ' which is derived by invagination from the epiblast, and represents a supra-oesophageal ganglion, developing in *Loxosoma* fibres and cells. It is 'apparently connected with the sub-oesophageal ganglion of the adult which is formed from a solid mass of epiblast cells in the floor of the vestibule, but in *Pedicellina* at a late period. Eyes, or masses of pigment imbedding each a transparent lens, are found in the dorsal organ of most species of *Loxosoma*, together with a pair of ciliated pits, or in *Pedicellina* a single pit. The larval *Loxosoma* develops two buds, one on each side of but quite distinct from, the dorsal organ. The larva itself probably dies away (?). The adult gives origin to buds, one on each side of the body, which are set free. The larval *Pedicellina* fixes itself by its oral extremity: the ciliated ring is retracted and degenerates, and the digestive tract undergoes a remarkable revolution in position. A part only of the original vestibular cavity persists, and the vestibular aperture of the adult is secondarily acquired. The aboral sucker and the 'dorsal organ' abort. The adult multiplies by gemmation from the creeping stolon. 'The Entoprocta, larval and adult, are true Trochospheres, possessing a ventral flexure of the alimentary canal, no true body cavity, and a pair of head kidneys.' 'The line between mouth and anus is ventral' (Harmer).

*Ectoprocta.* The zooids, or polypides, form a colony, or zoarium, which is sometimes erect and either lamellate, or branching, and plant-like, or else adherent to some foreign object, either living, e.g. crab, sea-weed, or inanimate. The colony is fixed with rare exceptions. In *Cristatella mucedo* it creeps about on a flat sole, and in the *Selenaridae* it is free and moves about by the action of the vibracula. The polypide itself is covered by a cuticle or ectocyst secreted by the ectoderm. This cuticle always remains thin and flexible on the anterior part of the zooid which forms the so-called tentacle-sheath, and can be invaginated and evaginated by the action of special muscles (p. 236). The cuticle of the posterior part generally thickens, and becomes resistant: it is gelatinous (*Alcyonidium*; *Lophopus*), or chitinoid, and usually more or less opaque and sometimes partially, or wholly, calcified. The calcareous matter in *Lepralia*, &c., is, however, said to be laid down between two layers of ectoderm cells, which are covered externally by a thin cuticle. The posterior region of the cuticle is known as zoöecium, and the collection of zoöecia forming a colony constitute the coenocœcium. The zooids are often polymorphic. In both *Ctenostomata* and *Cheilostomata* certain of them may be modified into stem-cells, and in the latter as Avicularia, and Vibracula (p. 237). The Oöecia and Root-fibres are probably to be regarded as organs (Vigelius). The ectocyst is lined by a soft layer



or endocyst formed apparently in marine Polyzoa by the fusion of two layers of cells. It has recently been stated, however, that an ectoderm layer may always be distinguished by the use of silver nitrate. In the *Phylactolaemata* a layer of ciliated epithelium lines the coelome, and distinct muscular layers, external circular, and internal longitudinal, intervene between it and the ectoderm, at least in *Alcyonella fungosa*. There is a common coelome for all the zooids in the colony of the *Phylactolaemata*, but in the *Gymnolaemata* the coelome of every zooid is isolated by septa. In these septa and in the walls of the zoöecia, where they touch one another there are in some forms, groups of perforations, or communication-plates, which are covered by a columnar epithelium and are connected by the funiculi (p. 235).

The mouth and anus are approximated, and the line between them, perhaps, marks a mid-ventral surface. The ganglion is situated between them. It is minute and double in *Phylactolaemata* where it has a narrow commissure encircling the oesophagus, and supplies nerves to the lophophore, tentacles (?) and digestive tract. Sensory cells resembling those of the *Entoprocta* have been detected on the tentacles of *Alcyonella fungosa*, &c. The mouth in the *Phylactolaemata* is overhung by a small ciliated mobile lobe, the epistome, perhaps homologous with the same structure in *Entoprocta*. It lies in the centre of a disc, or lophophore, either circular (*Gymnolaemata*), or horse-shoe shaped, i.e. crescentic (*Phylactolaemata*), along the edges of which are ranged in single series a row of tentacles which are postoral in position. They are hollow, and their cavities are extensions of the coelome: they are covered on the aboral and adoral surfaces by ciliated epithelium, on the action of which depends the food supply. Their number varies much; they are flexible and move swiftly bending to one or the other side, or coiling and uncoiling together in a spiral. Muscular bands have been detected inside them on the aboral and adoral surfaces. In the *Phylactolaemata* the bases of the tentacles are protected externally by a thin membrane or calyx. The alimentary canal retains a U-shaped curvature. It consists of a pharynx, followed in many instances by a ciliated oesophageal region, separated by a slight constriction from a stomach, the cells lining which contain a brown pigment. There is interposed between the stomach and the oesophagus in *Ctenostomata* a gizzard with thickened muscular walls, and containing gastric teeth or pointed processes. The stomach is tied to the endocyst by one or more funiculi, and is often V-shaped, as in *Membranipora* (Fig. 10 A, p. 235). The bent up pyloric portion is always ciliated in *Gymnolaemata*. The length of the intestine varies. The coelome is roomy, and contains a liquid in which float corpuscles derived, it is said, from the funicular tissue.

The *Phylactolaemata* are hermaphrodite, as are some *Gymnolaemata*;

in others this appears to be the case with certain zooids in a given colony, whilst the remaining zooids possess a ripe ovary or a ripe testis only. It is possible, however, that a testis or ovary may be developed at some other time in these cases. Both ovary and testis are produced by the growth of cells derived from the funicular tissue or the endocyst. The ovary is often placed at the upper end of the zoöcium, the testis at the lower. The ripe products are set free into the coelome, where the ovum may be impregnated by the spermatozoa of the same individual. In two species of the genera, *Alcyonidium* and *Membranipora*, the spermatozoa have been seen to escape through a flask-shaped and ciliated inter-tentacular organ placed on the anal aspect of the body, and opening both externally and into the coelome. It has been found in female as well as male zooids, and is perhaps to be considered as a nephridium. The number of ova in the ovary is very variable (2 to 30). Some of the ovarian cells form a follicle for the growing ovum. The ripe ova pass into an Oöcium or marsupial chamber in *Cheilostomata*, where they are probably impregnated by the spermatozoa of another zooid, and develop into larvae which escape through the Oöcial aperture. In *Farrella* and *Hypophorella* the ovum escapes by a special aperture at the base of the tentacles. In some *Phylactolaemata*, e.g. *Alcyonella*, and some *Gymnolaemata*, e.g. *Valkeria*, a rudimentary tentacular and digestive system is produced by budding in a zoöcium in which the perfect organs have been lost (*infra*). The ripe ovum passes into the tentacular sheath thus formed, is fertilised and developed into a larva which escapes through the opening of the sheath. In many instances, however, the ovum or the larva must be set free solely by the death and decay of the parent. A special individual—a gonocœcium, or a gonocyst—is sometimes developed in which ova are found. The former occurs in *Crisia* (*Cyclostomata*), some *Cheilostomata*, and in *Alcyonidium* (*Ctenostomata*), the latter in some *Cyclostomata*, but the anatomy of these structures is not understood. The ovum undergoes total segmentation. In *Phylactolaemata* it forms a hollow cyst ciliated externally, with walls formed of two layers of cells. The colony is derived by gemmation from this cyst. There are three forms of larva among *Gymnolaemata*, the bivalved larva of *Flustrella* and of *Membranipora*, the latter known as *Cyphonantes*: the larva of other *Cheilostomata*, and *Ctenostomata*, and that of *Cyclostomata*. The Cheilostomatous and Ctenostomatous larva has an aboral face separated by a ciliated ring or corona from an oral face. In both there is an aboral calotte or retractile disc, surrounded by, or bearing sense-hairs, sometimes regarded as the homologue of the foot-gland of the *Entoprocta*. On the oral face are two structures: one the 'anterior ectodermal furrow' of Vigelius, 'oral furrow' of Nitsche and Claparède, the 'fente' of Barrois, the other, the 'sucker' of Vigelius, 'stomach' of Barrois, both produced

by invaginations of the ectoderm. The sucker appears to be the organ by which the larva ultimately fixes itself; and it might, therefore, be considered, at least functionally, as the homologue of the foot-gland of *Loxosoma*. The larva of *Cyclostomata* is ciliated and barrel-shaped. At one end is the mouth leading into a stomach. At the other is a prominence, the homologue of the ciliated disc inclosed in a cylindrical sheath, the homologue of the corona (?). When a larva fixes itself, its organs, whatever they are, appear to undergo atrophy, and the tentacles, digestive tract, muscles, and nervous system of the adult zooid, make their appearance. The *Phylactolaemata* also reproduce by statoblasts or winter buds formed from the funiculus. The cells at one pole of the bud grow round the remaining cells, and form at their inner ends the chitinous investment and chitinous marginal air-cells of the fully formed statoblast. The statoblasts are discharged on the death and decay of the parent, and the whole colony in *Pectinatella* is at this time set free, and floating along the stream scatters them over a wide area. The same is true of *Cristatella*. The statoblast remains quiescent through the winter season. In spring it gives origin to a small non-ciliated, but fully formed individual, which fixes itself, and produces a colony by gemmation. All Polyzoa increase by budding, and the bud appears to be formed by tissue elements derived from the corresponding elements of the parent (see p. 236). In all the marine Polyzoa the tentacles, digestive tract, and its retractor muscles, with the nervous system of the individual are lost in the older parts of the colony. They degenerate into the 'brown body.' A new set of organs is produced from the endocyst by budding, and the brown body appears to pass into the new stomach where it may break down and perhaps be partially digested. It or its remnants are eventually expelled.

The *Phylactolaemata* are confined to fresh-water. The *Gymnolaemata* with the exception of *Paludicella* are marine, and are most plentiful near the shore, and at moderate depths. Certain *Cheilostomata* were, however, dredged at great depths in the voyage of H.M.S. Challenger, e.g. in the North Atlantic at 2750 fathoms, in the North Pacific at 3125. The *Cyclostomata* and *Cheilostomata* occur fossil. The first-named appear in Cambrian and Silurian strata, the second are sparingly represented in the older strata, but become numerous in the Upper Greensand, whilst the *Cyclostomata* diminish in numbers from Tertiary strata to the present time. Of living genera *Stomatopora* among *Cyclostomata*, and *Hippothoa* among *Cheilostomata* are said to appear in Silurian times. Many Jurassic genera still survive.

The class Polyzoa is subdivisible as follows :

I. *Entoprocta*. Lophophore praeoral; mouth and anus within the lophophoral

area; no coelome; a pair of nephridia; hermaphrodite. *Loxosoma*, non-colonial; *Pedicellina*, colonial. See note 1, p. 705.

II. *Ectoprocta*. Lophophore post-oral; anus external to it; a large coelome; sexes sometimes separate (?). Colonial.

i. *Phylactolaemata*. Lophophore horse-shoe shaped; a moveable epistome overhanging the mouth; fresh-water; *Cristatella*, *Pectinatella*, *Lophopus*, *Alcyonella*, *Plumatella*, *Fredericella*.

2. *Gymnolaemata*. Lophophore orbicular; no epistome; marine with the exception of *Paludicella*.

i. *Cyclostomata*. 'Cell mouth,' i.e. aperture left when tentacle-sheath is retracted, not guarded by an operculum or processes; zoëcia tubular; most genera are fossil; e.g. *Crisia*, *Diastopora*, &c.

ii. *Ctenostomata*. 'Cell-mouth' guarded by seta-like processes; zoëcium never calcareous; stem and root-cells often present; e.g. *Alcyonidium*, *Vesicularia* (= *Valkeria*), *Paludicella*, &c.

iii. *Cheilostomata*. 'Cell-mouth,' guarded by a thickened and moveable operculum; oral area to a great extent membranous; ova usually matured in oëcia; avicularia and vibracula often present; e.g. *Aetea*, *Scrupocellaria*, *Flustra*, *Membranipora*, *Lepralia*, *Eschara*, *Cellepora*, &c.

*Ectoprocta*. *Loxosoma*, Harmer, Q. J. M. xxv. 1885, with lit. cited; *Pedicellina*, Nitsche, Z. W. Z. xx. 1870, *its life history*, Harmer, Q. J. M. xxvii. (2), 1886; Barrois, A. Sc. N.; (7), i. 1886.

*Ectoprocta*, see p. 238. *Fresh-water Polyzoa*, Jullien, Bull. Soc. Zool. de France, x. 1885; *Polyzoa (Cheilostomata)*, Busk, Challenger Reports, x. 1884.

*Fossil Polyzoa*, Zittel, Handbuch der Palaeontologie, Abth. i, Palaeozoologie, i, 1880, p. 575.

*Ectoderm*, &c., Ostroumoff, Z. A. viii. 1885.

*Intertentacular organ*, Farre, Ph. Tr. 127, 1837, pp. 408, 412; Hincks, A. N. H. (2), viii. 1851, p. 355; Id. Brit. Marine Polyzoa, i. p. lxxxix.

*Special aperture for escape of ova*; in *Farrella* (= *Laguncula*), P. J. van Beneden, Mém. Ac. Roy. Belg. xviii. 1845, p. 18; in *Hypophorella*, Ehlers, Abhandl. K. Ges. der Wissenschaften, Göttingen, xxi. 1876, p. 66 (not seen).

*Rudimentary tentacle sheath*, &c., for escape of ova; in *Alcyonella*, Metschnikoff, Bull. Ac. Imp. St. Petersburg, xv. 1871, p. 507; Nitsche, Z. W. Z. xxii. 1872, p. 467; in *Valkeria*, &c. Joliet, A. Z. Expt. vi. 1877, p. 262.

*Floating colonies of Pectinatella*, Kraepelin, Z. A. vii. 1884.

*Embryology of Phylactolaemata*, Reinhard, Z. A. iii. 1880; cf. *on Metamorphosis of do.*, Ostroumoff, Z. A. ix. 1886; *of Gymnolaemata*, Barrois, Journal de l'Anat. et Physiol. xviii. 1882; cf. A. N. H. (5), x. 1882; Id. A. Sc. N., i. 1886; Vigelius, Mitth. Zool. Stat. Naples, vi. 1886; *of Cyclostomata*, Ostroumoff, Z. A. ix. 1886.

*Oëcium of Bugula*, Vigelius, op. cit. p. 512.

*Gonoecium and Gonocyst*, Hincks, 'Marine Polyzoa,' i. p. xcvi; p. 418.

## PTEROBRANCHIA.

The two marine genera *Rhabdopleura* and *Cephalodiscus* are contained in this group; the former found near the Shetland and Lofoten Islands, and on the Norwegian coast at depths of 90, 200, and 40 fathoms respectively<sup>1</sup>; the latter taken by the 'Challenger' expedition in 200 fathoms off the Patagonian coast.

*Rhabdopleura* forms indefinitely branching colonies, attached to various foreign objects. The zooids are all connected by a stem, and are contained in a tubarium, or connected system of hollow tubes composed of a hyaline material, which is secreted by the buccal shield of the zooids. The axial part of the tubarium, both main axis and branches, is adherent. The tubes of the zooids are more or less erect. The latter originate from the axis laterally, and the axial tube is divided by transverse septa into compartments, one to each zooid and its tube. *Cephalodiscus* buds, but the buds are detached at a certain stage of growth. Its zooids and their descendants inhabit cavities in a gelatinous branched mass with fimbriated edges probably secreted by the buccal shield as in *Rhabdopleura*. The head of the zooid bears in *Rhabdopleura*, on either side a flexible arm, the two edges of which are beset each with a single row of about fifteen ciliated flexible tentacles. Arm and tentacles are alike supported by a mesoblastic skeleton. *Cephalodiscus* is provided with twelve similar arms, six on each side, similarly beset with tentacles, and each of its arms terminates in a knob. Between the bases of the arms in both genera alike, and overhanging the mouth is a mobile disc or buccal shield. Its surface is ciliated in *Rhabdopleura*, and its shape extremely changeable. Not only does it secrete the tubarium, but it is an organ of locomotion by means of which the zooid creeps up its tube. The body in both genera is more or less ovoid, and gives origin on its oral aspect, and somewhat posteriorly to a flexible stalk or stem ("gymnocaulus"). This stem ends freely in *Cephalodiscus*, and bears at its extremity one or two buds. In *Rhabdopleura* the stem is branched correspondingly with the tubarium. It contains an axial skeleton, similar to that supporting the arms and tentacles, one surface of which is covered by muscle cells. The part of the stem to which the zooid is immediately attached, and which traverses the zooid tube, retains its soft nature. Contraction of its muscle cells retracts the zooid towards the base of its tube, the stalk itself being thrown into coils simultaneously. When the muscle cells relax, the elasticity of the skeleton probably comes into play, and aids the movement of the zooid up the tube. But the ectoderm of the branched part of the stalk, contained in the main axis and the branches of the colony,

<sup>1</sup> *R. compacta* comes from deep water off the coasts of Antrim (Hincks, Marine Polyzoa, i. p. 581, Pl. 72, Figs. 8, 8a, 9).

secretes an external hard brown chitinous coat. It is therefore rigid, and is termed 'pectocaulus' by Professor Ray Lankester. It becomes adherent to, and eventually sinks into the substance of the tubarium on its attached aspect. The mouth lies beneath the epistome. The alimentary canal is ciliated, and has a U-shaped curvature as in Polyzoa. The anus is situated on a more or less projecting papilla at the head-end of the body, but on the opposite side to the mouth. There is a small coelome which extends into the stalk. It is lined in *Rhabdopleura* by fusiform cells, sometimes branched, occasionally stretching from the body-wall to the digestive tract. The ectoderm cells of the arms, tentacles, epistome, and to a lesser degree of the stalk, contain in *Rhabdopleura* some an orange, others a black, pigment; and there is a special aggregation of black pigment at one end of the epistome, possibly a rudimentary eye. *Cephalodiscus* has a pair of eyes apparently placed on the oral aspect above the mouth, and hidden by the buccal shield. *Rhabdopleura* has a ciliated sensory (?) tubercle at the base of each arm on its aboral aspect. No nervous system and no nephridia have been detected. The testis in *Rhabdopleura* is an elongated sac opening by a special pore anteriorly and aborally. Ova have been found in *Cephalodiscus*. Both organisms reproduce by budding. While the buds are detached in *Cephalodiscus*, they remain connected by the pectocaulus in *Rhabdopleura*. The young buds in this genus are formed on the soft stalk or gymnocaulus of a zooid, which appears itself to remain for a time in an arrested condition, i. e. its arms are rudimentary, its buccal shield deeply bifid anteriorly, its gymnocaulus in a state of growth. The youngest bud is the one nearest to it. The buds are successively isolated with increasing age from one another by transverse septa which divide the axial tube into compartments (*supra*).

The affinities of Pterobranchia are at present doubtful. In the absence of all embryological evidence it is not possible to say whether the buccal shield or epistome is prae-oral as it is in Brachiopoda and Vermiformia, or post-oral, as it appears to be in the entoproctous Polyzoa; nor again whether or no the flexure of the intestine is dorsal or ventral. The class is accordingly treated as independent here.

Ray Lankester, 'Polyzoa,' Encyclopaedia Britannica (ed. ix.), xix. p. 434.

*Rhabdopleura*, Id. Q. J. M. xxiv. 1884.

*Cephalodiscus*, McIntosh, A. N. H. (5), x. 1882.

## COELENTERATA.

METAZOA in which a gelatinoid substance, the supporting lamina or mesoglaea<sup>1</sup>, intervenes between the epi- and hypo-blast of the embryo or

<sup>1</sup> The term 'mesoglaea' is due to Mr. G. C. Bourne (Q. J. M. xxvii. pt. 3, 1887). It seems inadvisable to apply either of the now synonymous terms 'mesoblast' and 'mesoderm' to the sup-

larva, and persists throughout life, holding the position of the absent mesoblast or intermediate cell layer of Coelomata. This mesoglaea varies in amount and consistency: it is homogeneous, sometimes partially fibrillate, and may be invaded by cells derived from the ecto- or endo-derm, or from both. The cells of the ectoderm may be uni- or multi-laminar. They may be differentiated into epithelium or covering cells, epithelio-muscle cells, muscle cells, pigment cells, gland cells, cnidoblasts, skeletogenous cells, sense with supporting cells, ganglion cells, and genital cells. The endo-derm is unilaminar, rarely multilaminar and then, as a rule, only in limited spots. Its cells may be differentiated, like the cells of the ectoderm, with the addition of skeletal cells, but skeletogenous cells, ganglion cells, and sense cells, with the exception of otolith cells, are rarely met with. Both ecto- and endo-derm are primitively unilaminar in the larva.

A persistence of the vertical axis passing through the Gastrula mouth as the long axis of the body, and a symmetry of form round this axis are typical of Coelenterata. When bilateral symmetry is established, or a lateral elongation of the body in a vertical plane takes place, an even balance with reference to the vertical axis just named is, as a rule, maintained<sup>1</sup>. Irregular growth, however, occurs in most Sponges.

There are four classes, *Ctenophora*, *Anthozoa*, *Hydrozoa*, and *Porifera*. The three first named possess peculiar offensive structures, either adhesive cells or cnidoblasts containing nematocysts, the former in the *Ctenophora*

porting lamella of Coelenterata, for the following reasons: (1) It appears typically as a clear layer between the epi- and hypo-blast of the embryo some time after their differentiation; (2) not only does it contain no cells at first, but may remain permanently in this condition; (3) when cells enter it, they never form a defined layer either sub-ectodermic or sub-endodermic; (4) it is frequently specialised in density and fibrillation; (5) though its cells, when present, may assume particular functions, the supporting lamina as a whole never gives rise to tissues in the same way as does the mesoblast. Apparent exceptions are (1) the early developed group of cells said by Metschnikoff to be derived from the endoderm in embryo Ctenophores, the source of mesoglaeal cells later on (see note 2, p. 720); and (2) the cellular mass filling the planula of certain Sponges. But according to Chun, mesoglaeal cells are derived in Ctenophores throughout life from the superficial and stomachal ectoderm; and the cells of the Sponge larvae in question appear to be the common source of both endoderm and mesoglaeal cells.

A gelatinous substance fills the blastocoele of Echinoderm larvae, the Nemertean *Pilidium*, etc.; but it appears before the epi- and hypo-blast are differentiated, and is, therefore, probably not homologous with a supporting lamella. Cells enter it either from the walls of the blastula or of the archenteron. They subsequently give rise to continuous cell-layers, and the jelly disappears at the same time. The cells referred to are therefore destined to a development never attained in any Coelenterate.

It is not likely that Coelomate forms are derived from Coelenterate. The latter are specialised from a simple gastrula type, from which the Coelomata have also sprung, but in a different direction. The great complexity often acquired by the Coelenterate ecto- and endo-derm points to the same conclusion.

<sup>1</sup> The converse of these three propositions appears to be true of the Coelomata. The principal axis of the Gastrula never persists as the principal axis of the body. Bilateral symmetry is always established, but may be disguised or lost; it is balanced with reference to the Gastrula axis, but this is not the case with the elongation of the body. Cp. p. 584, on the Trochosphere, &c. For points connected with the mesoblast and coelome, see General Introduction.

and a few *Hydrozoa*, the latter in one Ctenophore, in the *Anthozoa* and *Hydrozoa*. All are aquatic, and with few exceptions marine. The larva is ciliated and, except in *Ctenophora* set free, as a rule, at an early stage of development.

With the absence of a mesoblast is correlated the absence of coelomic spaces of all kinds, of a circulatory, specialised respiratory and nephridial systems. The genital cells are sub-epithelial, or in *Porifera* mesoglaeal.

The mesoglaea is a proteid substance, sometimes as dense as hyaline cartilage, sometimes excessively soft and watery, e. g. it contains 95.392 % of water in *Rhizostoma Cuvieri* (= *Pilema pulmo*). This percentage may be exceeded when the seawater is less saline than usual; e. g. *Aurelia aurita* from Kiel has 97.90 %. Fibrillae are very commonly present. They vary in character, size, mode of disposition, whether reticulate, tangential, or vertical to the surface. They are probably derived by condensation of the jelly: but in some instances very delicate fibrils have been traced into continuity with the ecto- and endo-derm cells. As to mesoglaeal cells, they may be wanting as in Craspedote Medusae: when present either simple or, as in *Ctenophora* and *Porifera*, specialised in various ways. They may be derived from the ecto- or endo-derm, or from both, and are sometimes set apart at an early period as in *Ctenophora* (note 2, p. 720). The mesoglaea itself is probably derived in some instances from the ectoderm, in others from the endoderm, e. g. in the taeniola of *Acraspeda*.

An epithelium cell is one that is solely protective: an epithelio-muscular cell is an epithelium cell with a basal muscular process, whereas a muscle cell is sub-epithelial in position. Muscle cells may become inclosed within the mesoglaea by the growth of the latter, and are then termed by Hertwig 'mesodermal muscles.' The term 'neuro-muscular' cell (Kleinenberg) has been applied to an epithelio-muscular cell, but there is no reason to ascribe any special nervous function to the cell portion of such a unit, any more than to the undifferentiated cell portion or muscle-corpuscle of a striated muscle-fibre. The term has recently been used by Korotneff in connection with certain remarkable branched ectoderm cells, the processes of which are in continuity with the longitudinal ectodermic musculature of some *Siphonophora* (Mitth. Zool. Stat. Naples, v. p. 235, Pl. 14, Fig. 13). The muscle substance is highly refractile, and is transversely striated in the subumbrellar muscles of Medusae.

A sense-cell is long, slender, provided with a cilium or stiff hair at the external end, and prolonged basally into 2-3 fine filaments which are connected to nerve fibres or processes of ganglion cells. A supporting cell is usually short and stoutish, its basal end prolonged into filaments which probably enter the mesoglaea. Such supporting cells occur wherever sense cells are present in numbers. In the eyespecks their outer ends are pigmented. The other terms require no explanation.

As to the endoderm, skeletal cells occur in the tentacles of many *Hydrozoa*, cf. p. 329 on Fig. 7, Pl. xiv, under C; skeletogenous cells are met with in some *Anthozoa Alcyonaria* (?); sense and ganglion cells have been detected in the prostomium of the Hydroid *Eucopeella* and on the mesenteries of Hexactinians.

For cnidoblasts, see p. 330, on Fig. 8, C, and for their contained nematocysts p. 331, on Fig. 9, both Pl. xiv.



When the ectoderm is multilaminar, its deeper cells may be undifferentiated, and of irregular outline as in some Hydroids, e. g. *Hydra*, stem of *Endendrium*, &c., and they are then termed sub-epidermic or interstitial cells. If they are differentiated three layers are generally distinguishable, an outer of epithelium, gland, and sense cells, &c., a middle of ganglion cells, and an inner of muscle cells, e. g. in *Hexactiniae* among *Anthozoa*. A multilaminar endoderm is very rare, but is seen in the stem of a few Hydroids, e. g. *Tubularia*, or in the hydranth of *Myriothele*, and perhaps in some *Anthozoa*.

The archenteron, or gastric cavity, is primitively more or less flask-shaped, but it may be produced into a system of canals, regular in *Ctenophora*, irregular in many *Porifera*, or be partially obliterated by the cohesion of its walls, as in the Medusa of *Hydrozoa*, or broken up by the development of radial ridges (mesenteries and septa) and a stomodaeal invagination in *Anthozoa*. In colonial forms it is continued through the stems, roots, &c., connecting the zooids; and inasmuch as it is ciliated either partially (most *Porifera*) or wholly (other Coelenterata), and the products of digestion may therefore be carried through all its parts from the special region where digestion occurs, it is often spoken of analogically as the 'gastrovascular system.' The *Ctenophora* are remarkable for possessing an ectodermic invagination or 'stomach' in which digestion takes place. The stomodaeum of *Anthozoa* is simply oesophageal in function.

Intracellular digestion has been observed in a variety of Coelenterata, the epithelial cells possessing in many instances the power of emitting pseudopodia and seizing nutrient particles. The cells may be those of the ectoderm, as in the machopolytes of certain *Plumularidae*, or in certain embryo or larval Hexactinians (*Actinia mesembryanthemum*: *Bunodes sabelloides*), or most commonly of the endoderm (*Beroe*; *Sagartia*, *Aiptasia* among *Anthozoa*; various *Hydrozoa*). In the *Porifera* the wandering mesoglaeal cells (in part) take an active share in the process of digestion; and Metschnikoff has compared with this process the destructive power exercised by mesoblast cells in the absorption of parts dead or dying, or of intrusive foreign bodies in Coelomata. See authorities quoted p. 249; cf. Claus, Z. A. iv. 1881. On *Porifera*, see also von Lendenfeld, Z. W. Z. xxxviii. p. 252, Poléjaeff's remarks in his 'Report on the *Calcarea*,' Challenger Reports, viii., p. 14, et seq., and the account of the class, *post*.

The four classes of Coelenterata seem at the present time to be distinct from one another. The *Ctenophora*, *Anthozoa* and *Hydrozoa* have in common the possession of offensive and defensive cell-structures, adhesive cells or cnidoblasts. The *Ctenophora*, however, have been recently derived by Haeckel from the *Hydrozoa*, and from the Anthomedusan family *Cladonemidae* in particular: see J. Z. xiii. 1879, SB. Jen. Ges. pp. 70-79. Two facts alone, leaving out of sight others, militate strongly if they are not decisive against his view, viz. the absence in all *Ctenophora*, even in development, of a gastral lamella uniting the endodermal canals, a structure which is present in all Medusae, and the fact that the tentacles are solid ectodermal structures, and do not contain an endodermic axis of any kind as do those of every *Hydrozoan*, whether hydroid or medusa. The position of the *Porifera* has been much debated. Histological structure, the presence of sperm, ova, of a blastula and gastrula, prove beyond doubt that a Sponge is not a colony of Protozoa as has been supposed. Stress has been laid on the absence of tentacles as showing an unlikeness to other Coelenterates; but tentacles are absent in the Ctenophoran

*Beroidea*, in the Hydrozoan *Protohydra*, *Microhydra*, *Limnocoedium* and some Medusae. The pores leading to the gastric cavity, or its parts, are a peculiar feature; but aboral pores are found in *Ctenophora*; pores on the tentacles, peristome, and body-wall and base in some *Anthozoa Zoantharia*; pores or subumbrellar papillae on the circumferential canal of some Hydrozoan *Leptomedusae*. These structures are, however, by no means homologous, and the pores of Sponges have a function found in no other Metazoa. Their great development renders possible the irregular and continuous growth of a Poriferan, and is no doubt correlated with a unique phenomenon, the fixation of the animal by the gastrula-mouth, afterwards obliterated, which has been noted in two thoroughly established instances. Add the collared endoderm cells and the absence of cnidoblasts and adhesive cells<sup>1</sup>, and the sum of peculiarities certainly gives the *Porifera* an isolated position among Coelenterata, but whether sufficient to erect them into a group of coordinate value is doubtful. They are retained here in this division of Metazoa on account of the resemblance in their fundamental structure (ecto-, endo-derm and mesoglaea) to what is typical of other Coelenterates in general.

For a remarkable ambulatory colonial Coelenterate, *Polypodium ambulans*, with non-tentaculate zooids, devoid of mesenteries, but resembling histologically an Actinian, see Korotneff, Z. A. ix. 1886.

## CLASS CTENOPHORA.

*Non-colonial, free-swimming and pelagic Coelenterata, globular, cylindrical, rarely band-like in shape. The mouth is at one pole of the principal axis, a sensory organ and otolithic mass with two excretory apertures at the other. Eight rows of ciliary or ctenophoral plates radiate meridionally from the sensory organ. There is, as a rule, a pair of tentacles, retractile into pouches, and provided with adhesive cells. Hermaphrodite. Exclusively marine.*

An axis passing through the otolithic mass and the mouth is the principal axis of the body. It has two poles, an oral and aboral. Two vertical planes at right angles to each other pass through this axis. One is parallel to the longer diameter of the stomach, and may be termed the stomachal or lateral plane: the other is parallel to the longer diameter of the funnel, and may be termed the funnel plane, median or sagittal plane. The funnel plane divides the body into a left and right half, the stomachal into an

<sup>1</sup> How far weight can be laid on this negative character is doubtful. Thread-cells are found in *Infusoria* among Protozoa; in *Aeolidia* (*Gastropoda*); and structures which are generally compared with them in *Turbellaria*. The late Professor Balfour thought it possible that the layers, i. e. 'ectoderm, endoderm and mesoblast did not correspond with the similarly named layers in the Coelenterata and other Metazoa.' He was influenced in his views by the peculiar character of the amphiblastula larva and by current opinions on the function of the collared cells—that they were respiratory, not digestive. There are, however, different forms of Sponge larvae; and authorities are even as yet by no means agreed as to the function of the collared cells.

anterior or dorsal, and a posterior or ventral half. Each half consists of two quadrants<sup>1</sup>. Two axes, a stomachal or lateral and a funnel or dorso-ventral axis, pass respectively through the stomachal and funnel planes. A horizontal plane at right angles to the planes of the principal axis may be termed the equatorial or dorso-ventral plane. The two tentacles lie one at each end of the funnel plane. The eight meridional vessels and ctenophoral rows are distributed four in each lateral half, or two to each quadrant of the body. The row of plates or the vessel in each quadrant which adjoins the funnel plane or tentacle, is termed 'subtentacular'; that which adjoins the stomachal plane 'subventral.'

The typical shape of a Ctenophore as seen in a *Pleurobrachia* is ovate, the long axis of the oval coinciding with the principal axis. The mouth leads into a flattened ectodermic stomach, the plane of the flat sides coinciding with the stomachal plane. Towards the aboral aspect, the stomach leads in turn into the endodermic funnel, the longest diameter of which coincides with the funnel plane. The funnel gives origin to two 'per-radial' vessels, which run more or less horizontally outwards in the funnel plane in opposite directions. At their outer ends these vessels bifurcate. And the four vessels thus formed belong one to each of the four quadrants and are known as 'interradial' vessels from the direction they take. A vessel to each tentacle springs from the angle or fork between each pair of interradians. The four interradial vessels bifurcate in turn giving origin to adradial vessels, eight in number, two to each quadrant. The adradials open one into each of the eight meridional or ctenophoral vessels which end blindly at their oral and aboral ends. The eight rows of ctenophoral plates coincide with the eight meridional vessels. A vessel originates from each of the perradial vessels close to its origin, runs in an oral direction close to the flat side of the stomach, and ends blindly. These two vessels are the 'paragastric canals.'

At the centre of the aboral pole is a pyramidal depression surmounted by a hyaline bell. The depression is elliptical or roughly hexagonal in outline, the longer axis of the ellipse or hexagon coinciding with the stomachal plane. The space inclosed is the central nervous system or sensory area. The ectoderm cells of this area are ciliated. Certain of them disposed in a circular row are provided with very long cilia which are bent like the figure 2, and are fused in groups to form four triangular cilia-plates. The tips of these plates give support to a spherical mass of agglutinated otoliths which consist of Calcium phosphate. Rows of similar but small plates, the four nerves or ciliated furrows, diverge outwards and inter-

<sup>1</sup> The 'stomachal' plane of Chun corresponds to the 'coeliac' plane of Agassiz, the 'sagittal' plane of Claus, Haeckel, and Hertwig, and the 'transverse' plane of Fol. Chun's 'funnel' plane is the 'diacoeliac' plane of Agassiz, the 'transverse' of Claus and Hertwig, the 'lateral' of Haeckel, and the 'tentacular' of Fol.

radially from the bases of the four cilia plates in question. They pass through four openings in the bell, divide each into two, and the eight nerves thus formed abut one against the first ctenophoral plate of each of the eight rows. The long axis of the sensory ellipse is prolonged outwards on each side, and in the same plane by the polar plates which in the adult are rectangular in outline. They are ciliated and their margins thickened. The central area of each polar plate leads into the bell by an aperture; its cilia work towards this aperture and renew the water within the bell. The central nervous system can be retracted by special muscles.

The funnel extends upwards beneath the central nervous system as the funnel vessel; it bifurcates and each branch forks again into two ampullae, making four in all, one to each interradius. Two, which correspond to the anterior left interradius and the posterior right, remain blind, whilst the other two are prolonged each into an excretory or anal tube opening externally in the right anterior interradius, and the posterior left just outside the polar area. These apertures are usually closed but are opened by the animal for the escape of water and faecal particles<sup>1</sup>.

The tentacles are two in number, and originate from a thickened basis which is sunk in a deep pit or tentacle sheath, the aperture of which is turned aborally. Consequently, the basis lies more or less close to the principal axis, in *Pleurobrachia* below, i. e. orally to, the origin of the funnel. The tentacle vessel, which is excessively short, is not prolonged into the axis of the tentacle, but gives origin to two ampullae which lie in its basis. The main axis of the tentacle is beset with a single series of simple branches. The whole structure is eminently contractile and can be completely withdrawn into its sheath.

The sexual organs are situated at the sides of each meridional vessel, the male on the sides corresponding to the four interradii, the female on those corresponding to the four radii, i. e. on the subtentacular and subventral aspects of the vessels. They take the form of bands coursing along the whole length of each vessel beneath the rows of ctenophoral plates. The genital products pass into the meridional vessels, thence to the funnel, the stomach, and out by the mouth.

The *Cydippidae* possess the typical structure above given. The aboral pole of the body may be produced into two or four processes situated in the funnel plane.

The *Lobatae* differ from the typical structure in several respects. The funnel axis is very short compared to the stomachal, and the right and left halves of the body are produced on their oral aspects into large spreading

<sup>1</sup> R. Hertwig (op. cit. *infra*, pp. 6, 7) found in a specimen of the Cydippid *Callianira bialata* four excretory pores, of which two at opposite angles, i. e. in corresponding interradii, were smaller than the other two. He observed the pores open from time to time; at the same time a bundle of cilia was protruded.

lobes. The two subtentacular rows of plates are short, and at their oral ends are situated the 'auricles,' which are processes of the body, either long and mobile, or short, the base sometimes of great extent reaching to the mouth. The aboral surface of the auricles is beset with fine ctenophoral plates, the movements of which are independent of those of the plates of the subtentacular rows. The central nervous system lies at the bottom of a deep and narrow furrow: the nerves are prolonged between the plates of each ctenophoral row. The mouth is wide, and there is an oral groove extending to the bases of the body-lobes. The interradial vessels spring from the funnel. The meridional vessels form loops on the body-lobes and communicate with the paragastric canals. The tentacle basis, which is of great length, lies close to the oral pole and there is no tentacle sheath. A tentacle furrow extends right and left to the auricles in which are lodged lateral tentacles. These are numerous and stretch to the right and left in the tentacle furrows in which they are upheld by peculiar bent ciliary plates or hooks, so that their ends only hang down freely. *Eucharis* alone possesses a simple chief tentacle. The sexual products are formed either in the short vessels which extend on either side from the main meridional vessels beneath each ctenophoral plate (*Eucharis*, *Bolina alata*), or in the walls of the vessels between successive ctenophoral plates.

The *Cestidae* have a band-like body, immensely elongated in the stomachal plane, and very short in the funnel plane. The subtentacular ctenophoral rows are reduced to a few plates (4-6) at the aboral pole, whilst the sub-ventral rows extend along the aboral margin of the body to its two extremities. The ctenophoral plates are placed obliquely. The interradial vessels originate from the funnel. The sub-tentacular meridional vessels course along the centre of each surface of the body and at its extremities fall into the sub-ventral vessels which follow the aboral margins, bend round the two extremities and unite with two vessels which follow the oral margin and are branches derived from the oral ends of the paragastric canals. An oral furrow extends right and left along the central line of the oral margin of the body. The tentacle basis has a great lateral length and is protected by a tentacle sheath. A tentacular furrow starts right and left from the sheath and reaches to each end of the body. There is no chief tentacle, but a number of lateral tentacles are lodged in the furrows in which they are supported as in *Lobatae*, their free ends hanging down into the water<sup>1</sup>. The sexual organs are developed in *Cestus* along the aboral margin of the body in connection with the sub-ventral vessels; in *Vexillum*

<sup>1</sup> R. Hertwig's account of the tentacular apparatus differs from Chun's. The latter traces all the lateral tentacles to the tentacle basis. The former thinks that they are freed periodically from the basis, but that they remain attached to a narrow band of epithelial cells and muscle fibres on the wall of each tentacular furrow, which dies away before it reaches the tentacle basis.

they are present only from place to place in pairs, 5-7 to each half of the body.

The *Beroïdæ* are conical or ovate in shape, a good deal broader in the stomachal than in the funnel plane. *Neis cordigera* has two large lateral lobes prolonged aborally. Tentacles and tentacular vessels are absent even in development. The central nervous system is freely exposed, i.e. not counter-sunk in the body, and the edges of the elliptical polar plates are produced into branched villiform processes. The mouth is of great size and expansible: the stomach voluminous, and its oral end armed with sabre-shaped cilia-plates which prevent the escape of the prey. There are no stomachal ridges (p. 723): the funnel is small and there is no vertical funnel vessel, but the two excretory vessels spring separately from the funnel, and the blind ampullae are extended to a great length beneath the polar areas. The perradial vessels are abortive; the vessels are large, the paragastric especially so: the latter divide at the oral margin into a right and left horizontal vessel, not united as generally stated into a circular canal. Into these horizontal vessels fall the corresponding meridional vessels. Both the paragastric and meridional vessels give off lateral branches. The latter traverse the mesoglaea in all directions in *Beroë ovata*. The branches of the sub-tentacular and sub-ventral vessels of the anterior half of the body unite *inter se* as well as with the paragastric branches: so too the corresponding branches of the posterior half of the body, but there is no lateral connection between the anterior and posterior networks in *B. ovata* as there is in *B. Forskalii*, and more especially in *Neis cordigera*. *Idya* has no branches from the paragastric vessels. The sexual products are placed at the sides of the meridional vessels and more or less in their lateral branches, especially in *B. Forskalii*: in *B. ovata* and *Idya* they extend along the canals nearly to the oral margins<sup>1</sup>.

The egg of Ctenophora is suspended in a large mass of jelly inclosed by a delicate membrane. As to the development the gastrula is epibolic: and the gastrula mouth is said by Chun to correspond with the aboral pole. The mouth and stomach are formed by an invagination of the ectoderm: the endoderm giving origin to the funnels and the various vessels. The muscular fibres in the mesoglaea are said to be derived from immigrant ectoderm cells both superficial and stomachal<sup>2</sup>. The ectoderm is at first

<sup>1</sup> In *Neis cordigera* the genital products are confined exclusively to the network of vessels. But von Lendenfeld believes that they are derived from cells of the endoderm (?) of the meridional vessels which withdraw into a layer of sub-epithelial cells present in this Beroïd, through which they wander to the spot where they ripen.

<sup>2</sup> This process of immigration may continue during life, according to Chun (op. cit. *infra*, p. 197). Metschnikoff denies the accuracy of Chun's and Kowalewsky's observations. His conclusions, briefly put, are as follows:—(1) The embryonic epiblast forms a ring of cells round the cells of the hypoblast, leaving a pore at each end of the principal axis, the blastopore and pseudo-blastopore. (2) A mass of small 'mesoderm' cells is formed from the hypoblast cells at the blastopore. (3) A

ciliated. The cilia-plates supporting the otoliths, the bell covering the sensory area, and the ctenophoral plates, are alike formed by the agglutination of cilia. The embryo is hatched at a period before its system of vessels and its other organs have acquired their adult condition. The *Lobatae* and *Cestidae* undergo a pronounced post-embryonal metamorphosis. The larva is at first a Cydippid-form resembling an adult *Mertensia*, and its funnel plane is longer than its stomachal. The young *Eucharis* has two tentacles at each end of the funnel axis, an upper which grows and develops lateral branches, and a lower which remains rudimentary. The lobes begin to make their appearance and the body becomes nearly spherical, and at last elongated in the stomachal plane. The larval tentacles are lost, and the tentacular apparatus of the adult are new formations. A sac or depression appears above each tentacle basis which grows, and in the adult extends above the level of the sensory area. Such sacs are found in no other *Lobatae*, and perhaps represent the tentacle sheaths of the *Cydippidae*. The *Mertensia*-like larva of *Cestus* differs from that of *Eucharis* in the branches of the tentacles which terminate in knobs laden with adhesive cells. It passes through a spherical stage and then into the band-like form of the adult. The larval tentacles are lost. The just hatched larval *Eucharis* becomes in summer sexually mature. Its sub-ventral vessels are dilated, and the dilatations contain both ova and sperm. The former, though only half the size of ova laid by an adult, undergo a normal development<sup>1</sup>.

The Ctenophora are transparent, pelagic, and are widely distributed. The *Cestidae*, however, do not occur in the northern and temperate seas. The *Lobatae* move their body-lobes energetically and the *Cestidae* are capable of serpentine undulations. In both cases the motions are caused by the contractions of the sub-ectodermic musculature (p. 722). The animals also sink and rise in the water, the former especially during the day time. In sinking an escape of fluid from the excretory pores has been noted. But, as a rule, all movement is carried out by the ctenophoral plates. The Cydippid *Lampetia Panzerina* applies its oral aperture to the surface of the water, or some solid object, and gradually expands the stomach to form a flattened sole upon which it glides along, probably by ciliary action. A similar expansion, but to a very much less marked degree, is observable in other *Cydippidae* and in the young Beroid. All Cteno-

process half-way between epiboly and emboly now takes place. The mass of mesoderm cells pass up the axis of the gastrula to its aboral pole; at the same time the epiblast cells close up the pseudo-blastopore, and are invaginated at the blastopore to form the future stomach. (4) The mesoderm cells multiply and give origin to (a) mesoglaeal jelly cells, and (b) to cells whence are derived in tentaculate forms the musculature of the tentacles. Metschnikoff observed *Callianira*, a *Cydippe*, and a *Beroë*. See Z. W. Z. xlii. 1885.

<sup>1</sup> This fact has been confirmed by Graeffe: see Arb. Zool. Inst. Wien, v. 1884, p. 362 (=p. 30 of his article).

phora are carnivorous and feed on various pelagic animals, but especially Crustacea. *Beroë*, however, preys on its congener *Eucharis*. Phosphorescence is general; its seat is in the vacuolate endoderm cells and the generative products. The ovum, embryo, and larva are especially luminous. Some of the Ctenophora are small in size, e. g. *Hormiphora*  $\frac{3}{4}$  in.: others attain large dimensions, e. g. *Eucharis multicornis* 10 inches or more: *Beroë Forskalii* nearly the same, and a full-grown *Cestus* 3-5 feet.

The ectoderm cells lose for the most part their outlines. But the 'glance' cells which contain a clear substance in clumps, the 'granule' or gland cells, the iridescent cells of *Cestus*, the cause of the deep blue colour when the animal is irritated, retain their individuality. Pigment cells are sometimes present, e. g. in *Beroë*. Cilia may occur scattered over the body, over the aboral pole, and in *Cestus* along the aboral margin of the body, and in the oral furrow. Cells with tactile points or bristles are found in the papillae situated on the body of *Eucharis multicornis* and *Deiopea caloktenota*<sup>1</sup>, on the aboral margin of *Cestus*.

A sub-ectodermic plexus of nerve fibrils, with nodal ganglion cells, has been found in some Ctenophora. Sub-ectodermic muscle cells occur on the body of *Hormiphora*, of *Eucharis*, on its broad aspect in *Cestus*: in the last longitudinally arranged. Circular fibres surround the tentacle sheaths, and the tactile papillae of *Eucharis* have a longitudinal coat.

The central nervous system or sensory area consists of delicate columnar ciliated cells. The bell is produced by the fusion of very long cilia in the larva: so too the four plates which support the otolithic mass. The meridional ciliated furrows or nerves commence at the bases of these plates as so many lines of ciliated cells, each line then dividing into two. The otoliths are formed in cells near the longer sides of the area, extruded and flicked against the mass to which they adhere. The margins of the polar plates consist of flagellate columnar cells, their central areas of flat polygonal cells, each with a cilia-plate.

The ctenophoral plates are transparent, rectangular, with margins somewhat split up, and composed of innumerable agglutinated cilia of relatively enormous length, derived from transverse ridges of cells. Their bases are usually close set, or connected by a few cells, or by a nerve in *Lobatae* and the young *Cestus*. The Mertensid *Charistephane* has but two plates in each row: in others they are numerous. Each plate is bent adorally near its base, but the bent portion is concave aborally, the direction in which it moves. Movement of one or of all the plates supporting the otolithic mass, is propagated adorally down the corresponding nerve. The animal can reverse the direction: it may also retain its position unchanged while the plates are moving.

The tentacles are solid, derived entirely from the ectoderm of their basis<sup>2</sup>. Their axis is gelatinous, divided by a septum in which are imbedded fine nerve-fibres, into a right and left half. Each half contains a bundle of muscle fibres.

<sup>1</sup> Von Lendenfeld believes that these bristles are defensive and not tactile, and that the gland cells scattered among them, e. g. on the papillae of *Eucharis*, are poison glands: Z. W. Z. xli. p. 679.

<sup>2</sup> So say Chun and R. Hertwig, but see note 2, p. 720.



A single fibre is oval or circular in section, homogeneous, nucleated when developing. The superficial cells of the axis are ordinary ectoderm cells in *Euplocamis stationis*, in others tactile cells, few in number, and adhesive cells which are replaced in *Euchlora (Owenia) rubra* by cnidoblasts on the main axis, but not its branches. An adhesive cell has a convex free surface studded with adhesive globules (p. 331), and contains a muscle filament in connection with the fibres of the axis. The outer part of the filament is spirally coiled to admit of extension when the cell is forcibly elongated by the struggles of the prey. The branches of a tentacle, and the lateral tentacles of *Lobatae* and *Cestus*, have the same structure as the main tentacle.

The mesoglaea is firm in *Cestidae* and *Beroïdae*, soft in others. It imbeds (1) amoeboid nucleated 'connective tissue' cells; (2) fine irregularly branched *nervous* filaments connected one to another, and to the muscle fibres<sup>1</sup>; (3) muscle fibres, composed of a sarcolemma, a clear cortex, a granular axial medulla with nuclei; few in number in the *Cestidae* alone; disposed radially between the stomach, funnel, ctenophoral vessels, and the surface of the body; circularly round the stomach and scantily round the body near its surface; meridionally near the surface, between the ctenophoral rows. The radial fibres are branched at each end, the others pointed. Circular fibres surround the mouth in *Cydippidae* and *Beroïdae*, and in all Ctenophora the sensory area. The latter can be deeply retracted into the mesoglaea: so too the ciliated furrows or nerves, and to a greater or less degree the rows of ctenophoral plates, e. g. in *Beroïdae*.

The stomach is lined by ectoderm, similar to that of the body-surface; 'glance' cells are sometimes wanting. Two stomachal ridges, covered chiefly by glandular or granular cells, *vis-à-vis* to one another, are present except in *Beroïdae*. A layer of longitudinal sub-epithelial muscles, and a nervous plexus external to it, are found in the stomach of that family, the musculature in other families as well.

The endoderm of the funnel and the vessels is unilaminar: its cells flat, polygonal, ciliated, except in the ampullae of the funnel vessels, at the sides of the paragastric vessels, and the outer aspects of the ctenophoral, where they are columnar, vacuolate, non-ciliated (?), and disposed in a single or double ridge. The two forms of cells pass one into the other. 'Ciliated rosettes,' or minute depressions into the mesoglaea, lined by small ciliated cells, occur in the flat epithelium of the funnel and vessels. Longitudinal and circular muscles are said to surround the vessels.

The genital organs are invaginations from the ectoderm (Hertwig). In *Beroïdae* they form continuous bands of cells; in *Callianira*, *Hormiphora*, *Euplocamis* close-set masses of cells connected to the ectoderm by cellular cords. The cell-masses grow into the endoderm. The testes have a sinus, except in *Beroë*, with an outer wall of flattish cells, and an inner of nucleated protoplasm, from which the spermatozoa are derived. The ovaries are solid, the cells of the outer wall vacuolate, of the inner transformed into ova.

The Ctenophora are classified by Chun as follows:—

I. *Tentaculata*. Tentacles present.

1. *Cydippidae* (= *Saccatae*): globular or cylindrical forms. Two long ten-

<sup>1</sup> They are possibly connected with the sub-ectodermic nervous plexus. The fine filaments which underlie the ciliary furrows, Chun's nerves, are probably nervous. They extend below the sensory area, where the different bundles anastomose. They are perhaps connected to the ciliated ectoderm cells.

tacles, simple (*Euchlora*) or beset with lateral branches. All the peripheral vessels end blindly.

(i.) *Mertensidae*, body compressed in the stomachal plane: sub-tentacular ctenophoral rows longer than the subventral; *Euchlora*, *Charistephane*, &c.

(ii.) *Callianiridae*, body similarly compressed: aboral pole with wing-like processes; *Callianira* (= *Eschscholtzia*).

(iii.) *Pleurobrachiadae*, body round in aquatorial section: ctenophoral rows similar; *Hormiphora* (= *Cydippe* in part), *Pleurobrachia*, *Lampetia*, *Euplokamis*.

2 and 3. Body compressed in the tentacular plane. Lateral tentacles contained in a furrow of the oral margin. Principal tentacle may be present as in *Eucharis*, or else wanting. Peripheral vessels communicate. Subventral ctenophoral rows longer than the subtentacular. Larval form a *Mertensia*-like Cydippid.

2. *Lobatae*, two lobes in the stomachal plane; *Bolina*, *Deiopea*, *Eucharis*, &c.

3. *Cestidae*, body band-like; *Cestus*, *Vexillum*.

II. *Nuda*. No tentacles.

4. *Beroidae*, the vessels have lateral branches, and communicate inter se, as well as by their branches; *Beroë*, *Neis*, *Idya*, &c.

'Ctenophorae' Chun, Fauna und Flora des Golfes von Neapel, i. 1880; Bau der Ctenophoren, R. Hertwig, J. Z. xiv. 1880, or 'Studien zur Blättertheorie,' iii. Jena, 1880: cf. L. Agassiz, Contribution to Nat. Hist. United States, iii. 1860, p. 155.

*Neis cordigera*, von Lendenfeld, Z. W. Z. xli. 1885; *Metamorphosis of Bolina Chuni*, Id. Proc. Lin. Soc. of New South Wales, ix. 1885, p. 929.

*Movements of ctenophoral plates*, Krukenberg, Vergleich. Physiol. Studien i. (3), 1880: cf. Id. *ibid.* on Eimer.

*Summary of researches on Development*, Allman, J. L. S. xvi. 1883; *Gastrula and formation of Mesoderm*, Metschnikoff, Z. W. Z. xlii. 1885.

## CLASS ANTHOZOA.

*Marine Coelenterata either free or fixed, simple or colonial. The mouth is an elongated slit in the centre of an oval disc or peristome which bears one or more circles of hollow tentacles. It leads into an oesophagus or stomodaeum of some length which projects into the gastric cavity, and is united to the body-wall by radial lamellate mesenteries. The generative organs are situated on the mesenteries and are of endodermic origin. There are no organs of special sense except isolated sensory cells.*

The body is usually columnar, rarely disc-like, terminated by the peristome at one end, and in many simple Anthozoa by a pedal disc or base at the other. But in most colonial forms its true shape is masked, the oral part only remaining free. It has a distinctly radiate appearance, but the axis of the mouth indicates a line of bilateral symmetry which divides it into two halves. The two ends of this line may be anatomically dissimilar owing to the structure of the corresponding mesenteries, hence

leading to a distinction of a dorsal or axial from a ventral or abaxial aspect. The mouth is rarely circular. It is usually closed with the exception of one end, or of both ends which remain open, leading into well marked grooves strongly ciliated known as gonidial grooves or siphonoglyphes. The oesophagus is an ectodermic involution. It leads into a central cavity the size and length of which vary. The part of the cavity which surrounds the oesophagus is divided into a series of radial chambers, completely or incompletely isolated by the mesenteries. These structures are covered by endoderm supported by a mesoglaeal lamella continuous with that of the body-wall, and with that of the oesophagus when they are, as some always are, complete. The mesenteries which do not reach the oesophagus are termed incomplete. When the mesenteries are paired, the two members of every pair inclose a space which is known as intra-septal, the spaces between adjacent pairs being termed inter-septal<sup>1</sup>. Their free edges are usually bordered by thickenings or mesenterial filaments, more or less convoluted. They are ciliated, and are sometimes entirely, sometimes partly, glandular, and usually contain nematocysts. They are applied to the food when swallowed and their glands secrete the digestive fluid. The tentacles are evaginations of the oral disc, simple or compound, contractile, sometimes invaginable. The peristome and tentacles, and sometimes the fore-part of the body, are retracted by special longitudinal retractor muscles developed in the endoderm on one aspect of all or some of the mesenteries.

Nematocysts are always present on the tentacles and in the mesenterial filaments, in the stomodaeum, and in the *Zoantharia Actiniaria* also on the body-wall and peristome. It appears to be rare for them to occur on the surface of the colony as they do in the Alcyonarian *Heliopora*. Their size varies, and they have usually simple threads: but in some *Actiniaria*, and in the Madrepore *Caryophyllia* the thread is beset with spirally arranged barbs of large size near its base.

The colonial Anthozoa are produced by gemmation or fission from a solitary form. The individuals or zooids may originate from a basal stalk or stolon, or from a lamella, in which case they usually remain isolated. But they often spring from the wall or side of the first zooid, and then usually form a massive colony in which the individuals are united by a plentiful common basis or coenosarc. They are generally connected by canals variously arranged arising from their gastric cavities. The latter, however, are sometimes imperfectly separated. In some instances the zooids become completely isolated.

A skeleton is present in many simple and nearly all colonial forms.

<sup>1</sup> For these spaces Mr. Fowler has suggested (Q. J. M. xxv. p. 578) the terms 'entocoele' and 'exocoele' respectively.

It may be (1) discontinuous in the shape of calcareous spicules, or (2) continuous and then (i) organic and horny, (ii) both organic and inorganic, i. e. calcareous, or (iii) solely calcareous. The discontinuous skeleton co-exists with the continuous either (i) or (ii) *supra*, but never with the lamellate form of (iii) *supra*. When the skeleton forms calyces, or tubes lodging the zooids of a colony, the deeper parts of the tubes or calyces may be successively closed off by calcareous partitions, usually horizontal and known as tabulae. Tabulae occur in *Tubipora*, and *Heliopora* among *Alcyonaria*, in many extinct *Rugosa* and a few living corals among *Zoantharia*<sup>1</sup>. The skeleton-producing cells appear to be derived from the ectoderm (except in *Pennatulidae*?); they may remain in continuity with it or be detached from it, in this case becoming mesoglaeal. The individual or colony may be either of separate sexes, or hermaphrodite<sup>2</sup>. Fission and gemmation may occur in solitary forms. There are two perfectly distinct sub-classes, the *Alcyonaria* and *Zoantharia*.

#### SUB-CLASS I, ALCYONARIA (= *Octactiniae*).

*Anthozoa which are colonial with the exception of a single family. The colony is sometimes free. The tentacles are eight in number, similar and pinnate: the mesenteries also eight and complete. The retractor muscles are well developed and placed on the ventral aspect of each mesentery. The siphonoglyph, when present, is single and ventral. The zooids are sometimes dimorphic and then are known as autozooids (= polypes) and siphonozooids (= zooids), the latter being of simplified structure. Calcareous spicules in the mesoderm are very rarely absent.*

The colonial *Alcyonaria* are distinguished from one another by the form of the colony and the character of the skeleton. As to the first, two principal groups are distinguishable. (1) The zooids originate from a system of basal tubular stolons (*Clavularia*), from a narrow band-like stolon (*Sarcodictyon*), or a disc-like expansion (*Symphodium* and *Tubiporidae*), as well as from tubes connecting the zooids at different heights as in *Clavularia viridis*, or from platforms s. external tabulae as in *Tubiporidae*. The consequence is that the individual zooids remain independent and separate. In certain fossil forms (*Favosites*) which appear to belong here the zooids are closely apposed. (2) The zooids are imbedded

<sup>1</sup> They occur also in the *Hydrocorallina* among *Hydrozoa*, and are consequently of no systematic importance.

<sup>2</sup> *Scytophorus striatus* among *Hexactiniae*, certain *Zoanthidae*, the *Cereantheae*, as well as some specimens of *Corallium* among *Alcyonaria*, are undeniably hermaphrodite. The question of sex is complicated by the fact that it is possible for the male and female organs to be developed at different times or on different mesenteries. Such at least is the case with certain *Hexactiniae*, according to de Lacaze Duthiers: see A. Z. Expt. i. 1872, pp. 309, 371. The instance of *Corallium* shows that one individual or one colony may be uni-sexual, another hermaphrodite.

in a well-developed coenosarc, and the fore-part or oral extremity of the body, which is sometimes invaginable, e. g. *Corallium*, sometimes not so, e. g. *Primnoa*, is the only region which projects freely. The colony however constituted is either attached or free. When attached the base is extended, if the colony is massive as in the *Alcyonidae*<sup>1</sup> and *Helioporidae*, or relatively small as in the *Pseudaxonia* and *Axifera*, the colony of which is a more or less branched and spreading structure, the branches of which are either free or only accidentally fused where in contact, e. g. in *Corallium*, or united to form a lattice-work. In the latter case they are all disposed in one and the same plane. The colony is free in the *Pennatulidae*. It has an elongated slender axis, the basal portion of which is more or less pointed and sunk in sand or mud. The exposed portion bears the zooids, (1) at its apex (*Umbellula*); (2) in a single row (*Protocaulidae*, *Protoptilidae*), or in numerous and irregular rows along one, the dorsal aspect and the sides, e. g. *Funiculina*, sometimes however leaving a narrow dorsal streak free; (3) aggregated on latero-dorsal leaflets as in *Pteroeides* and *Pennatula*; or (4) confined to one aspect of a terminal kidney-shaped expansion as in *Renilla*.

The skeletal structures are not less distinctive than the character of the colony. The discontinuous or spicular skeleton is only absent in the non-colonial *Monoxenia* and the colonial *Helioporidae*. It is the only skeleton present in the *Tubiporidae* and *Alcyonidae*, the spicules in the first-named being united by minute serratures into a continuous tube for each zooid, except near its oral extremity where they are free. It is present in other Alcyonaria in conjunction with other forms of skeleton mentioned below. The spicules themselves are lens-like, cylindrical, acicular, flattened or stellate, sometimes smooth, or roughened with pointed or warty processes. They are composed of Calcium carbonate with traces of Magnesium carbonate and are tinged with Iron, hence often imparting colour to the colony. The calcite has the typical form of minute rhombohedra; and in the spicule, layers of rhombohedra alternate with fine layers of an organic substance which is most developed superficially. It is rare for the spicules to project freely beyond the surface of the body as they do in the leaflets of *Pteroeides*.

The organic horny skeleton may form either an external sheath or an internal and central branched axis. The first form is a cuticular secretion of the ectoderm, and occurs only in *Clavularia* (*Cornularidae*), and *Sarcodictyon*, where it is thin near the oral extremities of the zooids but thickens towards their bases. Inasmuch as the spicules of *Clavularia* near the base may also be coated with horny layers which become connected to one another and with the external sheath as well, the zooids acquire a firm

<sup>1</sup> *Alcyonium digitatum* sometimes occurs in free ball-like colonies.

support in this region. A horny axial skeleton is found as a simple rod in *Pennatulidae*, or as a branching rod in *Pseudaxonia* and *Axifera* where, however, it is attached by a basal expansion to some foreign object. It is lamellate and then may consist of horny and calcareous layers alternating; or be divided into successive joints of alternately horny and calcareous nature, e.g. in *Isis*; or it may contain cavities filled with a spongy or calcareous mass; or finally be impregnated throughout with calcareous matter. Its centre is sometimes hollow, filled with a spongy material or secondary calcareous deposits. In some instances, e.g. *Sclerogorgia*, the horny joints of *Melitheia* and *Mopsea*, the axial skeleton appears to be composed of spicules with horny sheaths which fuse together, whilst the hard calcareous joints of the two last-named genera consist almost exclusively of coherent spicules. *Corallium* has an entirely calcareous axial skeleton which is formed by the fusion of calcareous spicules at first separate. The horny or partially horny, partially calcareous axis of the *Axifera* differs from that of the *Pseudaxonia* in being covered by a superficial epithelium which is invaginated basal ectoderm. An epithelium also covers the surface of the axis in *Pennatulidae* but its origin is uncertain<sup>1</sup>. The horny sheaths of the spicules, like the spicules themselves, are derived from mesoglaeal cells which have in the first instance an ectodermic origin; and the calcareous cementing material which unites the spicules of *Corallium* is probably similarly derived<sup>2</sup>. The calcareous skeleton of *Heliopora* is peculiar, and is composed of tubes large and small the adjacent walls of which appear to fuse. The large tubes form calyces for the autozooids

<sup>1</sup> The axial skeleton of *Pennatulidae* is contained within a septum which separates a dorsal from a ventral axial chamber, both in communication with the siphonozooids. The septum in question is produced, according to Wilson, in *Renilla* by a growth of endoderm cells from the aboral extremity of the primitive zooid. It consists of an axial and two superficial layers of cells continuous at the growing edge of the septum. Smooth oval calcareous spicules appear in the axial cells at an earlier date than the acicular spicules of the deep ectoderm cells. An adult *Renilla* has no axial skeleton, but Wilson's observation suggests that the epithelium covering the axial rod of other Pennatulids and the rod itself are of endodermic origin.

The dorsal and ventral chambers of the peduncle in *Renilla* are lined by endoderm, beneath which is a layer of longitudinal and circular endodermal muscles. Longitudinal muscles occur also in the septum.

See Wilson, Ph. Tr. 174, 1884, pp. 765-771, and pp. 776-782.

<sup>2</sup> The facts detailed in this account of the skeleton are chiefly taken from von Koch. The skeletal elements may be classified as follows:

(1) *Exoskeletal*: horny cuticle of *Clavularia*, &c.; axial skeleton of *Axifera*, in which the skeletal epithelium is in continuity with the basal ectoderm.

(2) *Mesoskeletal*, (a) of *ectodermic origin*; spicules; their horny sheaths; axial skeleton of *Pseudaxonia* where no epithelium is present; tubes of *Tubipora*; calcareous axis of *Corallium*; calcareous lamellate skeleton of *Heliopora*;

(b) of *endodermic origin*: axial rod of *Pennatulidae*.

It is a mistake to consider the spicules, &c. as exoskeletal because the cells which give origin to them are of ectodermic descent. The fact that the cells are detached and wander into the mesoglaea deprives them of their ectodermic character.

whilst the small tubes lodge the siphonozooids. The calcite is laid down in lamellae and it is coloured blue by an organic pigment. The surface of the skeleton is covered superficially by a layer of cells or calyco blasts from which the hard structures are derived<sup>1</sup>.

Skeletal structures to be noted are the external and internal tabulae of *Tubiporidae*, the septa and tabulae of *Helioporidae*. The external tabulae (=platforms) of *Tubipora* are developed as rims close to the oral extremities of the zooids. These rims either surround neighbouring tubes or fuse with adjacent rims. They are at first soft and consist of ectoderm with a core of mesoglaea, but as they increase in size endodermic canals spring from the gastric cavities of the zooids and ramify in the mesoglaea. Spicules are formed at the same time and gradually unite into a firm skeleton. The internal tabulae are formed by a shrinkage, at the level of the platforms, of the endoderm and the lamina of mesoglaea lining the skeletal tube and the simultaneous formation of layers of spicules on the surface of the mesoglaeal lamina. These tabulae assume various shapes. The calcareous septa of *Heliopora* are ridges projecting inwards at the mouths of the calyces, usually twelve in number, but sometimes more, up to sixteen. The internal calcareous tabulae or horizontal floors are flat-bottomed cups added within the cavities of the calyces and tubes. In both genera the internal tabulae limit the deep dying or dead region of the colony from the superficial and growing region.

As to the zooids themselves, when the mesoglaea of the colony is plentiful their anterior or oral extremities are invaginable; when it is scanty they are usually only contractile. The tentacles are hollow and set one over each of the eight perigastric chambers; they are pinnate, and are sometimes invaginable as in *Corallium* and *Heliopora*, but are usually only contracted when the fore-part of the zooid is invaginated. The oesophagus or stomodaeum is of some length; its walls are transversely folded in invagination. The siphonoglyphe is absent in all the *Axifera* hitherto examined, probably also in the non-colonial genera. It is well developed in the *Alcyonidae*, feebly however in the autozooids of *Sarcophyton*. It is wanting in the autozooids of *Pennatulidae*, of *Heteroxenia*, and *Paragorgia*, but present in their siphonozooids. The mesenteries are thin. The retractor muscles, which are usually well-developed, are borne upon the homologous aspect of each mesentery, in such a way that the two mesenteries which limit a chamber corresponding to one extremity of the mouth have the muscles on the surfaces turned to each adjoining lateral chamber, whilst the two limiting the chamber at the opposite extremity of

<sup>1</sup> The calyco blasts of *Heliopora* give origin, according to Professor Moseley, to a fibriloid organic substance which undergoes calcification, and is afterwards removed (?), seeing that little or no organic matter is to be detected in the older parts of the skeleton. Judging from Prof. Moseley's figures and description, the calyco blasts are of undoubted ectodermic origin.

the mouth, have them on the surfaces turned to its cavity. The first is termed the dorsal chamber, the second the ventral. The three lateral chambers on each side have consequently each a single muscle projecting into their cavities from the surfaces of the mesenteries turned towards the ventral aspect of the zooid. The two mesenteries inclosing the dorsal chamber are frequently of great length, and in the bud they usually develop more rapidly than the remaining mesenteries. The two mesenterial filaments of the dorsal mesenteries are composed of a border or ridge of high columnar cells, each with a single powerful cilium backed by flattened endodermic cells such as cover the surfaces of the mesenteries. The columnar cells are derived from a down-growth of the lower edge of the oesophagus; they are therefore ectodermic. Their cilia always produce an ascending current<sup>1</sup>. The mesenterial filaments of the remaining mesenteries are composed entirely of endoderm cells which become columnar and for the most part glandular, but possess a single cilium. Thread cells of minute size occur among them. They develop before the dorsal filaments in the zooid originating from the egg. The sexes appear to be separate as a rule, and the colonies are even of one sex. In *Corallium*, however, hermaphrodite individuals may occur, and the zooids of a single branch or of neighbouring branches in a colony may be of different sexes. The genital products are attached to the faces of a mesentery and possibly of particular mesenteries, in pedunculate capsules, always few in number. They are derived from the endoderm.

The autozooid always has the typical structure above given. The siphonozooid differs from it in the absence of tentacles and retractor muscles; in the great development of the siphonoglyphe; in having the two dorsal, and sometimes the two ventral mesenteries, longer than the rest, the first named only having mesenterial filaments<sup>2</sup>; and in being sexless. Such zooids occur in *Sarcophyton* and *Heteroxenia* among *Alcyonidae*, and in *Pennatulidae*; among *Pseudaxonia* in *Paragorgia* and *Siphonogorgia* where they bear ova, and also in *Corallium* where it is stated that they develop into autozooids. Similarly certain zooids found in the Pennatulids *Haliscyprum* and *Virgularia*, which differ however from siphonozooids in having genital organs and traces only of the dorsal mesenterial filaments, develop into autozooids when they have discharged their sexual function.

<sup>1</sup> The only filaments present in *Xenia* and *Sympodium* are the two dorsal. Haacke, Z. A. vii. 1884.

<sup>2</sup> Wilson says (op. cit. p. 725) that the siphonozooids of *Renilla* have no mesenterial filaments. According to Professor M. Marshall (Trans. Roy. Soc. Edinburgh, xxxii. p. 145) the siphonozooids of *Umbellula gracilis* possess a single tentacle; and the larger siphonozooids of *Pennatula phosphorea* var. *aculeata* have a long abaxial process formed probably by elongated calyx teeth (op. cit. p. 126). A single large siphonozooid terminates the axis of the colony in *Renilla*. Water is constantly discharged by it; hence 'exhalent zooid' = Haupt-zooid of Kölliker. The other siphonozooids are small, clustered and inhalent.



The gastric cavities of the zooids of a colony are connected by systems of tubes variously arranged in different Alcyonarians, and lined by endoderm. The buds originate as outgrowths from these tubes, with an ingrowth of ectoderm to form the stomodaeum. A definite arrangement of the zooids in a colony is frequently observable, their dorsal aspects being turned in the same direction.

The ectoderm may be unilaminar or, as on the tentacles, multilaminar. It is ciliated in the latter position and in the stomodaeum. The endoderm is unilaminar. Its cells may be flattened or columnar, and in some instances at least, e.g. in *Corallium*, are ciliated throughout. The retractor muscles of the tentacles, oral disc, and stomodaeum are derived from it. The mesoglaea is more or less hyaline, sometimes fibrillate, and often contains stellate or branched cells.

The *Pennatulidae* are phosphorescent, and the phosphorescent material is contained in eight cords of cells attached to the gastric aspect of the stomodaeum of both auto- and siphono-zooids.

Development sometimes takes place within the parent, e.g. *Sympodium*, *Corallium*, *Clavularia petricola*, sometimes external to it, e.g. *Alcyonium*, *Renilla*; and the ova may be attached to the parent externally by a gelatinous material as in *Clavularia crassa*. Segmentation is very irregular and does not always extend at once to the centre of the ovum. In *Renilla* there is a small and transitory segmentation cavity, but as a rule the embryo is a solid mass of cells. The ectoderm is differentiated as a superficial layer: the endoderm arises from the central mass as a layer of cells underlying the ectoderm; the remainder of the mass degenerates and is absorbed. The oesophagus is a hollow, e.g. *Sympodium*, or solid, e.g. *Renilla*, ingrowth of ectoderm. The mesoglaea is derived from the base of the ectoderm cells, many of which pass into it; that of the mesenteries may originate from the endoderm. The tentacles are at first simple and conical. The spicules appear in cells derived from the ectoderm, and the central axis of *Gorgonia* is formed after the attachment of the larva as a small basal plate, which subsequently grows upwards as a papilla.

Few fossil *Alcyonaria* are known. The *Tubiporidae* are probably represented in Silurian, Devonian, and Carboniferous strata by *Syringopora* and its allies. *Corallium* is found from Jurassic times onward; a Pennatulid occurs in the upper Chalk, and the family *Helioporidae* has several representatives in Silurian and Devonian strata. The *Favositidae* from the same period are probably Alcyonarian<sup>1</sup>.

<sup>1</sup> See Moseley, Challenger Reports, ii. p. 121, and Hickson, Q. J. M. xxiii. pp. 569-74; cf. Nicholson, A. N. H. (5), xiii. pp. 29-34.

The classification of the *Alcyonaria* is by no means settled in details. The following groups however may be distinguished.

I. Non-colonial forms = *Proto-Alcyonaria* (Hickson).

*Haimeidae*. Three genera only; *Monoxenia*, from Arabian coast; *Haimea*, from Fiji Islands; *Hartea*, from west coast of Ireland.

II. Colonial forms.

1. *Cornularidae*. Zooids originating from a tubular stolon, e.g. *Clavularia*, a band-like stolon, *Sarcodictyon*, or a basal expansion, *Symphodium*. They are usually free; but *Clavularia viridis* has connecting tubes between the zooids from which new zooids may spring.

2. *Tubiporidae*. Zooids originating from a basal disc and connected by platforms from which new zooids spring; spicules uniting to form a continuous system of tubes and platforms; *Tubipora*.

Hickson unites 1 and 2 into a group, *Stolonifera*.

3. *Alcyoniidae*. Zooids forming a more or less massive colony; rarely dimorphic as in *Sarcophyton* and *Heteroxenia*; no skeletal structures save scattered calcareous spicules; gastric cavities of zooids remarkably long; *Alcyonium*, &c.

*Coelogorgia*, from Zanzibar, which forms branching colonies with tubular axes, and one or two allied forms perhaps belong here.

4. *Pseudaxonia*. An axial branched skeleton present, derived entirely from cells of the mesoglaea. This axis consists of fused calcareous spicules in the *Corallinae*, e.g. *Corallium rubrum*; of calcareous spicules cemented by horny lamellae in the *Sclerogorgiacea*; of alternating joints, one set composed of spicules united by horny lamellae, the other of fused spicules, *Melitheacea*, i.e. *Melitheia* and *Mopsea*.

*Siphonogorgia* and *Paragorgia* with a spicular axis form a transition to 3. They have dimorphic zooids; so too probably *Corallium*.

5. *Axifera*. An axial branched skeleton present, derived from a layer of ectoderm cells invaginated from the base of the colony; skeleton lamellate, horny, or horny and calcareous; in *Isis* composed of alternating horny and calcareous joints; *Primnoa*, *Gorgonia*, &c.

6. *Pennatulidae*. Colony free, with a base or peduncle sunk in sand or mud. Zooids dimorphic; confined to the exposed part of the colony. An axial skeleton generally present, covered by an epithelium, probably of endodermic origin. Some are phosphorescent. *Virgularia*, *Funiculina*, *Pennatula*, *Renilla*, *Umbellula*, &c.

7. *Helioporidae*. A calcareous skeleton composed of lamellae of calcite, as in the Madreporarian Zoantharia. Zooids dimorphic. Siphonozooids reduced to short closed tubes. The calcareous cups for the zooids are closed below by horizontal tabulae, which are formed successively during the growth of the coral, one at some little distance above another. *Heliopora*, from the Philippine Islands.

*General literature*. Milne Edwards and Haime, *Histoire Nat. des Coralliaires*, 3 vols., Paris, 1857-1860. Klunzinger, *Korallthiere des Rothen Meeres*, (with lit.) 3 pts., Berlin, 1877-1879. *On the skeleton*, von Koch, *Biol. Centralblatt*, ii. 1882-83.

*Monoxenia*, Haeckel, *Arabische Korallen*, 1876, p. 7; *Hartea*, P. Wright, *Q. J. M.* v. 1865; *Haimea*, Milne Edwards, *Histoire Nat. des Coralliaires*, Paris, i. 1857, p. 104.

*Clavularia*, Hickson, P. R. S. xl. 1886, p. 322; von Koch, M. J. vii. 1881. *Sarcodictyon*, Herdman, Proc. Roy. Phys. Soc. Edinburgh, Session 1883-84. *Tubipora*, Hickson, Q. J. M. xxiii. 1883. *Sarcophyton*, Moseley, Challenger Reports, ii. 1881, p. 117; *Corallium*, de Lacaze Duthiers, Histoire Nat. du Corail, Paris, 1864: cf. Moseley, Q. J. M. xxii. 1882. *Isis Neapolitana*, von Koch, M. J. iv. 1878; *Gorgonia verrucosa*, Id. ibid.: *various Axifera*, Id. Mitth. Zool. Stat. Naples, iii. 1882. *Pennatulidae*, Kölliker, Challenger Reports, i. 1880: Id. Abhandl. Senckenb. Ges. vii. 1879; viii. 1872; *Report on the Oban Pennatulidae*, A. M. and W. P. Marshall, Birmingham, 1882; *Pennatulida dredged by H. M. S. Triton*, A. M. Marshall, Trans. Royal Soc. Edinburgh, xxxii. pt. 1, Session 1882-83; *Umbellula*, Kölliker, Festschrift zur Feier des 25-jährigen Bestehens d. phys. med. Ges. in Würzburg, 1874; cf. Lindahl, A. N. H. (4), xiii, 1874, and von Willemoes-Suhm, ibid. xv. 1875. *Renilla*, Wilson, Ph. Tr. 174, 1884. *Heliopora*, Moseley, Challenger Reports, ii. 1881.

*Skeleton*, von Koch, M. J. iv. 1878; Id. M. J. vii. p. 484; Id. Biol. Centralblatt, ii. 1882-83. *Development in Gorgonia*, Id. Mitth. Zool. Stat. Naples, iii. p. 550. *Skeleton in Corallium, &c.*, Nicholson, A. N. H. (5), xiii. 1884.

*Siphonoglyphe*, Hickson, Ph. Tr. 174, 1883. *Mesenterial filaments*, Wilson, Mitth. Zool. Stat. Naples, v. 1884; *ditto of Xenia and Sympodium*, Haacke, Z. A. vii. 1884.

*Phosphorescence of Pennatulidae*, Panceri, Atti Ac. Napoli, v. 1873; cf. Q. J. M. xii. 1872.

*Development of Renilla*, Wilson, Ph. Tr. 174, 1883; *of Clavularia and Sympodium*, Kowalewsky and Marion, An. Mus. Nat. Marseilles, i. 1883.

*Classification*, von Koch, M. J. iv. 1878, p. 474; Hickson, Ph. Tr. 174. p. 699.

## SUB-CLASS 2, ZOANTHARIA (= *Hexacoralla*).

*Anthozoa which may be simple or colonial, and in the latter case furnished as a rule with either an organic or calcareous continuous skeleton derived from the basal ectoderm. The tentacles are usually simple. They are arranged in one or more circles, the members of a circle or of different circles being often dissimilar in size. The mesenteries and the retractor muscles are never disposed as in Alcyonaria: the former are very generally paired, and then tentacles may correspond to the inter- as well as to the intra-septal spaces. The number of both tentacles and mesenteries is very generally, but not universally, some multiple of six<sup>1</sup>. One or two siphonoglyphes are often present. Dimorphism is known only in one instance.*

<sup>1</sup> The Zoantharian mesenterial filaments are described on p. 241. It has been suggested by Wilson that the median lobe is of ectodermic, the two lateral lobes of endodermic origin. Histology, as pointed out by Fowler (Q. J. M. xxvii. p. 8), points in the opposite direction. But there is one difficulty in the way of any such derivation, viz. the filaments of incomplete mesenteries are constructed on the same type as are those of complete. As the former set of mesenteries are never in contact with the stomodæum, it is not possible for them to acquire a band of ectoderm cells. See on Alcyonarians, p. 730, *ante*.

There are three distinct subdivisions of living Zoantharia, the *Actinaria*, *Antipatharia* and *Madreporaria*.

The *Actinaria* or *Malacodermata* are distinguished in the first place by the absence of an organic or inorganic skeleton. The animal is usually solitary, and either free, or adherent to the surfaces of foreign bodies, and creeps about by means of a pedal disc, or it lives immersed in sand or mud. It is rarely colonial and fixed. There are six tribes.

(1) The *Hexactiniae* have all the mesenteries paired. Two pairs placed one at each end of the mouth, termed directive mesenteries, to each of which corresponds a siphonoglyphe, differ from the remaining pairs which are generally numerous, in having the retractor muscles on the interseptal surfaces instead of the intraseptal. The number of primary pairs of mesenteries is six, two directive and two lateral on each side of the body. In the *Sagartidae* and *Amphianthidae* the six pairs in question are the only complete mesenteries, whereas in other Hexactinians, so far as is known, the secondary mesenteries are also complete: the tertiary and quaternary are always incomplete. The tentacles are numerous, and frequently of great length. There is always a marginal set, and sometimes an intermediate as well as circumoral,—the two latter often termed 'accessory'.<sup>1</sup> They differ, like the mesenteries, in age, and therefore sometimes in size, but there is a general tendency to equalisation in this respect. When they are numerous they are arranged in concentric circles, the oldest nearest to the centre of the disc. Structurally speaking, they are evaginations of the oral disc, which correspond to both the intra- and inter-septal spaces. They are usually contractile, and furnished with a terminal pore. They become altered in character in some deep sea forms; i.e. the terminal pore enlarges; the tentacle itself may be reduced to a short wide-mouthed tube or stomidium, or to an aperture with ring-like margin, which may almost disappear; and finally in *Liponema* it becomes a simple opening in the peristome. When the animal is irritated the tentacles shorten. At the same time the outermost margin of the disc is very generally strongly contracted over the tentacles and mouth by the action of an endodermal sphincter or Röttken's muscle (p. 240), rarely completely absent. *Acontia* (p. 241) are present in the *Phellidae* and *Sagartidae*, and may be protruded through the mouth, by cinclides, or by rupture of the body-wall. The inner stomata are always, the outer sometimes, present. The genital products are either borne upon all the mesenteries, e.g. in *Corallimorphidae*, or they are confined to those of lower order, and are at least not developed on the

<sup>1</sup> In the family *Stichodactylinae* the disc is large and covered with tentacles in radial series either of one form and simple, or of two and then simple, mixed with ramose or foliate tentacles, or of various shapes. So too in the family *Thalassianthinae* the disc is covered with dendritic appendages. See Andres, 'Le Attinie,' Monograph ix. (1), 1884, p. 264 and p. 299.

primary, e. g. in *Sagartidae* and *Liponemidae*<sup>1</sup>. The *Amphianthidae* live attached to fragments of the stems of *Axifera*, and like *Gerardia* (*infra*, p. 737) have the sagittal or antero-posterior axis short, and the transverse elongated. In *Halcampa* the aboral end of the body is rounded, and it is pierced by numerous (24?) small openings. Its mesenteries are reduced to the primary six pairs<sup>2</sup>. The *Hexactiniae* live usually attached to rocks, or when the base is feebly developed, immersed in sand or mud. The *Minyadinae*, which probably belong to this tribe, are pelagic. The base may be inverted and serve as an air vesicle, but in *Nautactis* is capable of eversion and attachment. It is perforated in *Dactylominyas* (*Oceanactis rhododactyla*).

(2) The *Paractiniae* of Hertwig differ from the *Hexactiniae* in having the mesenteries multiples of 8; *Sicyonis* has 64: but *Polyopsis* 36, there being in Hertwig's opinion two redundant pairs in this case. *Polyopsis* has the tentacles reduced to stomidia, and has a rounded aboral pole.

(3) The *Monauleae*, represented by *Scytophorus striatus*, have seven pairs of complete mesenteries, one only of which is directive. The single siphonoglyphe corresponds to it. The animal is hermaphrodite: the testes are situated near to the base, the ovaries at a higher level.

(4) The *Edwardsiae* possess eight mesenteries, all complete, all bearing reproductive organs. There are two pairs of directive mesenteries; the remainder are not paired and have the retractor muscles turned in the direction of one of the two pairs of directive mesenteries, hence termed ventral. There are two siphonoglyphes. The arrangement is therefore neither Alcyonarian nor Hexactinian. The tentacles vary in number with age (12-36), and are more numerous than the mesenteries, a fact which probably denotes the loss of mesenteries by reduction. The body is divisible into three regions; the middle one (=scapus) is covered by a tough mucoïd investment; the posterior is pointed but not perforated. The animals live immersed in sand or mud, in holes of rocks or under the roots of seaweeds.

(5) The *Zoanthidae* have the mesenteries paired as in the *Hexactiniae*, but each pair consists typically of a complete mesentery, the macro-septum, which has a mesenterial filament, and bears genital organs, and of an incomplete mesentery, the micro-septum devoid of both the structures named. The directive mesenteries are as in *Hexactiniae*, but one pair con-

<sup>1</sup> In *Ophiodiscus* the mesenteries of the fourth order are devoid of mesenterial filaments and muscles, and bear the genital organs, the mesenteries of higher orders being muscular and sterile. So too perhaps in *Polystomidium*. See also note, p. 726.

<sup>2</sup> The base is rounded also in *Ilyanthus*, in *Siphonactinia* (= *Peachia*) and *Philomedusa*, but whether perforated or not is uncertain. The mesenteries and retractor muscles of *Siphonactinia* are apparently restricted in number and peculiarly disposed, its base perforate according to Faurot, C. R. 98, 1884. It must be borne in mind that the present arrangement of the *Hexactiniae* in families, &c. is not founded throughout on anatomical structures: it can only be regarded as temporary.

sists of two macrosepta, the other of two microsepta. The former is termed ventral and to it corresponds the single siphonoglyphe. The remaining pairs of mesenteries are disposed so as to constitute two zones, a dorsal and a ventral. The former always has, even in the youngest specimens, five pairs of mesenteries, including the directive pair. On each side of the latter there is a pair of the typical Zoanthidan structure, and then a pair, either of the typical structure or composed of two macrosepta. The first-named disposition is termed the microtype, the second the macrotype. The ventral zone contains a variable number of mesenterial pairs according to age, but all of the typical structure, with the exception of the directive pair. In both the dorsal and ventral zones the mesentery immediately adjoining the directive pair is a macro-septum. New pairs are intercalated only in the interseptal space on either side of the ventral directive pair. The tentacles are disposed in two circles; one set corresponding to the intra-septal chambers, the other to the inter-septal. Röttcken's muscle is well developed and embedded in the mesoglaea except in *Palythoa*. The mesoglaea is filled with islands or branching cords of cells derived from the ectoderm, and it is traversed by radial nucleated muscle-fibres. It also contains, except in the genera *Zoanthus* and *Mammilifera*, foreign bodies,—particles of sand, calcareous fragments, spicules of Sponges, shells of *Foraminifera* or *Radiolaria*. The sexes are united in *Zoanthus*, separate in the colonies of *Epizoanthus* and *Palythoa*: not known in the other colonial genera. The animals are fixed and colonial or free. Of the former, *Zoanthus* has branched stolons; *Mammilifera* stolons with a tendency to form lamellae; *Epizoanthus* a lamellate base; *Palythoa* a band-like base, whilst in *Corticifera* the zooids are imbedded in a coenosarc. The stolons, lamellae, or coenosarc are traversed by a system of canals which communicate with the gastric cavities of the zooids at their bases. The colonies are fixed to stones except in the genus *Epizoanthus*, which grows either upon empty shells of Mollusca, on the rooting spicules of *Hyalonema*, or on a shell inhabited by a Hermit Crab, and then the substance of the shell is resorbed by the coenosarc. The free-living *Zoanthidae* comprise the genus *Sphenopus*, in which the body is drawn out into a hollow peduncle terminating in a disc sunk in sand, &c., and an unnamed dioecious genus with buds originating from the base of the peduncle.

(6) The *Cereantheae* have numerous complete mesenteries, not disposed in pairs nor multiples of 6. There is a single siphonoglyphe which determines a ventral aspect. Two median mesenteries, which correspond to this siphonoglyphe are minute, and from their position are termed directive. The mesentery on either side of these two is of very great length and reaches to the aboral pole. The remaining mesenteries diminish in size to the middle dorsal line, the spot where new mesenteries are added. There are no retractor muscles, but each surface of a mesentery has feebly

developed transverse muscles<sup>1</sup>. The body is elongated and pointed aborally where it is perforated by a pore. It is covered by a tough investment of mucus, discharged nematocysts, and foreign bodies derived from the soil in which the animal lives immersed. The tentacles are in two circles, one marginal and long, the other circumoral and shorter. The former have a series of slit-like pores on the oral aspect. There is a subectodermic layer of plaited longitudinal muscles, not present in any other *Actiniaria*, which thins away in the dorsal median line, denoted externally by a furrow. The animal is hermaphrodite. Sterile and fertile mesenteries are said to alternate one with another.

So far as concerns the histological structure of *Actiniaria*, it agrees more or less closely with that of *Tealia*, described on pp. 241-42. The ectoderm sometimes secretes a cuticle, e. g. in *Phellia* among *Hexactiniae*, and in *Zoanthus*. The consistency and degree of development of the mesoglaea is liable to variation; it is homogeneous, with or without cells, or fibrillate. The muscle cells either lie evenly on the surface of the mesoglaea, or the latter is thrown into supporting folds or plaits, or may even completely inclose the cells. The endoderm cells of *Cereanthus* bear many cilia, not a single flagellum, as in *Tealia*.

The *Antipatharia* are degenerate, but the different genera in various degrees. The ectoderm of the base secretes an organic or horny lamellate skeleton. *Gephyra Dohrnii* is the least modified. Its zooids are either isolated or in small groups united by their bases, and fixed by their basal plates to the stems of the Axiferan *Isis* which they embrace. The tentacles number about eighty and are disposed in circles. The mesenteries are numerous, and bear each a mesenterial filament. *Gerardia* forms colonies growing upon the stems of *Gorgonia*, on rocks, shells, &c. There are twenty-four tentacles, a large and a small alternating, and twenty-four mesenteries all complete. The zooids are united by a reticulum of vessels which communicate with the interseptal spaces. *Antipathes* is also colonial. The basal skeleton is erect, and carries rows of lateral branches, sometimes branched in turn. It is tubular, and the tube crossed from place to place by partitions; it is covered with small spines, and is inclosed in an epithelial ectodermic (?) sheath. The zooids are disposed in a line on the branches, usually on the aspect looking upwards, i. e. towards the apex of the stem. They have six short tentacles. The zooid is elongated in the axial plane

<sup>1</sup> In large specimens the mesenterial filaments undergo a change close to the lower border of the stomodaeum. They are drawn out into a number of simple or branched 'mesenterial threads.' These structures commence as small papillate projections of the mesentery, bordered of course by the mesenterial filament. The papillae grow out, become filiform, and may branch. Hence a cross section of such a thread shows as it were two mesenterial filaments back to back. An acontium differs from a mesenterial thread (1) in being attached to the surface, not the edge, of a mesentery; (2) in being simple and filiform, and single in cross section; and (3) in containing very large numbers of nematocysts.

of the branch, the mouth transversely to that axis. Two mesenteries only are complete, and they correspond to the long axis of the body: they have mesenterial filaments, and carry the sexual products. Two short mesenteries correspond to each end of the shorter diameter, and two still more reduced lie one on either side of each complete mesentery. There are consequently ten mesenteries in all. A canal traverses the colony beneath the bases of the zooids, but whether or not it is in connection with them is uncertain. The surface of the colony secretes in *Gerardia* and some species of *Antipathes* a viscid mucus which entangles foreign bodies, such as spicules of *Axifera*, and Sponges, grains of sand. The nematocysts of the ectoderm in the two genera named are aggregated into groups. The sexes appear to be separate.

The *Madreporaria* are simple or colonial, and differ most markedly from other Zoantharia in the presence of a continuous calcareous skeleton secreted by cells or calyco blasts, which either actually are, or represent the basal ectoderm<sup>1</sup>. The skeletal structures are therefore, strictly speaking, external to the animals to which they belong. The form of the skeleton is very variable. In a typical simple, i. e. non-colonial Madreporarian, it consists of a theca, which is as a rule attached by a base, large or small, to some foreign object, but it may, as in *Flabellum*, &c., become free when adult. The theca is excavated terminally by a depression, the calycle or calice in which the animal is lodged, the soft parts extending over its lip to a variable extent. The theca is sometimes flattened, e. g. *Bathyactis*, *Fungia*, and it may then, as in the genera named, be covered completely on its lower surface by soft tissues. The inner aspect of the calycle is not smooth, but bears a number of radial calcareous ridges or septa, differing in size and extent, and accordingly distinguishable into systems, primary, secondary, &c. Certain of these septa may meet in the centre of the cup, where they form a pillar or columella, which may be prolonged more or less upwards. They may unite together in various degrees, and there may be at or near their central ends one or more circles of plate-like upgrowths, known as pali. The outer surface of the theca may be marked with ridges or costae, which do or do not correspond to the septa, and are separated by intercostal spaces: it may be covered to a greater or less height by an epitheca or calcareous layer distinct from the theca itself, which is sometimes extended into radicles<sup>2</sup>. In the colonial forms the shape of the colony depends on the mode of growth and multiplication of the individual; it is massive, branched, lamellate, cup-shaped, &c. The soft parts of the zooids may

<sup>1</sup> Vegetable parasites are often found in the coralla of *Madreporaria*, *Heliopora*, and the coenosteum of *Millepora*. See Moseley, 'Hydrocorallinae,' Challenger Reports, ii. p. 30; Martin Duncan, P. R. S. xxv. 1877, and Quart. Journal Geol. Soc. xxxii. 1876.

<sup>2</sup> For definitions of descriptive terms relating to Corals, see Martin Duncan, J. L. S. xviii. pp. 200-2.



become independent, or remain in continuity over larger or smaller regions. As the coral grows, portions of the skeleton often become exposed to a variable extent, and the exposed surface, like the exposed surface of a simple coral, is attacked by the water, and by organisms, vegetable or animal. The calyces are in the majority of colonial corals connected by a calcareous coenenchyma or common skeleton, which is either perfectly solid, or excavated by internal spaces left during growth, but not connected with the calyces nor open in the macerated state; or it is traversed within and without by tubular channels which lodge in the living condition canals connecting the gastric cavities of the zooids, and therefore in the macerated skeleton open superficially. Hence the division of *Madreporaria* into two great sections, the *Aporosa* and the *Perforata*. The skeleton itself is composed of calcareous ellipsoids, themselves made up of typical rhombs of Calcite. Little is accurately known as to its development. In *Astroides calycularis* it appears first as a calcareous ring beneath the base of the solitary larva and the foreign object to which it is fixed. The ring becomes a disc, and on the upper surface of the disc are formed twelve radial ridges, the first septa, which bifurcate at their outer extremities. They correspond to vertical folds of the base of the zooid, within the hollow of which they are laid down. It is a disputed point whether or not the wall or theca arises by a fusion of the outer ends of the septa (von Koch) or is a ring-like thickening of the base independent of the septa (de Lacaze Duthiers). The epitheca appears at the spot where the ectoderm of the base passes into the ectoderm of the wall of the zooid. Of the twelve septa, six grow more rapidly at first than the remaining six, a difference afterwards equalised. A second series of twelve septa, and then a third of twenty-four appear. The young *Astroides* begins to bud and form colonies. In the larger calyces the second set of twelve septa become equalised with the first twelve, and a fourth series of forty-eight septa is intercalated. An even and regular development of septa in cycles is probably the rule: but (1) cycles may become equalised, and (2) irregularities affecting a part or the whole of a calyx may occur. Hence there are many difficulties to be encountered in interpreting the skeleton of corals<sup>1</sup>. Moreover 'nearly allied

<sup>1</sup> Von Koch has recently given an account (M. J. xii. (1) 1886) of the morphology of the Madreporarian skeleton according to his latest views. He regards (1) the epitheca as formed on the outer surface of the wall of the zooid, (2) the theca as concentric with it, and (3) the two structures as separated by spaces crossed by mesenteries and continuous with the intra-calycular portions of the inter- and intra-septal chambers at the free edge or lip of the theca. The theca and epitheca are, however, never separated, so far as the specimens and descriptions accessible to me show, by anything more than a minimal space, and there is no evidence for the existence of soft parts between them. The epitheca appears to be secreted by the free edge of the soft parts or limbus covering the theca. At present it is by no means a settled point whether or no the theca may grow in such a way that it cuts the mesenteries, as von Koch contends it does, into an extra- and an intra-thechal portion, or whether the edge or limbus of the zooid simply overlaps the edge of the theca. It is probable that both modes of growth occur. Mr. G. C. Bourne informs me that in

species are in the young condition very closely alike, and sometimes indistinguishable; and 'in the very early stages the young of even widely different species of the same genus are almost absolutely alike' (Moseley), facts especially noted in the genus *Flabellum*. Tabulae occur in *Pocilloporidae* and a few *Poritidae*.

As to the zooids they are, in the majority of instances properly examined, Hexactinian in structure. The tentacles do not appear to be perforated by an apical pore. They may correspond to the intraseptal chambers alone, e.g. in *Rhodopsammia parallela*, or to the interseptal as well, the more usual arrangement. They are simple in form and often armed with batteries of aggregated nematocysts. The mesenteries may be only twelve in number, all complete (*Stylophora*, *Madrepora*), or, when the calyces are large or the animal solitary, much more numerous and some complete, others incomplete. They are disposed in the typical Hexactinian mode. The septa are contained only in the intraseptal chambers, or in the interseptal as well. Septal stomata have not been described nor Rötteken's sphincter muscle. Sexual organs may be present on all the mesenteries, or confined to those of a certain order, or, as in *Madrepora Durvillei*, to two specially elongated mesenteries. The sexes appear generally to be separate even in the colonies. In the coral last named a remarkable dimorphism occurs between the zooids in respect of the mesenteries<sup>1</sup>.

*Seriatopora* differs in several respects from typical *Madreporaria*. Its calyces are elongated and disposed lengthwise on the branches of the coral, and are traversed by a longitudinal plate. There are twelve tentacles in two cycles, and twelve mesenteries, two of which, towards the basal or ventral end of the calyx, are of great length, and alone have mesenterial filaments and genital organs. The chambers to which they belong are greatly prolonged and received into deep pits in the calyx. There are three complete septa and two rudimentary on each side. The form and arrangement of the mesenteries and septa bring about a marked difference between the two ends of the zooids or calyces. The colony is unisexual. *Pocillopora* closely resembles *Seriatopora*.

The zooids in a colony are either isolated, e.g. *Cladocora*, or where there is a coenosarc, they are connected by a superficial canal system as in *Stylophora*, *Seriatopora* and *Pocillopora*, by a deep system as well in *Madre-*

*Fungia* the synapticulae or plates connecting the septa commence as points on the opposing surfaces of two adjoining septa, which grow, meet and fuse, perforating the intervening mesentery in the process. The edge of the flattened theca grows similarly; an extrathecal space underlies it, divided into radial chambers by the aboral continuations of the mesenteries and connected to the intrathecal space peripherally as well as by canals passing through the theca itself.

<sup>1</sup> Fowler states (Q. J. M. xxv. p. 588) that there are acontia(?) and peristomial cinclides in *Flabellum patagonicum*. Mr. G. C. Bourne tells me that he has observed the protrusion of much convoluted mesenteries from peristomial cinclides in *Maeandrina*.

*poraria Perforata*, or by their gastric cavities, as in *Coeloria*, *Maeandrina*, &c., corals in which they are disposed in linear series.

Asexual reproduction has been observed in few of the non-colonial *Actiniaria*. Part of the limbus may separate off in some *Hexactiniae* and develop into a new zooid: such a process is known as scissiparity (p. 241). Fission occurs commonly in *Anemonia sulcata* (= *Anthea Cereus*), and may be the cause of the occurrence of twin individuals in *Actiniloba dianthus*, &c. The colonial forms increase in various ways which have been classified by von Koch under the two heads of internal and external gemmation. In the former, the young calycle originates with the parental, and is derived partly or entirely from it: in the latter, it is external to it altogether. Internal gemmation occurs (1) as *fission-budding*, in which the original calycle is constricted into two parts, e.g. in *Mussa*; (2) as *septal budding*, seen in the Silurian *Stauria* and its allies, where the so-called primary septa become in part the walls of the young calyces; (3) *tabular budding*, in which the young calyx is produced from the parental, but is completed by the development of a pocket-shaped floor or wall. As to external gemmation, the bud is either formed (4) from the wall of the parental theca, and adheres closely to it as in *Favosites*, which is probably, however, an Alcyonarian; (5) in *coenosarcal budding* from the tube of the coenosarc, e.g. *Madrepora*, or of the coenenchyma (?), e.g. *Rhodopsammia*; or (6) in *stoloniferous budding*, from a stolon, as occurs in some extinct operculate Corals<sup>1</sup>. Individuals are sometimes found with a new but smaller calycle symmetrically formed within an old calycle with which it corresponds completely. This is termed 'rejuvenescence' by von Koch. In *Fungia* there is a small fixed stock simple (or branched?) from which the apical zooid-portion is detached, a new zooid arising by gemmation from the pedicle. The process may be repeated 3-4 times. The detached zooid is  $1\frac{1}{8}$  in. in diameter and shows a scar of detachment which disappears during subsequent growth (Moseley)<sup>2</sup>.

<sup>1</sup> Of these various modes, (1) and (2) are often termed simply 'fission,' and (3) 'calycular gemmation,' very common in the extinct *Rugosa*. Fission may be quite imperfect; e.g. Dana states that the long lines of the Maeandrine corals are due to the lengthening out of the peristome and the formation of a series of mouths, the elongated and many-mouthed disc being fringed by a line of tentacles on either side. (4) Is termed by von Koch 'Zwischenknospung,' and does not occur in any living coral. (5) Is a very usual form, and is commonly spoken of as 'parietal gemmation.' As to (6) it is, strictly speaking, only a mode of (5), inasmuch as every stolon contains coenosarcal tubes. There can be no doubt that the stolons of extinct Anthozoa contained similar extensions of the coelenteron. According to Martin Duncan, the epithelial roots of the living *Rhizotrochus* are hollow and open into the calycle.

<sup>2</sup> The *Fungia* stock is probably never branched, but two or three stocks may grow close upon one another. Stutchbury states that the pedicle of the stock becomes bare of soft tissues when the terminal part is detached. The mode in which the second zooid buds from the stock is not known. Semper mentions in his paper (Z. W. Z. xxii.) several interesting facts relative to the asexual multiplication of Madrepores. *Blastotrochus nutrix* is simple, properly speaking, but from the bare sides of the theca originate buds which drop off. The pedicle of the bud left *in situ* forms

Development is only known, and that imperfectly, in some Hexactinians, in *Cereanthus*, in the Madreporian *Caryophyllia* and *Astroides*<sup>1</sup>. It may take place externally to the parent as in *Cereactis* (= *Actinia*) *aurantiaca*, but more generally within it, and then it is probable that the ovum is fertilised in the ovary. An invaginate Gastrula is found in *Actinia* (sp.?) and *Cereanthus*, and probably in *Caryophyllia*. In other instances (*Adamsia Rondeletii*=*Actinia* (*Sagartia*) *parasitica*; *Astroides*) the endoderm probably originates by delamination from a central mass of cells as in Alcyonaria. The ciliated larva is usually free-swimming and elongate, sometimes with a long posterior bunch of cilia; but in some cases (*Cereactis aurantiaca* and occasionally in *Actinia equina* = *A. mesembryanthemum*) it quits the parent as a young Actinian. It usually assumes the Actinian condition while in the free-swimming stage. A single tentacle, corresponding to one end of the mouth, may appear first of all as in *Actinia equina*; or there may be two, one at each end of the mouth, as in *Heliactis* (*Sagartia*) *bellis*, but the number may be greater, e. g. four in *Cereanthus*. The twelve primary mesenteries in *Hexactiniae* are probably developed in the following order:—(1) a pair at each end of the mouth, but one before the other, with retractor muscles turned away from one another; (2) a second pair, the future directive mesenteries, with retractor muscles similarly disposed in the intraseptal spaces of (1); (3) a pair on the right and left sides of the mouth with muscles also similarly disposed. The members of these two lateral pairs, however, become coordinated with the members of (1), to form two right and left pairs with retractor muscles turned towards one another. The remaining mesenteries arise in pairs in the interseptal spaces<sup>2</sup>.

The *Actiniaria* are found in all seas and at depths not greater than 2900 fathoms: and the deep sea yields a distinct fauna in which a tendency to disappearance of the tentacles and to variations in structure and arrangement of the mesenteries is observable (R. Hertwig). Some of the *Madreporaria* descend to great depths, e. g. *Bathyactis symmetrica* from 70–2900

another bud, but if it drops off a scar remains, laying bare the coelenteric cavity of the coral. Buds may develop from the sides of the scar. He has also shown that a pedunculate and fixed *Flabellum*, his *Fl. variable*, may detach the upper part of its body. The part set free is the *Fl. Stokesii* or *Fl. Oweni* (according to age) of Milne Edwards: the attached part, the *Fl. spinosum*, and the original parent form the *Fl. aculeatum* of the same author. Semper mentions that in the simple Fungid genus *Diaseris* the coral has several mouths; that the lobes of the corallum may break away to form new zooids, new lobes being developed after such a separation. He observed a *Fungia* when reversed, i. e. turned topsy-turvy, forming a number of zooid mouths around the edges of its base.

Semper regards the budding of the *Fungia*-stock and the pedicle in *Blastotrochus* as instances of Alternation of Generations, the stock and the pedicle being asexual. Nothing, however, is definitely known as to the ultimate fate of the structures in question.

<sup>1</sup> The *Astraea* of Kowalewsky appears to be the same coral as *Astroides*.

<sup>2</sup> There is considerable uncertainty as to the time, mode, &c. of appearance of the tentacles and mesenteries. O. and R. Hertwig have revised (J. Z. xiii. p. 539) de Lacaze Duthiers' conclusions with reference to Actinians, as stated in the text. For a summary of observations, see Balfour, *Comp. Embryology*, i. pp. 139–143.

fathoms. With one or two exceptions the deep sea forms are widely distributed and most of them occur also in shallow water. *Leptopenus*, however, is an instance of a coral limited to the deep sea (1500–2250 fathoms). The majority form the well-known coral reefs. These structures, which are absent from the west coasts of America and Africa, are for the most part confined within the limits of 30° North and South of the equator, where the mean temperature of the sea does not fall below 68° F., growing in water of, as a rule, not greater depth than twenty fathoms and for the most part less, different genera and species flourishing at different depths. The coral banks may follow the coast line of the land either closely as ‘fringing reefs’; at a distance, sometimes great, as ‘barrier reefs’; or they inclose spaces of water, the ‘lagoons,’ and then constitute ‘atolls.’ They are formed in the first instance on sub-marine banks and elevations mostly of volcanic origin, combined with deposits of mud and calcareous matter; and their subsequent extension depends on various factors, ‘the temperature, solvent power, currents, tides, and waves of the sea;’ on ‘the amount and direction of the supply of pelagic food, the up-building of calcareous deposits to the zone of reef-builders, the outward vigorous growth of the coral-masses, and their death and decay’ forming a fresh extension of ground ‘and the solution of their skeletons in the inner parts of the reefs’ (Geikie). Neither subsidence nor upheaval of the land are necessary factors, though both may occur, especially the latter. There are large numbers of fossil *Madreporaria* known. The existing fauna appears to be but sparingly represented in Palaeozoic times during which flourished a series of extinct and peculiar forms (*infra*). Some of the existing groups were, however, formerly more numerous than at present, e. g. *Turbinolidae* in the Chalk and Eocene.

The sub-class *Zoantharia* is divisible into the *Actiniaria*, *Antipatharia*, and *Madreporaria*, the characters of which, as well as of the tribes of *Actiniaria*, have been already given.

The classification of the *Madreporaria* presents great difficulties. The anatomy of their soft parts has been little investigated, and the characters of the skeleton alone are not sufficient basis for any sound classification. Moreover, these characters are not trustworthy in all respects; see p. 739. A principal division into *Perforata* with a skeleton or coenenchyma, perforated throughout by cavities which lodge, so far as is known, coenosarcal tubes, and *Aporosa* in which the corallum is not so perforated, has been universally recognized. The most recent re-arrangement of the sub-groups of these two main divisions is by Martin Duncan, J. L. S. xviii. 1885.

The Palaeozoic Corals are for the most part classified as *Rugosa* s. *Tetracoralla*, but the assemblage is probably artificial. The corallum is simple or colonial, but there is no coenenchyma; it is free or fixed. The septa are arranged in four systems, which are either disposed in a bilaterally symmetrical manner and for the most part feathering from a primary chief septum and two lateral septa, or else are regularly

radiate. One or all of the four primary septa (if such are distinguishable) are marked out by size and strength, or by a slight development, in which case they lie in a septal furrow. The septa usually alternate, a large one of the first order and a short incomplete one of the second order. The calycle is usually provided with tabulae and vesicular endotheca, i. e. secondary calcareous deposit. Reproduction was sexual, or asexual, by calycular, or by parietal gemmation. The most interesting forms are the Operculate corals, with one or four moveable opercula marked internally by septa: the horn-shaped *Cyathaxonia*, simple with well-marked radial septa and median columella, to which the living *Duncania* is perhaps allied: *Stauria*, which forms *Astraea*-like masses with four principal septa in the calycle arranged like a cross, from which the remaining septa tend to radiate, multiplying by septal gemmation (p. 741): *Zaphrentis* and *Menophyllum*, simple forms with a deep furrow or fossula lodging the principal septum, and the other septa radiating towards it: *Cystiphyllum* with a series of calycles one above the other, filled with layers of vesicular endotheca, the vesicles arranged radiately to the axis of the corallum.

See general literature, p. 732.

*Actiniaria*, see pp. 244-5. Add the following: *Cereanthus*, O. and R. Hertwig, Die Actinien, J. Z. xiii. p. 565; *apertures in tentacles of*, von Koch, M. J. vi. 1880, p. 355. *Edwardsia*, O. and R. Hertwig, op. cit. p. 582. *Zoanthidae*, Erdmann, J. Z. xix. 1886.

*Antipatharia*. *Gephyra*, von Koch, M. J. iv. 1887, p. 78 of Appendix dedicated to von Siebold; *Gerardia*, de Lacaze Duthiers, A. Sc. N. (5), ii. 1864; *Antipathes* (chiefly *A. sub-pennata*), Id. ibid. iv. 1865; *A. larix*, von Koch, op. cit. p. 75.

*Madreporaria*. *Deep-sea forms* (with lit.), Moseley, Challenger Reports, ii. 1881. *Stylophora*, von Koch, J. Z. xi. 1877. *Cladocora*, von Heider, S.B. Akad. Wien, lxxxiv. Abth. 1, 1881. *Flabellum and Rhodopsammia*, Fowler, Q. J. M. xxv. 1885; *Madrepora*, Id. ibid. xxvii. 1887. *Stephanotrochus*, W. L. Sclater, P. Z. S. 1886, pt. 1. *Fungia*, G. C. Bourne, Q. J. M. xxvii. 1887. *Seriatopora and Pocillopora*, Moseley, Q. J. M. xxii. 1882. *Reef-building Corals*, Quelch, Challenger Reports, xvi. 1886. *Classification*, Martin Duncan, J. L. S. xviii. 1885 (for technical terms, see pp. 200-2); also Quelch, op. cit. p. 38.

*Skeleton*, Fowler, *supra*; von Koch, M. J. v. 1879; *development in Astroides*, von Koch, Mitth. Zool. Stat. Naples, iii. 1882; *increase in number of septa, and on the theca*, Id. M. J. viii. 1882; *relation of soft parts to skeleton*, Id. M. J. xii. 1886.

*Asexual reproduction*, Semper, Generationswechsel, &c., Z. W. Z. xxii. 1872; on *Fungia*, see also Moseley, Notes by a Naturalist on the Challenger, 1879, p. 524; cf. *general papers, supra, and remarks* in Dana, Coral Islands, pp. 28-38; in *Palaeozoic Corals, &c.*, von Koch, Palaeontographica, xxix. 1882-83

*Coral Reefs*, Geikie, Nature, xxix. 1883-84 (*summary of recent views with lit.*); Guppy, On the recent Calcareous Formations of the Solomon Group, Trans. Roy. Soc. Edinburgh, xxxii. pt. 3, Session 1884-85. Coral Reefs, Darwin (ed. 2), 1874; Corals and Coral Islands, Dana (ed. 2), 1875.

*Fossil Corals*, Zittel, Palaeontologie, Abth. 1, i. 1876-80; cf. Moseley on *Heliopora*, Hickson on *Tubipora*, Nicholson on *Corallium*, cited note p. 731; *Operculate Corals* (by Lindström), Moseley, Nature, xxviii. 1883.

## CLASS HYDROZOA.

*Marine, rarely freshwater, Coelenterata; free or fixed; simple or colonial. There are two forms of zooids, the Hydroid and the Medusa, the former asexual except in Hydra, the latter alone, or one of its degenerate forms, sexual. Both forms of zooids usually possess tentacles: the mouth is circular or square: the gastric cavity either simple, or provided with four ridges, or in the Medusa partly obliterated, leaving pouches or canals radiating from a central cavity. Sensory cells and ganglion cells may be found in the Hydroid; aggregated sense-cells, ocelli and auditory organs, nerve rings or ganglionic centres in the Medusa. The generative organs are either ecto- or endo-dermic. The sexual zooid is developed from the asexual, either directly by metamorphosis, or indirectly by gemmation or fission, thus giving rise to an Alternation of Generations.*

There are two principal types of the Hydroid. One, the Hydromedusan or Craspedote type, consists typically of an oral and stomachal region (hydrocephalis), with or without tentacles, borne upon a peduncle (hydrocope). The tentacles are variable in shape and disposition, rarely tubular, usually solid. The mouth is placed at the extremity of an oral cone, and is sometimes extremely dilatible; the gastric cavity is simple, but its endoderm cells are sometimes thrown into ridges by the contraction of the musculature. The second or Acrasped type, the *Scyphostoma*, has a squarish mouth in the centre of a peristome, which is fringed by a circle of solid tentacles; a somewhat flask-shaped body and a short peduncle. Its gastric cavity is traversed by four equidistal longitudinal ridges, into which the mesoglaea enters. The Hydroid is (1) a permanent locomotor sexual form, multiplying by gemmation, but only temporarily colonial,—*Hydra*: (2) a larval form which passes by a metamorphosis into a Medusa, which may multiply by gemmation but is only temporarily colonial, its hydriform progeny alone in some instances attaining the Medusa-stage,—*Trachymedusae*, Acrasped *Pelagia*: (3) A non-sexual but permanent form, sometimes solitary, usually however multiplying by gemmation, which is rarely discontinuous, but as a rule continuous, giving origin to colonies,—most *Hydroidea*, *Acraspeda*: (4) a locomotor sexual form, probably derived by the specialisation of (3), and never multiplying by gemmation—Acrasped *Depastridae* and *Lucernaridae*.

The Medusa<sup>1</sup> is a bell or disc-shaped organism with the mouth at the apex of a manubrium, which depends from the centre of the concavity of the bell or disc. The mesoglaea of the aboral aspect of the bell is much thickened to form the umbrella s. exumbrella, that of the oral remains thin, and is known as subumbrella. The rim of the bell may carry hollow or

<sup>1</sup> See p. 247, *ante*, and Fig. II.

solid tentacles, and the mouth may have solid marginal tentacles. The gastric cavity in the bell is generally partially obliterated. Organs of special sense are generally present. Sexual organs are developed on the walls of the manubrium, gastric cavity, or radial canals, from the ectoderm, or in the gastric cavity from the endoderm. Asexual reproduction by gemmation, very rarely by fission, occurs in some *Craspedota*. The Medusa swims by alternate contractions and expansions of the bell. It is derived (1) by direct metamorphosis from a larval Hydroid,—*Trachymedusae*, Acrasped *Pelagia*: (2) by gemmation from a hydroid colony,—*Hydroidea*: (3) by the multiple transverse fission of a Hydroid,—most *Acraspeda*, (4) by gemmation from a Medusa,—some *Craspedota*.

The hydroid of the *Craspedota* may become polymorphic (pp. 757–8), and the Medusa be degenerate (pp. 762, 768) or devoid of mouth, and simply a locomotor or hydrostatic organism (pp. 771–2).

In one order, the *Siphonophora*, precocious gemmation takes place in the embryo to form colonies containing polymorphic hydroid individuals, and generally medusoid as well. The *Siphonophora* are consequently to be regarded as the most specialised group in the class.

Skeletal structures in the Hydrozoa are confined to the Hydroid, and are secreted by the ectoderm. They occur in two forms, most commonly as a chitinoid investment, the perisarc, more rarely as a calcareous coenosteum. The axial endoderm cells of the solid tentacles have a tough cell membrane and vacuolated contents.

The sexes are, as a rule, separate in the individual. Segmentation is total, and generally equal: the larva a free swimming planula<sup>1</sup>.

The Hydrozoa are widely distributed and almost exclusively marine; a few are fresh-water, but some of the marine forms are tolerant of brackish or even of fresh-water (p. 748). They are essentially carnivorous. Some of the Campanularian *Hydroidea*, some Craspedote and Acrasped Medusae, and especially among the latter the genus *Pelagia*, some *Siphonophora*, e.g. *Diphyes*, *Abyla*, &c., are phosphorescent. Fossil forms are rare. Two extinct groups, the Silurian *Graptolithidae*, and the Silurian and Devonian *Stromatoporidae*, are generally considered as Hydroids. A few Medusae have been described from the Jurassic Solenhofen slates, and one from the Chalk. One or two of them appear to belong to the *Trachymedusae*, the remainder to the *Acraspeda*.

There are two sub-classes, the *Craspedota* and *Acraspeda*.

<sup>1</sup> Metschnikoff has classified the formation of the endoderm in this class as follows: (A) Multipolar, and then (1) by *primary delamination*, i. e. transverse fission of the cells of the single layered embryo (*Geryonidae*, *Eudendrium*); (2) by *immigration* of cells on all sides (*Aeginopsis*); (3) by *secondary delamination*, i. e. arrangement of the cells (*Aglaura*, *Rhopalomena*, most degenerate Hydroidean Medusae); (4) by a combination of the foregoing (*Polyxenia leucostyla*). (B) hypotropic, and then by (1) immigration at one pole (Hydroidean Medusae); (2) by invagination (many *Acraspeda*). See Embryol. Studien an Medusen, Wien, 1886, pp. 70, 71.



Various views have been held as to the relation and nature of the Medusa. That it is merely a specialised sexual organ, or that it is a colonial organism, no person with a knowledge of its development and varieties of form, would maintain at the present day. It is generally held to be a zooid, polymorphic with a Hydroid and specialised for the purpose of reproduction, this function having become restricted to certain individuals of a Hydroid colony which are detached, and have acquired special facilities for locomotion in order to disseminate the race. Another view, strongly advocated by W. K. Brooks, which appears to have much in its favour, is to the effect that the primitive Hydrozoon was a free Hydroid<sup>1</sup> which gradually acquired a more and more perfect organisation for swimming: that when it had thus become a larval stage in an ontogeny, it began to multiply by gemmation: that its progeny were at first all detached and became Medusae, but that at a later stage of evolution some remained in connection with one another in the Hydroid stage, whilst the development of the Medusae became accelerated *in situ*: that finally the Medusa has in many instances become by acceleration of the development of its sexual products a degenerate sessile organism.

The points in favour of this view, as applied to the Craspedota, are, briefly put, the following:—(1) The direct development of the *Trachymedusae*, see pp. 752–3. (2) The existence of a free sexual Hydroidean—*Hydra*; and of a free hydroid larva, the Actinula, in two genera of *Hydroidea*, unless the latter is to be regarded as an instance of precocious development. (3) The fact that the development of the Medusa in the *Hydroidea* is abbreviated as shown (a) by the way in which the bell and velum are formed not by simple growth but from an entocodon or ectodermic thickening<sup>2</sup> a structure not seen in *Trachymedusae*, and (b) by the fact that it is so commonly degenerate (p. 762), and (c) that it is very generally produced on the hydrocephalis, a place where hydranths never bud, or on a blastostyle, a specialised Hydroid. (4) The fact that among the *Hydroidea* closely related genera differ greatly in the character of their reproductive zooids (p. 768), and that the development of the sexual cells is accelerated in many instances (pp. 767–8). (5) That the Medusa is not purely a reproductive organism but feeds, &c., like any other organism, and that its specialisation is as Brooks says ‘to enable it to live out its own life.’ (6) The fact that a Medusa may reproduce itself, but as a Medusa only, by budding. What is true of the *Craspedota* appears to be true also of the *Acraspeda*. *Pelagia* develops directly from the ovum; others, so far as their development is known, by strobilisation (p. 782), a process which has probably been attained by abbreviation, though it is perhaps not necessary to assume with Claus that the primitive Acrasped Hydroid was a colonial organism (cf. Untersuchungen über die Organisation, &c., der Medusen, p. 18). Götte has recently advanced the view that the subclass in question should be separated from the Hydrozoa, and that it should be united with the Anthozoa and Ctenophora in a division of Coelenterata to be termed ‘Scyphozoa.’ But he appears to exaggerate the degree to which the ectoderm is

<sup>1</sup> Brooks says ‘a solitary swimming hydra or actinula.’ Why ‘swimming’ is not clear. The natatory Hydroid of the *Trachymedusae* is a larval form, but a free adult would more probably be a creeping form, much like *Hydra*. Swimming, unless effected by cilia, requires a specialised organ for the purpose.

<sup>2</sup> For an endodermic entocodon in *Coryne pusilla* see Weismann, Die Entstehung der Sexualzellen bei der Hydromedusen, p. 53, and for the way in which an entocodon may have originated, *ibid.* pp. 259–60.

invaginated as a stomodaeum in the *Acraspoda*, and to lay too much stress on the four taeniolae and stomach pouches. The strong general anatomical resemblances between the *Acrasped* and *Craspedote* Medusae outweigh any such considerations. See his *Abhandlungen zur Entwicklungsgeschichte der Thiere*, pt. iv. 1886.

Metagenesis, or Alternation of Generations in the Hydrozoa, has therefore probably arisen from the larva acquiring the power of forming a colony by gemmation, certain of its progeny only attaining a sexual development. It has itself become at the same time specialised in structure.

The genus *Hydra* is probably a direct descendant of the primitive Hydrozoon. Its peculiarities point in this direction. The ambulatory Medusae *Clavatella* and *Eleutheria* have been supposed to be intermediate forms between a hydranth and a Medusa, but an entocodon is present in the development of the latter by budding from the Medusa.

For the remarkable form known as *Tetraplatia* s. *Tetrapteron volitans*, see Claus, *A. M. A.* xv. 1872; Viguier, *C. R.* 100, 1885.

*Toleration of freshwater by strictly marine forms*, e. g. *Eucope*, *Obelia*, *Sarsia*, *Turritopsis*, *Aurelia* and its *Scyphostoma*, *Q. J. M.* xx. 1880, p. 483-4. *Crambessa Tagi* is estuarine. Cf. Romanes on the physiology of the freshwater Medusa, *Nature*, xxii. p. 179.

*Origin of Medusae and the significance of Metagenesis*, W. K. Brooks, *Mem. Boston Soc. Nat. Hist.* iii. pt. 12, 1886.

*Terms used in describing Medusae*. Haeckel, *Deep-sea Medusae*, *Challenger Reports*, iv. 1882, pp. v-cv, pp. 143-154.

*Fossil Medusae*. List in Haeckel's *System*, *Dk. Med. Natw. Ges. Jena*, i. 1879, p. 646.

*Phosphorescence*, McIntosh, *Nature*, xxxii. p. 477; Panceri, *Atti Accad. Napoli*, vii. 1875-7; Allman, *Gymnoblastic Hydroids*, p. 145; cf. *Nature*, xxx, Verrill, p. 281, Meldola, p. 289.

## SUB-CLASS I. CRASPEDOTA.

### (*Cryptocarpa*, *Gymnophthalmata*, *Hydromedusae*).

*Hydroid form, either a free and temporary larval stage, or permanent, and then either free or fixed, solitary or colonial either temporarily or permanently. It may or may not be tentaculate; its tentacles rarely hollow, usually solid; its mouth prominent and gastric cavity simple. It is sometimes polymorphic. The skeleton is either a chitinoid perisarc, or more rarely a calcareous coenosteum. Asexual reproduction takes place very rarely by fission, generally by gemmation; and in the permanent hydroid forms some only of the buds become sexual zooids.*

*The Medusa has a tubular manubrium, the margin of the bell even or lobed, and provided with an inturned velum, a double nerve ring (inner and outer), and sensory organs either ocelli or auditory organs; the latter either tentaculocysts or ectodermic otocysts. It may become sessile and degenerate to a greater or less extent. The sexes are separate; the sexual cells typically of*

ectodermic origin, but sometimes, especially in the degenerate forms of sexual zooid and the Siphonophora, formed in the endoderm. Marine with few exceptions.

There are three orders, *Trachymedusae*, the *Hydroidea*, and *Siphonophora*.

The order *Trachymedusae*, the *Trachylinae* or second sub-legion of *Craspedota* of Haeckel, contains Medusae which possess tentacles with a solid axis, sometimes replaced in the adult by hollow tentacles, and tentaculocysts or auditory tentacles, with an axis of endodermal otolith cells. Ocelli are rare. Development is direct by metamorphosis from free hydroid larvae, and there is an Alternation of Generations only in one parasitic species. 'Sporogony,' or development from a non-sexual spore, occurs in a few instances. There are two sub-orders, the *Narcomedusae* and *Trachomedusae*.

In the *Narcomedusae*, the exumbrella is flattish, rarely bell-like, and is divided into a central and peripheral part by the insertion of the tentacles. Its substance is firm and traversed by radial, branched and anastomosing fibres. The peripheral portion is divided into lobes, one lobe between every two tentacles. The lobes are connected together by the subumbrella and by well-marked intervening streaks or 'peronia,' of ectoderm containing cnidoblasts, continuous with a marginal band of cnidoblasts and ciliated sense-cells, and reaching from the latter to the bases of the tentacles. A nerve extends from the outer ring beneath each peronium. In the *Peganthidae*, however, the subumbrella is also divided, the peronia are very rudimentary, and the lobes are united by the velum. The subumbrella corresponds solely to the peripheral region of the exumbrella, the central portion being occupied by the stomach. The velum is broad; it is either horizontal or hanging vertically downwards. In locomotion the lobes of the bell are turned inwards with the velum.

The tentacles may be in number only two, or four, or eight, but in the majority more numerous, but never more than thirty-two. In the *Aeginidae* their number follows a geometrical progression, but in the other three families it is irregular. Their ectoderm consists of cnidoblasts and sensory cells, some ciliated, some provided with stiff sense-hairs. The axial endoderm cells are developed in a single row, but may be numerous at the base, and are continued as the tentacle-root for some distance along the exumbrellar aspect of the stomach. The tentaculocysts may be only four in number, alternating with the four tentacles in *Cunantha*, generally more numerous, often several hundreds in number. They are inserted on the marginal band of the lobes (*supra*). The auditory ectoderm cells have long auditory hairs: the axial endoderm cells are in a single row, as a rule two to four, rarely more in number. Of these one, or two to four, contain one or more calcareous otoliths, as a rule of regular crystalline figure, rarely, as

in the *Solmaridae*, globular. The tentaculocyst is frequently borne upon an auditory ectodermal papilla composed of sense-cells with long auditory hairs. 'Otoporpaë,' or meridional streaks of ectodermal cnidoblasts extending centripetally on the exumbrella from the bases of the tentaculocysts are found in the *Cunanthidae* and *Peganthidae*.

A prominent manubrium is present in some *Cunanthidae* and in many *Aeginidae*, but not in other instances. In the last-named the mouth is generally four lobed: it is always extremely dilatable. The central stomach cavity is usually flattened. In the *Cunanthidae* it is produced into radial pouches, a pouch corresponding to each tentacle. Every pouch is connected to the pouch on either side by a separate 'festoon' or loop-canal, which follows the edge of the corresponding lobe. The two festoon canals originating from each pouch are separated at their roots by a peronium. The *Peganthidae* have a central stomach and festoon canals derived from it corresponding to each lobe: the *Aeginidae* a variable number of interradial pouches extending into each lobe, and festoon canals derived from the central stomach as well. In the *Solmaridae* the festoon canals are obliterated: the stomach may be simple and central, or prolonged into radial or interradial pouches.

The sexual organs are developed on the subumbrellar aspect of the stomach, either as a simple ring which may extend in some *Cunanthidae* either on to the radial pouches, or become restricted to them. The ring may be resolved in some *Peganthidae* into a number of separate interradial pouches, as it always is in *Aeginidae*. In *Solmaridae* all three conditions may obtain.

Most *Trachomedusae* have a firm, stiff, semi-globular, or broad bell. In the *Aglauridae*, however, it is bell-shaped, cylindrical, or eight-sided and prismatic; and the exumbrella is excessively thin. The velum is broad and stout, and hangs downwards when the Medusa is floating. The margin of the exumbrella has a strongly developed ring of cnidoblasts, and where the solid tentacles are sub-marginal, as in all *Geryonidae* and some *Petasideae*, there are peronia, beneath which the roots of the solid tentacles, when cast off, persist in connection with the circumferential canal. The exumbrella is prolonged in the *Aglauridae* and *Geryonidae* into a long 'gastric peduncle,'—a solid cylindrical process of its gastric aspect, which is in the last-named usually longer than the height of the bell, and therefore projects from the bell-cavity. Mesogonia occur in the *Pectyllidae*: see p. 786.

The tentacles are usually numerous, and may even be disposed in several rows one above the other. Eight, four radial and four interradial, occur in some instances, four radial in *Petanus* alone, reduced to two in *Dipetanus*. The primitive tentacles are always solid, but radial hollow tentacles communicating with the circumferential canal are present in *Olindias* and *Pectanthis*, and appear in the *Geryonidae* in the course of

growth. Those of the *Pectyllidae* terminate in suckers<sup>1</sup>. The solid tentacles have the usual structure: their cnidoblasts are very variously arranged, scattered, gathered into rows, rings, or on a terminal capitulum: ciliated cells and sense-cells furnished with stiff sense-hairs are present as well. The latter in the Trachynemid *Marmanemidae* may be aggregated in a patch or a circle at the apices of the tentacles, in longitudinal rows along them, or in 'tactile combs' situated in pairs at the bases of the tentacles as well as between them. The ectodermal musculature of the solid tentacles is striated.

The tentaculocysts are primitively four and interradial, and so persist in *Petasus* and *Dipetasus*, but they are usually displaced by the unequal growth of the bell-margin, or the formation of interradial tentacles; there are usually four radial tentaculocysts as well, and then the eight organs take an intermediate or adradial position. The number is seldom increased; e. g. *Olindias* has one to two hundred or more. Among *Geryonidae* the *Liriopidae* have eight, the *Carmarinidae* twelve, half radial, half interradial, and doubling the number of the radial canals. They are free always at first, and persist in this condition in the family *Aglauridae*, the Petasid sub-family *Petachnidae*, and the Trachynemid *Pectyllidae*, but in the Petasid *Olindiadae*, the Trachynemid *Marmanemidae*, and the family *Geryonidae* they become inclosed by the growth of the ectoderm of the bell-margin in vesicles, which in the last-named are sunk within the exumbrellar mesoglaea. The endodermal axis consists of two to three, rarely four cells, the apical cell dilated, and lodging a single rounded or ovate calcareous otolith. The ectoderm consists in part of auditory sense-cells. Marginal bulbs and cirri (p. 761) are occasionally present.

The manubrium is very muscular, short when attached to a gastric peduncle (*supra*), elongate in other instances. The mouth has four lobes, or in the *Carmarinidae* six, beset with cnidoblasts: it is, as a rule, extremely dilatable, even exceeding the diameter of the bell, e. g. in *Liriopé*, and may then be used as a sucker. There are radial canals, four in *Petasidae*, as in the Geryonid *Liriopidae*, eight in others, except the *Carmarinidae*, where there are six; they are united by a circumferential or marginal canal. In the Petasid *Olindias*, the Trachynemid *Pectis*, and in some *Liriopidae* and *Carmarinidae* centripetal radial canals originate from the marginal canal between the radial canals, but fail to reach the base of the manubrium. Their number is variable, but increases with age. The sexual organs are

<sup>1</sup> These tentacles are solid in *Pectis* and *Pectyllis*, and arranged in vast numbers along the edge of the bell: some of them are sessile. In *Pectanthis* they are aggregated in sixteen bundles, two bundles between each pair of radial canals. *Pectanthis* was observed by Haeckel alive: it was able to climb up the glass sides of an aquarium by means of its suckers, or to anchor itself with the bell-margin downwards or reversed. See his report on 'Deep Sea Medusae,' Challenger Reports, iv. 21, and Pl. VIII.

developed on the radial canals, in the *Aglauridae* alone sometimes at or near the base of the manubrium. They either occupy the whole sub-umbrellar wall of the canals, or are divided by radial muscles into two halves. They have a narrow base in the *Aglauridae*, and depend into the bell cavity: and in the *Geryonidae* they are leaf-like, the apex of the leaf being turned towards the bell-margin<sup>1</sup>.

The ovum is naked, as it always is in Craspedote Medusae. The smallest Medusan ovum known is that of *Cunina proboscidea* (·024 mm.), the largest that of *Polyxenia (Solmissus) albescens* (1.5 mm.). Segmentation is regular; in *Polyxenia (Solmoneta) flavescens* var. *leucostyla* variably irregular; in *Aglaura hemistoma* irregular. There is a solid morula, or in *Geryonidae* a blastula. The endoderm in the latter is derived by primary delamination, i. e. transverse fission of the cells: in the former in various ways; (1) by immigration of cells at any point, *Aeginopsis (Solmundella) mediterranea*; (2) by secondary delamination, i. e. by arrangement of the cells in two layers, *Aglaura hemistoma*, the Trachynemid *Rhopalonema velatum*; or (3) in a mixed mode, primary or secondary delamination, immigration, *Polyxenia leucostyla*.

In the *Narcomedusae* the further development of some *Solmaridae*, and the life history in part of some *Cunanthidae* have been traced. As to the former, *Solmundella* s. *Aeginopsis mediterranea*, *Solmoneta* s. *Polyxenia flavescens*, var. *leucostyla*, have an elongated ciliated free-floating larva—the two ends of which become transformed into the two primary tentacles, the central region acquiring a mouth. In the latter of the two named, two tentacles have been observed developing at right angles to the two first, and a tentaculocyst appearing in each interval between the tentacles. Later stages with eight and twelve tentacles have been seen, but the number of tentaculocysts present was not constant. The central part of the bell is produced by the growth of the aboral part of the body within the circlet of tentacles: the peripheral part by the growth of a ridge in the same zone with the tentacles or to their oral side. But the development of this region has been more accurately traced in some *Cunanthids*. The lobes are produced by the more rapid growth of the parts between the tentacles; the peronia by the union of the ectoderm fringing the outer surface of the margins of adjacent lobes, whilst the velum appears to be an outgrowth of their inner or oral aspect. The segmentation of the egg in the *Cunanthidae* has never been observed. The life histories of several members of the family, so far as known, are most remarkable. (1) *Cunocantha (Cunina) octonaria*, parasitic in the bell of the Anthomedusan *Turritopsis*. The first noted stage (? developed from an ovum) is proboscidiform with a

<sup>1</sup> A female specimen of *Geryonia hexaphylla* (= *Carmarina fungiformis*, Haeckel, 'System', p. 297) was found by Schulze to be hermaphrodite: see A. N. 41 (2), p. 404.

mouth and near the aboral pole two short tentacles. The young animal adheres by its proboscis to the margin of the bell of its host. It then migrates into the cavity of the bell and affixes itself by its tentacles, two new tentacles appearing between the two first formed, whilst the oral end of the body elongates remarkably, and may be inserted into the mouth of the *Turritopsis*. At the same time it develops as many as six to seven buds at its aboral pole which become larvae similar to their parent, and are detached. The ridge, from which the peripheral part of the bell is formed, appears in the same zone as the bases of the tentacles, the number of which is increased by the development of four more. The ridge grows out at its summit into intertentacular lobes, each of which bears a tentaculocyst. The larval Medusa is now set free. The oral proboscis shortens, the stomach pouches acquire their adult character, and the generative rudiments are formed. A somewhat similar larva has been observed in the bell of *Rhopalonema velatum*. (2) *Cunina proboscidea* (= *C. vitrea*). In this species, in *C. rubiginosa* s. *rhododactyla*, and apparently in *C. (Cunocantha) Köllikeri*, an asexual reproduction or sporogony occurs in both males and females, which has been accurately worked out in the first-named of the three. Immature sexual cells with a granular protoplasm wander from the sexual organs into adjacent parts. They multiply by fission. Eventually one cell ingulfs another, and the ingulfed cell divides and forms a morula. If the inclosing cell lies in the endoderm of a festoon canal further development of the inclosed cell into a ciliated lens-like body with ecto- and endoderm takes place. It escapes from the supporting cell, and is eventually converted into a Medusa. During its growth it develops buds at the aboral pole, one after another in *C. proboscidea*, which are detached, but may remain in connection with a stolo prolifer in *C. rubiginosa*. Gemmation does not appear to take place in *C. Köllikeri*. In the two last named the Medusa becomes a true Cunanthid though differing in the number of its segments from its parent, e. g. *C. Köllikeri* is eight-rayed, its young twelve. In *C. proboscidea* the young sexually mature Medusa differs entirely from its parent<sup>1</sup>. (3) *Cunina (Cunocantha) parasitica*. The life-history of this form is only partially known but is probably connected with a sporogony. It is parasitic in *Geryonia proboscidualis* s. *Carmarina fungiformis*<sup>2</sup>. The youngest stage observed consists of a colossal cell with pseudopodia adherent to the bell-margin of the host, and partially inclosing a morula composed of a cap of ciliated ectoderm cells and an irregular mass of entoderm cells.

<sup>1</sup> See Metschnikoff, Embryologische Studien an Medusen, Wien, 1886, pp. 119, 120.

<sup>2</sup> A sporogenetic brood seems to be capable of wandering. Metschnikoff states (op. cit. p. 122) that he has found embryos and buds of *Cunina rubiginosa (rhododactyla)* in *Polyxenia (Solmissus) albescens*. Hence the budding larvae found in various Geryonids may belong to an identical species.

The nomenclature of the *Geryonidae* appears to be in much confusion. The two specific names given in the text are used by Metschnikoff for the same medusa.

The ecto- and endo-derm cells grow each in a single layer round the colossal cell, leaving a slit-like or triangular opening by which it protrudes its pseudopodia. The elongate or triangular larva now swims about and settles eventually on the gastric peduncle of its host. It begins to bud, whilst the colossal cell atrophies, and is then transformed into a clavate sac, not quite  $\frac{1}{2}$  in. long, with walls composed of an ectoderm, longitudinal ectodermal musculature, a supporting lamina, and an endoderm with muscle fibres (? circular). This sac, when full-grown, carries buds in numbers up to about 100, which develop into eight-rayed *Cuninae*, and are detached. The cycle therefore includes an Alternation of Generations, and Metschnikoff has suggested that there may be three generations, (1) a true *Cunina*, (2) a sac-like larva (*supra*), and (3) a *Cunina*-like Medusa with peronia but no festoon-canals.

As to the *Trachomedusae*, *Aglaura hemistoma* has an elongate larva with an axis of endoderm cells in a single row. The mouth is formed at one pole, and near it the first two tentacles, and then at right angles to them two more. In the *Geryonidae* mesoglaea makes its appearance as soon as the endodermal sac is complete. A patch of thickened ectoderm is then formed at one spot and the endoderm sac gradually approaches and at last comes into contact with it, becoming, sooner or later, flattened. The edge of the patch thickens, while its centre becomes thin. The primary radial solid tentacles (four in *Liriope*, six in *Geryonia*) appear in connection with the thickened edge which gives origin to the margin of the umbrella and velum, whilst the central disc becomes the ectoderm of the subumbrella and manubrium. The mouth breaks through in its centre. The interradial solid tentacles, in number equal to the radial, next appear. During growth the Medusa undergoes changes. The oral peduncle grows down, carrying the manubrium with it; the hollow radial tentacles of the adult spring from the margin of the bell, whilst the solid radial tentacles drop off; the solid interradials are lost in some genera, not in others<sup>1</sup>.

The hydroid appearance of the larva is much masked in the Geryonids by the early development of mesoglaea, in *Cunocantha parasitica* by parasitism. In other instances, especially in *C. octonaria*, it is exceedingly well-marked, and it has a resemblance to the *Actinula* larva of certain *Hydroidea* (p. 765).

The *Trachymedusae* are marine, unless the freshwater *Limnocodium*, of unknown habitat, and a Medusa, lately found in Lake Tanganyika (Central Africa), belong to the order<sup>2</sup>. Some of them have been dredged at great

<sup>1</sup> The solid radial and interradial tentacles differ from one another in shape, &c. Brooks states that in *Liriope scutigera* the interradial tentacles are lost or retained irregularly. Hence the point is not, at least not always, as Haeckel considers it to be, of diagnostic value. See Mem. Boston Soc. Nat. Hist. iii. p. 383.

<sup>2</sup> By Allman *Limnocodium* was placed among *Leptomedusae*. There are three points about



depths in the sea; e.g. *Pectyllis* at 1250 fathoms, *Pectis* at 1260, *Cunarcha Aeginoides* at 1675, and *Aeginura myosura* at 2150. The majority of the *Trachomedusae* are small, the *Geryonidae* excepted: the *Narcomedusae* are small or of moderate size. The two giants are the Petasid *Olindias Sambaquiensis* and the Geryonid *Carmaris Goltshii*, both of which attain a diameter of four inches.

The *Hydroidea* s. *Polypomedusae*, the second order of Craspedota, contains both non-colonial and colonial hydroids, fixed with the exception of *Hydra* and *Protohydra* (?). The hydroid, or in a colony the hydranth, is a purely nutritive zooid, except in *Hydra*, where it has sexual organs (p. 328, *ante*). The free sexual zooid, or Medusa, which is frequently arrested in development and consequently sessile, arises by gemmation either from the coenosarc, from a hydranth, blastostyle or Medusa.

The non-colonial hydroids are the freshwater genera *Hydra* and *Microhydra*, the marine *Protohydra*, *Tiarella*, *Heterostephanus*, *Corymorphidae*, and *Monocaulus*, in all of which a hydrorhiza is absent<sup>1</sup>. In the colonial forms the hydranth is attached directly to the hydrorhiza in *Hydrocorallina*: by its hydrocope in some instances, e.g. *Clavatella*, *Hydractinidae*: or, as is most usual, by a more or less branched hydrocaulus<sup>2</sup>. A hydrorhiza is sometimes but feebly developed, as in *Myriothela*: but in most instances it is filiform, or reticulate and spreading, giving origin to new zooids or stems<sup>3</sup>. In *Hydractinia* and *Podocoryne* it

it which makes its position doubtful. (1) It has organs at the base of the velum on its exumbrellar aspect, which appear to be auditory though they possess no otoliths. They are said by Professor Lankester to be tentaculocysts, but his description and figures do not place the matter quite beyond doubt. (2) It has floating embryos, and the bell-cavity seems to be closed at first, a mode of origin not found in any Trachymedusan, so far as is known, certainly not in *Liriope* and *Geryonia*, a point incontestably established by the recent researches of Brooks and Metschnikoff. As the female has never been observed, the origin of the embryos from ova is not certain. (3) It is possible that the small columnar Hydroid, devoid of tentacles and enveloped in a tube of mud, found by Mr. A. G. Bourne on the roots of a *Pontoderia* growing in the tank at the gardens of the Royal Botanic Society, Regent's Park—the place where *Limnocoidium* appeared—may belong to the life-history of the Medusa. If so, it is the solitary instance of a *fixed hydroid stage among Trachymedusae* met with up to the present time.

<sup>1</sup> The hydrocope of *Hydra*, *Protohydra*, and *Tiarella* ends in a disc; of *Heterostephanus*, the *Corymorphidae* and *Monocaulus* in a pointed extremity, but it is furnished in the two last-named with long extensile filamentous processes which probably anchor it in the mud or sand in which it is immersed.

<sup>2</sup> In some species of *Eudendrium* the main stem and origins of the branches may be fascicled, i. e. consist of a number of separate but closely apposed coenosarc tubes contained each in their own perisarc: see Hincks, *British Hydroid Zoophytes*, i, and Allman, *Gymnoblasic Hydroids*, under the genus. *Corydendrium* has the same peculiarity, and the further one that from the mode of growth of the colony, 2-3 perisarc tubes may be inclosed in a common perisarc tube: see Weismann, *Entstehung der Sexualzellen bei den Hydromedusen*, Jena, pp. 35-6. The erect growing species of the genus *Lafocia* have the stem composed of several tubes. *Anisicola Halecioides* has a second stem accompanying the hydranth-bearing stem, which itself bears no hydranths, but is connected to the primary stem at short intervals: see Jickeli, M. J. viii. p. 636.

<sup>3</sup> In *Coppinia* the thecae for the hydranths and blastostyles are closely packed, hiding the

forms an incrusting felt-work of tubes, the chitinous perisarc of which is thickened in the intervals, that of adjoining tubes fusing<sup>1</sup>. So too in the *Hydrocorallina*, where the chitinous perisarc is replaced by a coenosteum or strong skeleton of Lime carbonate, and the hydrorhiza constitutes incrusting or more usually erect lamellate or columnar, &c., branching structures, simulating certain corals properly so-called. Pores or depressions in this calcareous structure, either scattered or aggregated into systems and sometimes furnished with raised walls, give shelter to the dactylozooids and gastrozooids (*infra*, p. 758) of the colony: and in the genus *Millepora*, newly grown strata of tubes are cut off from older and deeper strata by calcareous platforms or tabulae. Similar tabulae cross the pores in the same genus, and in two genera of *Stylasteridae*.

*Hydra* is destitute of any natural or adventitious protective coat: *Microhydra* invests itself with a coating of mud, &c., held together by a secretion: *Protohydra* and *Corymorpha nutans* have a delicate cuticula. In other instances a perisarc is present, thickish, brownish in colour, and composed of lamellae; but in *Tiarella* its outer portion is gelatinous. It is secreted by the cells of the ectoderm, and is resorbed by them in places where budding is taking place. It usually commences in the Tubularian hydroids as a very delicate layer upon the hydrocephalis aborally to the tentacles, is thicker on the hydrocope, and thickest on the hydrocaulus and hydrorhiza<sup>2</sup>. It is confined to the two last named in the *Campanularia*-like hydroids of *Eutima*, *Octorchis* and *Aequorea*; but in most other Campanularian hydroids there are perisarcal hydrothecae for the hydranths, and gonothecae (or gonangia) for the blastostyles. The edge of a hydrotheca may be thin, and thrown into plaits when the animal is retracted, or cut into moveable or fixed teeth. In some *Sertularidae* it is furnished with a valve-like operculum.

The hydranths are usually very small in size; the largest known, a *Monocaulus*, does not exceed  $1\frac{1}{2}$  in. in length. When they are attached to a branched stem, they are disposed either terminally or laterally on the branches; and in the latter case they may be pedunculate as in *Tubulariae* and *Campanularidae*, or sessile and are then arranged either in a single row as in *Plumularidae*, or in a double row opposite or alternate one to

reticulate hydrorhiza from which they spring; see Allman, *Gymnoblasic Hydroids*, pp. 54-5, and notes with Fig. 27.

<sup>1</sup> A living *Hydractinia* with calcareous skeleton has been described by Carter from West Africa (*A. N. H.* (4), xix. p. 50; *ibid.* (5), i. p. 300). Calcareous species from the Chalk and Pliocene, a pseudomorphic siliceous species from the Greensand are also known, together with extinct allied (?) genera: see Carter, *op. cit.*; Steinmann, von Meyer's *Palaeontographica*, xxv. 1878.

<sup>2</sup> *Perigonimus Cidaritis* (Weismann, *Entstehung der Sexualzellen*, &c. p. 116) is invested by a coat of mud, even extending on to the tentacles; *P. palliatus* has a gelatinous coat (Allman, *op. cit.* p. 325); *P. vestitus* a perisarc roughened by grains of sand (Allman, *op. cit.* p. 326). In the Tubularian *Bimeria* the perisarc covers the hydranth and the bases of the tentacles.

another as in *Sertularidae*. The hydranth itself varies somewhat in the shape of the hypostome, the relative proportions of the hydrocephalis and hydrocope, and the sharpness with which the latter is marked off from the former by a constriction or neck<sup>1</sup>. The tentacles of *Hydra*, *Myriothela*, and *Polypodium* (p. 766), are tubular, those of other Hydroids are, with a few partial exceptions, solid, possessing a notochord-like axis of modified endoderm cells generally disposed in a linear series. They are either filiform or capitate. In the former the cnidoblasts are scattered along them in, for the most part, irregular groups containing micro- and macrocnidia, intermingled; in the latter they are restricted to the swollen end, and contain almost exclusively macrocnidia. The tentacles are either arranged in a single adoral whirl, all similar in size, or alternately large or small, their bases sometimes united by a thin ectodermic lamella, e.g. in *Campanopsis*, *Laomedea*, &c.; or in two or more whirls of similar members, e.g. *Tubularia*, or of dissimilar, e.g. *Stauridium*, *Cladonema*, *Pennaria*, *Tiarella*. Or they are more or less irregularly scattered like the filiform tentacles of *Clavidae*, and the capitate tentacles of some *Corynidae*. In *Cladocoryne* the scattered tentacles are branched as well as capitate. They are usually numerous, but are reduced to two in *Lar Sabellarum* and *Amphibrachium Euplectellae*, to one in *Monobrachium*, and are absent altogether in *Microhydra* and *Protohydra*.

The hydranth is sometimes modified for special functions, and the following must be regarded as polymorphic forms of it. (1) The *blastostyle*, a hydranth comparatively rarely developed in *Tubulariae*, the function of which is solely to produce sexual zooids<sup>2</sup>. It may possess a mouth and

<sup>1</sup> The base of the hydranth of *Eudendrium* is surrounded by an ectodermal ring containing cnidoblasts separated by a furrow from a ring of gland cells. In *E. ramosum* some of the hydranths are furnished with a single basal horn-like process—the cnidophore—armed terminally with a battery of cnidoblasts, and capable of executing slow movements. See Weismann, op. cit. p. 94, and Mitth. Zool. Stat. Naples, iii. 1882. A glandular ring occurs in some Campanularidans: von Lendenfeld, Z. A. vi. p. 69.

<sup>2</sup> According to Allman (op. cit. ante, p. 336), the blastostyle of *Eudendrium* is formed by the atrophy of the hydranth, every stage being present in one and the same colony. Weismann, on the contrary (op. cit. ante, pp. 97, 103), states that it differs from a hydranth in development and structure from the first. The hypostome is absent, but the female has a double circle of small tentacles and a minute mouth, organs absent in the male. Both *Cladocoryne* and *Eudendrium ramosum* (as well as other species of the latter genus, judging from Allman's figures) are instances in which gonophore-bearing hydranths and blastostyles may be found side by side. The blastostyle of the female *Halecium* gives origin to two hydranths at its apex (Allman, op. cit. p. 58, Fig. 29, and Hincks, op. cit. ante, i. p. 221). The blastostyle of the thecate Campanularians is expanded distally into a disc, hollow at least in some instances, in which rhythmical contractions, due to the presence of ectodermic muscles, occur in *Eucopella*, as in the gonophores of *Coryne pusilla*. The blastostyle in *Eucopella* and *Laomedea* is broken up into a number of tubes which open into the terminal hollow disc. The gonophores in *Eucopella* are borne upon one of these tubes, in *Laomedea* in connection with a central spadix. See von Lendenfeld, Z. W. Z. xxxviii. pp. 537-544; Allman, op. cit. ante, pp. 47-8, and Fig. 20. The homology of the pedicle bearing medusae in *Corymorpha*, and *Monocaulus* or gonophores in *Tubularia* does not seem to be known. It always springs from the hydrocephalis.

tentacles as in *Podocoryne*, the latter reduced to ectodermic knobs in *Hydractinia*, or tentacles and no mouth as in *Myriothela*; or it is, as is more commonly the case, e. g. in all *Campanulariae*, destitute of both structures. (2) The *Dactylozoid*, a mouthless hydranth, modified for solely defensive and offensive purposes. Such zooids are universal among *Hydrocorallina*. They are long and filiform in the *Milleporidae*, and bear a variable number of short scattered capitate tentacles, but in the *Stylasteridae* are devoid of tentacles. A circle of them surrounds each gastrozoid of *Millepora* and some *Stylasteridae*. They communicate by several apertures with the coenosarc. Under this heading should also be included the three following: (i) The *spiral zooids* of *Podocoryne*, mouthless and tentaculate, tubular in *P. carnea*, with a solid endodermal axis in *P. Haeckelii*: the similar zooids of *Hydractinia*, which are tubular and possess small ectodermic tentacles<sup>1</sup>. (ii) The highly extensile tentacle-like and apparently solid zooids of the Campanularian *Ophiodes*, attached singly to the hydrocope or in numbers to the hydrorhiza. They are capitate, and the terminal knob supports numerous cnidoblasts. There appear to be very similar structures seated on the hydrorhiza of *Oplorhiza* and *Lafoëina* and below the hydrothecae of *Halecium Gorgonidae*<sup>2</sup>. (iii) The structures known as *nematophores*, *sarcothecae*, *guard-polypes* or *macho-polyps* which are confined to the Campanularian family *Plumularidae* and are in close relation to the thecae of the ordinary hydranths. They are tentaculoid with a solid endodermal axis, longitudinal ectodermic muscle cells, and are capitate. The knob in one form contains cnidoblasts, sense cells, supporting cells, sub-epithelial ganglion cells, and radial muscles; see Pl. xiv, Fig. 8, and p. 330. In some species the cnidoblasts are replaced in the guard polypes situated in front of the hydranths by cells containing adhesive globules similar to the structures so called in Ctenophora. And in the genus *Aglaophenia* certain guard-polypes of this last-named kind placed behind the hydranths, possess a basal ectodermic thickening with cnidoblasts, ganglion cells, &c., protrusible from an aperture of the theca separate to that by which the macho-polypes themselves are protruded. The macho-polypes are usually disposed in a median and two lateral rows<sup>3</sup>. (3) The *Gastrozoid*, a term applied to the

Weismann considers (*Entstehung der Sexualzellen*, &c. pp. 245-6) that the blastostyle is correlated with the degeneration of the Medusa (pp. 760, 768, *post*). A Medusa-bearing blastostyle occurs in *Podocoryne* alone among *Tubulariae*, but the Campanularian Medusa is invariably developed from one.

<sup>1</sup> The spiral zooid is confined to the edge of the colony bordering the aperture of the Gastropod shell on which the colony is planted, or of any accidental hole in it. The zooids are found in the colonies of both sexes, not in the male only, as Grobben thought. See Weismann, *Entstehung der Sexualzellen*, &c. pp. 63-65.

<sup>2</sup> See note, p. 6, in Allman's *Plumularidae*, Challenger Reports, vii.

<sup>3</sup> Von Lendenfeld states that the guard animal with cnidoblasts is protruded when the colony is disturbed; the one with adhesive cells, on the contrary, retracted; and that in the third variety above described the part or head with adhesive cells is protruded for holding fast the prey, the basal thickening, on the contrary, if the colony is roughly disturbed, the two parts being retracted under

digestive zooid of *Hydrocorallina*. It is relatively short, and large, with a wide mouth, and in the *Stylasteridae* is sometimes devoid of tentacles. The base of the gastric cavity gives off many communicating tubes to the coenosarc. (4) A *spine* occurring in the genus *Podocoryne* alone<sup>1</sup>. (5) The clasps of *Myriothela*, simple filiform structures, with a sucker-like extremity, which bear each one an ovum during its development.

In many *Plumularidae* a ramulus, hydrocladium or theca-bearing portion of a branch, becomes modified to form a *phylactocarp* for the gonothecae which here occupy the position of hydrothecae. This phylactocarp, to which numerous machopolytes are attached, varies in structure and in the degree to which the ramulus is modified. It may form a cage completely open, nearly closed, or altogether closed, e. g. in *Aglaophenia pluma*, where it receives the special name of *corbula*<sup>2</sup>.

The coenosarc connecting the hydranths and other members of the colony is nearly invariably a simple tube. But in *Tubularia indivisa*, *Corymorpha* and *Monocaulus*, the endoderm cells of the stem proliferate, leaving only tubular passages: and in some *Plumularidae* the main stem and principal branches are hollow, with a number of peripherally placed endodermal tubes, communicating laterally with one another, all inclosed in a common thin ectoderm and perisarc<sup>3</sup>. See also note 2, p. 755.

The sexual zooid or Medusa has the typical structure detailed on pp. 247-8, and Fig. 11<sup>4</sup>. The Medusae of the *Hydroidea* constitute Haeckel's first sub-legion of Craspedota, the *Leptolinae*, in which there are either ocelli or ectodermic otocysts. There are two groups, the *Anthomedusae* and *Leptomedusae*. The former possess ocelli and never otocysts: their generative products ripen in the walls of the manubrium, and their radial canals usually number four, very rarely six to eight, and they are derived from Tubularian Hydroids. The latter may have ocelli, but generally

reversed conditions. He also observed that the third variety has at first cnidoblasts in its terminal knob, but that during growth the nematocysts are lost, their cells undergo degeneration, and certain supporting cells develop adhesive globules. Metschnikoff has observed the ectoderm of the machopolytes in two species of *Plumularia* ingest not only carmine suspended in the water, but the dead hydranths of the colony: see Q. J. M. xxiv. p. 94.

<sup>1</sup> Spines also occur in *Hydractinia*; but, judging from Allman's figure, their structure is unlike that of the spines of *Podocoryne*.

<sup>2</sup> It is impossible to explain the structure of the phylactocarp without figures. For details; see Allman, *Plumularidae*, Challenger Reports, vii. pp. 10-15; and for the development of the corbula, Id. *Gymnoblasic Hydroids*, pp. 59-60, and Fig. 30. In *Cladocarpus*, the phylactocarp is a super-added bifurcating branch, and in *Pleurocarpa* it consists of phylactocarpal appendages in the shape of ribs taking the place of the proximal hydrocladia of a branch.

<sup>3</sup> See Allman, *Gymnoblasic Hydroids*, pp. 124-6; Id. *Plumularidae*, Challenger Reports, vii. p. 4; Agassiz, *Natural History of United States*, iv. p. 267; Hamann, J. Z. xv. p. 30.

<sup>4</sup> The Medusae *Eleutheria dichotoma* and *Clavatella prolifera* have so feebly developed a bell that they are incapable of swimming, and only creep about. See Allman, op. cit. ante, pp. 31, 212, 384, and Pl. XVIII; Hincks, op. cit. i. p. 71; Haeckel, *System der Medusen*, pp. 105-7, and Hartlaub, Z. A. ix. 1886. The Medusae in question appear to be distinct, not, as Haeckel considers them, one and the same species: see Allman and Hincks.

possess vesicular otcysts; their generative products ripen on the sub-umbrella in the course of the radial canals, which are in number from 4, 6, 8, 16, 32, 80, to several hundreds, and they are derived from Campanularian Hydroids. In both groups the Medusa may after its detachment grow in size, develop additional radial canals, tentacles, &c., and it may become sexual before its full development is attained.

The bell of the *Anthomedusae* is, as a rule, of greater depth than breadth, conical or a four-sided pyramid in shape, and of a firm consistence<sup>1</sup>. Meridional ridges or a network composed chiefly of cnidoblasts may be present on the exumbrella. The velum is broad. The manubrium is cylindrical with a simple mouth and is surrounded by the genital products in the *Codonidae*: usually quadrangular in cross section in the other families, the genital products being variously arranged in bands. The mouth is furnished with four lobes in the *Tiaridae*; four solid capitate simple or branched oral tentacles in the *Margelidae*; and in the *Cladonemidae* it varies, resembling one or other of the three families named<sup>2</sup>. Tentacles to the bell may be entirely absent (*Amaltheidae*), or there may be only one (*Euphysidae*); there are occasionally two, e. g. *Gemmaria*, *Ctenaria*, but usually at least four, and when thus restricted in number they correspond to the ends of the radial canals. Their number may be increased in the *Tiaridae*, *Margelidae* and some *Cladonemidae*, the additional tentacles springing from the circumferential canal. They are sometimes grouped in bunches, and in the *Cladonemidae* are either feathered or branched. Their root is bulbous, and the eye is situated on this bulb, usually on its outer aspect, but on its inner in those species that habitually carry the tentacles reflexed, e. g. in *Lizzia*. Most *Anthomedusae* are small, some *Codonidae* and *Cladonemidae* not exceeding  $\frac{1-2}{25}$  in. The *Tiaridae* are of fair size, and some species of *Turris* and *Tiara* attain a diameter of  $1\frac{1}{2}$  in.

The *Leptomedusae* contrast with the *Anthomedusae* in the following points. The bell is flat, its breadth greatly exceeding its depth; it is relatively soft, and hence assumes very different forms during contraction, and may even be reversed, as not infrequently happens in *Obelia*. Exumbrellar ridges are rare. The velum is feebly developed. The manubrium does not project much: the mouth has usually four lobes, often of some length: the atrium is quadratic or polygonal, and the radial canals spring from its angles<sup>3</sup>. The latter vary from four (*Eucopidae*), eight (*Meliceridae*, &c.),

<sup>1</sup> In *Sarsia* the subumbrella separates from the gastral lamina along eight lines so as to form eight closed pouches. See the description of *S. tubulosa* by F. E. Schulze in his '*Syncoryne Sarsii*,' Leipzig, 1873, pp. 15-16.

<sup>2</sup> Complete absence of the manubrium and mouth has been observed in individuals of a *Bougainvillea*: Mereschkowsky, A. N. H. (5), iii. 1879.

<sup>3</sup> The manubrium is exceedingly small in *Obelia* and *Aequorea*, and is absent in *Staurostoma* and *Staurophora*, in which the mouth is a cruciform slit. Cf. Haeckel, op. cit. ante, pp. 130, 148.

to a larger number, e. g. 200 or more, as in *Aequorea*. They are variously branched in some instances. The genital organs are usually confined to the radial canals but may extend to the manubrium, or be divided, one part lying at the base of the manubrium, the other on the radial canals, as in the *Octorchidae*. They appear as simple radial bands, divided sometimes into two parts when radial muscles are present in the subumbrella. If long they may be thrown into hollow folds, if short take the form of dependent pouches. The tentacles are usually tubular with bulbous basis, in number 2, 4, 8, 16, or several hundreds. Other marginal appendages are (1) *marginal cirri* present in a few genera of all the families, solid filaments scattered between the tentacles, spirally coiled at their extremities, with swollen ends armed with cnidoblasts: (2) *marginal bulbs* occurring only in the ocellate families and in certain genera, short, thin, with bulbous ends, provided, at least in some cases, with sense hairs: (3) *marginal tubercles* present in some vesiculate genera, more or less conical eminences tipped with cnidoblasts, usually black, and containing an evagination of the circumferential canal, and frequently opposite to (4) the *marginal funnels* or *subumbrellar papillae* which, unlike the preceding, are placed at the base of the velum to the inner or subumbrellar aspect of the circumferential canal. These papillae are conical, hollow, with a terminal pore, and their lining endoderm cells are filled with brown granules and concretions. They are without doubt excretory organs. Ocelli are found in the two families *Thaumantidae* and *Cannotidae*, seldom in the *Eucopidae* and *Aequoridae*, usually on the outer aspect of the tentacle-bulbs, rarely on the marginal cirri or bulbs, or on the bell-margin itself in great numbers, e. g. *Orchistoma*. Otocysts are characteristic of the families *Eucopidae* and *Aequoridae*. They lie at the base of the velum, projecting to its outer aspect. The *Eucopidae* are small in size, averaging  $\frac{1-2}{5}$  in., some, however, such as *Obelia*, do not exceed  $\frac{1-2}{25}$  in. The majority of *Leptomedusae*, however, range from  $\frac{2-4}{5}$  in. and upwards. Some *Aequoridae*, indeed, are the largest of all Craspedota, e. g. *Aequorea Forskalea* reaches from 8 to nearly 16 inches.

The Medusan eye consists of sense-cells with pigmented (black, brown, violet, red) supporting cells, with basal ganglion cells connected to the outer nerve-ring. A cuticular lens is sometimes present, e. g. in *Lizzia*. The otocyst is primitively a groove lined by the ectoderm cells of the subumbrellar side of the velum; certain of these cells contain each a single calcareous otolith, and others connected to the inner nerve ring are converted into sense-cells. Such otocysts are found in *Mitrocoma Annae*. But in other instances the groove is very deep and the ectoderm cells at its margins proliferate and meet, thus turning it into a vesicle.

The sexual zooid is very commonly degenerate, and is always so in

the two Campanularian families *Plumularidae* and *Sertularidae*<sup>1</sup>, and the following stages may be enumerated (Weissman): (1) *Medusoid*. There are no tentacles, and as a rule no velum, no organs of special sense, nor mouth to the manubrium, detached when ripe, e.g. *Pennaria*<sup>2</sup>. (2) *Sessile Medusoid*. The bell has either incomplete canals or none at all, but there is a bell-mouth and cavity, e.g. *Tubularia*, female *Cladocoryne*. (3) *Sessile Gonophore*. Bell devoid of cavity and mouth, but with a gastral lamella, subumbrellar and manubrial ectoderm laminae, e.g. *Clava*, *Hydractinia*, *Plumularia*. (4) *Sessile Gonophore*. Bell with gastral lamella, subumbrellar and manubrial ectoderm forming a single lamina if present: female *Campanularia*, *Opercularella*, *Halecium*. (5) *Sporosac* = *Sporophore*. A sessile gonophore without trace of medusoid structure, e.g. *Cordylophora*, male *Campanularia*<sup>3</sup>. The term 'spadix' is applied to the central closed endodermic structure representing the manubrial cavity in a gonophore or sporosac. It is sometimes branched, e.g. in *Cordylophora*. An alteration in the place and mode of origin of the generative products usually accompanies these changes, but not always to the same degree in the two sexes: see pp. 767-8, *post*.

As to the *Hydrocorallina*, the generative products of *Millepora* are developed in small capsules in the course of the coenosarcal canals; of *Stylasteridae* in a sporosac formed in the course of the same canals and lodged in an ampulla or cavity of the coenosteum<sup>4</sup>.

Asexual reproduction takes place by fission or gemmation. Fission is rare. It occurs in the hydroid *Protohydra Leuckarti*, where it is binary and transverse; in *Polypodium*, where it is longitudinal (*infra*, p. 766); and in certain Leptomedusans, *Stomobranchium mirabile* (= a young form of *Mesonema coerulescens*), in *Phialidium variabile*, and *Gastroblasta Raffaelei*.

<sup>1</sup> The medusae produced by *Syncoryne (Coryne) mirabilis* are said by L. Agassiz to be set free in March, but in April to be sessile and more or less arrested in development; cf. Allman, *op. cit. ante*, p. 278, and *lit. cited*. *Campanularia volubilis* is said by Du Plessis to bear medusae in summer, gonophores in winter (A. N. 41 (2), p. 412). See also Wagner, *Wirbellosen des Weissen Meeres*, Leipzig, 1885, p. 78.

<sup>2</sup> The *Meconidium* of *Gonothyrea* is a medusoid which is not detached; and the male is more arrested than the female. See Weismann, *op. cit. ante*, pp. 135-7, 139, and Allman, *op. cit. ante*, pp. 55-8, Fig. 28.

<sup>3</sup> The Tubularian *Dicoryne conferta* has a remarkable free swimming ciliated sporosac with two solid tentacles attached to the base of the spadix. The spermatozoa surround the spadix, but in the female there are only two ova, one on either side of it. See Allman, *op. cit. ante*, p. 226. In *Sertularella polyzonias* the gonophore is suppressed and the genital products ripen in the walls of a blastostyle: see Weismann, *op. cit.* p. 166, note p. 252, p. 265. On the nature of the blastostyle cf. p. 757, *ante*, and note 2.

The development of a sporosac after discharging the generative products into a hydranth has been described in *Cordylophora* by Allman, and L. Agassiz has observed a similar case in *Rhizogeton*: cf. Allman, *op. cit.* p. 204. Some doubt is perhaps permissible on the subject.

<sup>4</sup> Quelch states that there are ampullae in *Millepora Murrayi*: see Reef Corals, Challenger Reports, xvi. p. 192; or *Nature*, xxx. p. 539.



In the first-named the manubrium divides, and then the bell. In *Phialidium* a second manubrium appears as a bud at the base of the first, and fission then takes place between the two. A third may be similarly formed in the course of a radial canal. *Gastroblasta* has the number of manubria increasing progressively by budding on the radial canals, and fission occurs between the oldest and second oldest. Sexual products were observed in the two last-named<sup>1</sup>. The detachment by fission of the end of a growing branch has been observed in some *Campanularidae*: and in one instance the fixation of the detached portion, the formation of a hydranth, and subsequently of a colony<sup>2</sup>. Gemmation is universal in the hydroid form, *Protohydra* only excepted: and is not uncommon in Medusae, for the most part belonging to the *Anthomedusae*. In *Hydra*, *Microhydra*, and *Tiarella* the hydroid form thus produced is set free, but the first-named may be temporarily colonial, the individual not only producing more than one bud, but its buds other buds in their turn before detachment. In all other instances the hydroid buds remain attached to one another, constituting a colony. They originate from the hydrocope of the first hydranth, and afterwards from the coenosarc in a definite manner. The buds in a hydroid colony which develop into sexual zooids may take origin from the hydrorhiza when the hydranths do so, from the branches of a colony, then occupying either the same or a different position to a hydranth, from the peduncle of a normal hydranth, from its hydrocephalis, from a blastostyle, or from a special peduncle of unknown significance (*Tubularia*, *Corymorpha*, *Monocaulus*)<sup>3</sup>. The buds borne by a Medusa invariably develop into a Medusa: they may be situated on the manubrium, on the tentacles or at their bases, on the radial canals, or circumferential canal, and gemmation may be continued through more than one generation.

The sexes are as a rule separate. *Hydra* and *Eleutheria* are hermaphrodite: abortive ova occur in the male of *Gonothyrea Lovéni*. Male and

<sup>1</sup> Lang thinks that Davidoff's *Phialidium variable* is not the Medusa usually so-called, but a younger form of his *G. Raffaelei*. A species, *Gastroblasta timida*, has been described by Keller in Z. W. Z. xxxviii. pp. 622 et seqq. It has four manubria, but fission was not observed. See on the whole subject Lang's paper in J. Z. xix. 1886.

<sup>2</sup> I. e. in Allman's *Schizocladium ramosum*; see op. cit. ante, pp. 151-3, Fig. 61. Detachment has been observed in *Obelia flabellata* and *O. (Laomedea) geniculata*: Wagner, Wirbellosen des Weissen Meeres, Leipzig, 1885, p. 69. Hincks thinks it occurs in *Campanularia neglecta* (A. N. H. (4), x. 1872, p. 391), and Allman in *Corymorpha nutans* (op. cit. p. 153). Hydranths have been observed with several oral cones in *Cordylophora lacustris* (Price, Q. J. M. xvi. 1876), and two hydranths on the same peduncle occasionally occur in *Hydractinia echinata* (Wagner, op. cit. Pl. I. Fig. 8); whether fissiparously produced or not is unknown.

<sup>3</sup> The medusa sometimes takes origin in the same place as does a hydranth, e. g. from the peduncle of a hydranth, the Tubularians, *Dendroclava*, *Bougainvillea*, some species of *Perigonimus*; from the stem of a colony, *P. muscoides*; from the hydrorhiza, some species of *Perigonimus*, the Campanularian *Eucopella*. As a rule it originates from the hydrocephalis of a hydranth, or from a blastostyle as in *Podocoryne* and most *Campanularidae*.

female gonophores grow on the same blastostyle in *Myriothela*, on the same stem of certain Sertularians, or on stems of the same colony in the Tubularian *Dicoryne*. The ovary may consist of but one ovum, e.g. in *Eudendrium*, *Campanularia flexuosa*; or of many, and in the latter case a certain proportion of the ova, e.g. in *Coryne pusilla*, *Tubularia mesembryanthemum*, *Plumularia Halecioides*, or all save one, e.g. in *Hydra*, *Tubularia indivisa*, *Myriothela*, undergo atrophy, and the products to which they give origin serve as food-material to the remainder. A vitelline membrane is absent in all ova borne by a Medusa, and as a rule when development takes place within a gonophore or in an acrocyst. When present it may be delicate, thickened, or shell-like as in *Corydendrium*, *Pennaria*, *Eudendrium capillare*. Impregnation and segmentation take place in *Hydra* before the ovum is laid. Development also frequently occurs within the gonophore, e.g. in *Cordylophora lacustris*, *Campanularia flexuosa*, *Stylasteridae*, &c. The Medusae *Bougainvillea superciliaris* and *Ametrangia hemisphaerica* are viviparous<sup>1</sup>. Segmentation is total, rarely very unequal as in *Clava squamata*, where the hypoblast is represented by two cells for a long time.

The embryo is usually from the first a solid mass of cells, the outer layer of which is ciliated and differentiated as epiblast: or there is a blastocoele, as in *Hydra* and most embryos produced from the eggs of Medusae, e.g. *Eutima*, *Obelia*, *Eucope*, *Aequorea*<sup>2</sup>. In the first case the internal cells arrange themselves in a layer: in the second the blastocoele is, sooner or later, filled with cells derived (1) by the growth and fission of the cells of the wall in general (*Eucope*), and the embryo has then become a planula, or of one pole, the most usual mode, or (2) by migration inwards (*Obelia*). The gastric cavity is formed as a central slit, or the peripheral endoderm cells devour the central, as in *Clytia* and *Obelia* (Metschnikoff), or it is in *Eutima* a remnant of the blastocoele. The planula leads a free existence, and then fixes itself, either by one pole or by its side. In the first case it lengthens and the mouth and tentacles appear at the free end, or it flattens into a disc, from the centre of which rises a bud, the future hydranth (*Clytia*, *Obelia*, *Eucope*, *Eudendrium*, *Campanularia*, *Plumularia*, *Sertularia*): in the second, either one end becomes hydrorhiza, the other grows and becomes the hydranth (*Tiara*, *Eutima*), or the hydranth-bud appears laterally (*Turritopsis nutricula*), or it forms a ramified and anastomosing hydrorhiza, from which buds are developed (*Turritopsis (Oceania) armata*). In *Mitrocoma Annae* the planula may become either hydrorhiza alone or hydrorhiza

<sup>1</sup> Cf. Wagner, *Wirbellosen des Weissen Meeres*, p. 74; Allman, *Nature*, ix. p. 74. In the last instance the planula is oval and non-ciliated. On the species, which is perhaps fissiparous, see Haeckel, *System*, p. 636.

<sup>2</sup> According to Metschnikoff, two or three blastulae may fuse in *Mitrocoma Annae*; but development proceeds normally.

plus hydranth. There may or may not be a perisarc. Peculiarities are,—the transformation of the superficial cells completely or incompletely into protective envelopes in *Hydra* (p. 327), and the development in *Tubularia* of the planula, while within the gonangium, into an Actinula, a hydroid form with a circle of tentacles, or sometimes, as in the adult, two circles, which leads a free existence for a short time before fixation. The planula of *Myriothela* develops similarly within the vitelline membrane, but the Actinula possesses a set of scattered provisional capitate tentacles in addition to a certain number of permanent tentacles.

The freshwater *Hydroidea* are the genera *Hydra* widely distributed, the American *Microhydra* from the neighbourhood of Philadelphia, the Russian *Polypodium* from the Volga (p. 766), and *Cordylophora*, European, American, and Australian. A Leptomedusan, *Laodice* (*Cosmetira*) *salinarum*, a modified form of the marine *L.* (= *C.*) *cruciata*, has been found in the variably brackish waters of the discharging canal of saltworks at Villeroy, near Cette, in S. France. *Polypodium* is in one stage parasitic (p. 766); a Leptomedusan *Mnestra parasites* lives attached by its manubrium and tentacles to the neck of the pelagic Gastropod *Phyllirhoe*. The marine *Hydroidea* are denizens of all seas; the genera are widely distributed, the species sometimes extremely restricted in their range. They live at very various depths from the surface downwards: the greatest number of forms between the lowest tide-mark and fifty fathoms. Some, however, only occur below one hundred fathoms. At very great depths they appear to be extremely rare. The colonies are as a rule of small or moderate size, but occasionally attain a great height, e. g. a Plumularian in the Pelew Islands that of a man. Deep water forms appear to be larger than those from shallow water. A *Monocaulus*, seven feet long when fully extended, has been dredged in nearly 3000 fathoms in the North Pacific. The colonies are attached to fixed or floating objects, and certain genera always affect a particular habitat, e. g. *Hydractinia* and *Podocoryne* a Gastropod shell tenanted by a Hermit Crab. Some usually grow upon other Hydroids, e. g. some species of *Lafoëa*; *Amphibrachium* within the canal system of the sponge *Euplectella*<sup>1</sup>. The Medusae are frequently carried by currents from the localities where their hydroid form grows. A few appear to swim habitually at a considerable depth below the surface. As to fossil forms a *Hydractinia* with calcareous skeleton is found in the Chalk, and in Tertiary strata (see note 1, p. 756, ante). There are some other allied (?) calcareous forms supposed to be Tubularian. The Silurian and Devonian *Stromatoporidae* perhaps belong to the same sub-order. The Campanularians are doubtfully represented by the *Rhabdophora* s. *Graptolithidae*, which commence in the Upper Cambrian and die out in the Upper

<sup>1</sup> Carter has found an undetermined hydroid in the sponge *Reniera* (A. N. H. (4), x. p. 50). See note 2, p. 781, post.

Silurian, and by a few other Silurian and Devonian forms. *Sertularella polyzonias* occurs in Miocene strata in Ayrshire: a Milleporan (*Porosphaera*) in the Chalk: *Stylaster* in Miocene strata.

The freshwater *Polypodium hydriforme* is a parasite in its first observed stage in the ova of the Sterlet (*Acipenser ruthenus*). It is then a cylindrical tube or stolon which gives origin to 16 buds, each of which divides once, forming 32 in all. Each bud acquires 24 hollow tentacles. The stolon breaks up when transferred to fresh water. The free *Polypodium* is 2 mm. long and  $4\frac{1}{2}$  mm. wide. It divides by longitudinal fission into 2 parts with 12 tentacles apiece, and these in turn into 2 with 6 tentacles apiece. All these forms grow, acquire 24 tentacles, and then divide again. *Polypodium* moves from place to place by means of its tentacles, on which it stands like stilts. Ussow, A. N. H. (5), xviii. 1886.

The hydranth is frequently detached in *Tubularia*, and may live some time in this condition, a new hydranth developing as a bud in its place. The two Tubularian genera *Nemopsis* and *Acaulis* are considered by Allman to be similarly detached hydranths, and the Hydroid of the former has been discovered by Brooks (Studies Biol. Lab. John's Hopkins Univ. ii. p. 468). A complete absence of hydranths during winter has been observed in *Eudendrium*, *Cordylophora* and *Hydractinia*, but the coenosarc persists and develops buds again at a more favourable season<sup>1</sup>. So too, when the destruction of Campanularidan colonies by parasitic Protophytes takes place, the hydrocope of certain hydranths may grow suddenly for an inch or so, and then develops a new colony at a higher level (von Lendenfeld, Z. A. vi. p. 42). The power of repairing injuries is very great, and propagation of the individual or colony by artificial section is possible, as in *Hydra* and *Cordylophora*.

A few points in the histology of the hydroid colony may be noted. The ectoderm forms an unbroken layer on the surface of the hydrophyton in the *Hydractinidae* and *Hydrocorallina*. Ectodermal ganglion cells occur on the arms, chiefly towards their bases (cf. *ante*, p. 329); also, but more sparingly as a rule, on the body, occasionally aggregated at its base, and even present in numbers in the coenosarc (*Eudendrium ramosum*). Sense cells are present, and the sense hairs may have great length as in the palpocils of *Syncoryne*. The ectodermal muscle cells, epithelial or sub-epithelial, are always disposed longitudinally. In the coenosarc the ectoderm is usually unilaminar, but it may be multilaminar as in *Eudendrium ramosum*, and its cnidoblasts are few and devoid of cnidocils. It is usually said not to contain muscle-cells, but they have been detected in *Campanularia* and *Plumularia*, where they cause slow rhythmic contractions of the cavity of the tube, and they are probably present in other instances. It secretes the perisarc, and is either in contact with it at all points or only here and there by cells with a striated structure; cf. von Lendenfeld, Z. W. Z. xxxviii. p. 534, and for the chitinous cells, *ibid.* p. 520. Where perisarc is to be absorbed the ectodermal cells enlarge; see *op. cit.* p. 542, and Weismann, Entstehung der Sexualzellen, &c. pp. 178 and 182. The other constituents of the ectoderm are epithelial cells, interstitial cells, and gland cells. As to the endoderm, ganglion and sense cells have been found in the hypostome of *Eucopella* and of other Campanularians (von

<sup>1</sup> This phenomenon is perhaps not uncommon: see Hincks, *op. cit.* p. xlv. On *Eudendrium* see Weismann, Entstehung, &c. p. 102; and on *Tubularia*, Allman, *op. cit.* p. 403.

Lendenfeld, Z. A. vi. p. 70). The notochord-like axial cells of the tentacles (p. 329) often become irregularly arranged in the adult, and they are in many instances united by a basal ring of similar cells, e. g. in *Tubularia*, *Eucopeella*. Other elements are epithelio-muscle cells, the processes of which take as a rule a circular direction, absent in *Campanularidae* and *Sertularidae*, except in the hypostome, e. g. of *Eucopeella* (? others); of glandular absorbent and excretory cells, cf. von Lendenfeld, Z. W. Z. xxxviii. pp. 522-5. Whenever muscle cells are well developed, the endoderm is thrown into prominent longitudinal rugae, at least in the contracted state of the hydranth. These rugae are more feeble in other instances.

The ambulatory medusae *Clavatella* and *Eleutheria* (see note 4, p. 759) have branched tentacles. The basal or first branch ends in *Clavatella* in a sucker, or in *Eleutheria* in a knob laden with cnidoblasts. The swimming form *Cladonema* has three similar adhesive processes to each tentacle, and Hincks has observed it reverse its bell and adhere by the processes in question while fishing for food with the manubrium (A. N. H. (4), x. 1872, p. 392<sup>1</sup>). The reversion and atrophy of the bell when the sexual products are ripe has also been observed in some instances, e. g. *Cladonema* (Allman, Gymnoblasic Hydroids, p. 359; Hincks, British Hydroid Zoophytes, i. p. xxviii.). Solid tentacles, i. e. with an endodermal axis, occur in some *Leptomedusae*, e. g. in *Obelia*. The exumbrellar ridges of *Eucopeella* have been examined by von Lendenfeld, who finds that they consist of a meridional nerve with ganglion cells, young cnidoblast cells, and an overlying epithelium of cnidoblasts and sense cells. The otocyst in the same medusa is connected to both nerve-rings, and contains a basal ganglion.

The sexual products originate from interstitial ectoderm cells in many medusae after they are detached, or even before, e. g. *Perigonimus*. In some species of *Obelia* they migrate from their place of origin at the base of the manubrium to the radial canals (Hartlaub). The ova pass into the endoderm, wander through it, and ripen partly in the endoderm, partly in the ectoderm of the radial canals. The male cells, however, ripen exclusively in the ectoderm. The ova of the medusa of *Podocoryne* originate in the gonophore-bud.

With the degeneration in development of the sexual zooid (p. 762, *ante*) the place in which the sexual cells first originate is altered. They may arise in the entocodon, e. g. in *Tubularia* (2), male *Clava* (3), *Pennaria* (1)<sup>2</sup>; in the endoderm of the gonophoral bud, e. g. *Coryne* (3); or in the coenosarc, but in different positions, e. g. at the place of origin of the gonophore itself, *Hydractinia* (3), male *Cordylophora* (5), female *Clava* (3), in the budding zone of the hydranth, from the hydrocope of which the blastostyle buds, male *Eudendrium racemosum* (3), *Gonothyrea* (1), *Campanularia* (female 4, male 5), or in a budding zone of a principal hydranth of the stem, female *Cordylophora* (5), and *Eudendrium* (5). They sometimes originate in the hydrorhiza, as in *Eudendrium capillare* (5) and *Eucopeella* (1). The sexual cells themselves in these cases are very commonly cells of the ectoderm, and they may migrate in it from one spot to another, e. g. female *Cordylophora*, male *Campanularia flexuosa*. They may pass into the endoderm,

<sup>1</sup> A partial reversion has been noted by Allman in a Medusa, *Circe invertens*, Nature, ix. p. 74; see p. 760, and note p. 751.

<sup>2</sup> The numbers in brackets correspond to the numbers affixed to the paragraphs on p. 762, and how what stage of degeneration the sexual zooid has reached.

wander through it, and pass back into the ectoderm, where they ripen as in the female *Eudendrium racemosum*. But they very frequently appear first in the endoderm, and wander through it to the place where they ripen in the ectoderm, e. g. female *Clava* and *Podocoryne*, male *Eudendrium racemosum*, *E. capillare*, *Gonothyrea Loveni*, female *Campanularia flexuosa*, *Eucopeella*, *Halecium*, *Sertularia pumila*, *Plumularia echinulata*, *P. (Anisicola) Halecioides*, *Antennularia antennina*, *Aglaophenia pluma*. It is rare for the sexual cells to ripen in the endoderm as in *Corydendrium parasiticum* and the male *Pachycordyle Neapolitana*. It is uncertain whether or no they ever originate really in any Hydroidean from endoderm cells. Such an origin has been asserted in *Eucopeella* by von Lendenfeld; in *Plumularia fragilis* by Hamann (J. Z. xv. p. 501); in *Campanularia flexuosa* by Fraipont and de Varenne; but in the last-named case it is doubted by Weismann (Entstehung, &c. p. 147), as it is in *Gonothyrea* (p. 133). The young cells lying in the endoderm may be immigrant ectoderm cells.

The forms of sexual zooids 1-4, p. 762, are to be regarded as degenerate medusae, not as forms tending to acquire a medusan structure. It is difficult to explain the presence of rudimentary and peculiar medusan organs, e. g. entocodon, gastral lamella, on any other hypothesis (cf. Weismann, Entstehung, p. 255), particularly when coupled with the remarkable facts above detailed concerning the sexual cells. Moreover, Hydroids obviously genetically related, may vary extremely in the character of their sexual zooids, e. g. *Podocoryne* has free medusae; *Hydractinia* sessile gonophores with gastral lamella, &c.; and in *Oorhiza* the female sporosacs, the only ones known, are seated in groups on the hydrorhiza, and have apparently a very simple structure (Mereschkowsky, A. N. H. (5), i. 1878, p. 325; Wagner, Wirbellosen des Weissen Meeres, p. 71); or again *Coryne* with sessile gonophores, *Syncoryne* with free medusae. Variations of this character and the mode of origin of the sexual cells, prove also that the sporosac (5, p. 762) is a degenerate medusa, at least in the *Campanulariae*. And Weismann concludes that the same is the case with the sporosac of the Tubularians (cf. Entstehung, pp. 244-252 and p. 291). Their frequent origin from a blastostyle favours the same view (op. cit. pp. 246-7). The physiological explanation of these changes is probably to be found in an earlier ripening of the genital products, a process benefiting the race and lessening the danger of its extinction (Weismann, pp. 262-65). See on the whole subject the work of Weismann's already quoted, or Moseley's abstract in Nature, xxix. 1883-4.

The ectoderm on the sides of the blastostyle in the *Campanulariae*, appears to be frequently multilaminar, and to invest the gonophores more or less loosely. The loose layers are termed gubernaculum by Allman. In *Eucopeella* the medusoid acquires a chitinoid capsule secreted by the ectoderm filling the cavity of its peculiar blastostyle<sup>1</sup>. The ova of the Tubularian *Wrightia (Atractylis) arenosa* undergo development in a gelatinous mass secreted by the walls of the sporosac. In many Campanularians, e. g. species of *Sertularia*, *Calycella*, a gelatinoid laminate receptacle, or acrocyst, is formed by the gonophore (? the loose layers of ectoderm) and passes with it out of the gonangium: the ova are fertilised and develop in it, the gonophore undergoing regressive metamorphosis (Allman, Gymnoblatic Hydroids, p. 48; Weismann, op. cit. p. 170). The Sertularian genus *Diphasia* has

<sup>1</sup> In *Campanopsis (= Octorchis)* the Medusa bud is protected by a layer of ectoderm cells, not by a perisarc layer, as is usually the case in Tubularians: see Claus, Arb. Zool. Inst. Wien, iv. p. 94 (p. 6 of paper).

this acrocyst protected by processes of the gonangium containing hollow extensions of the tissues of the blastostyle, and together constituting a marsupium (Allman, op. cit. pp. 50-3; Hincks, British Hydroid Zoophytes, p. 244). The Anthomedusan *Eleutheria* has a cavity aboral to the atrium and opening into the bell by six interradial canals. The genital products are formed in the walls of the cavity, which is also a brood-pouch (Hartlaub). So too in *Pteronema* and *Clavatella*<sup>1</sup>.

Brooks has shown in the planulae of the Anthomedusan *Turritopsis* and the Leptomedusan *Eutima*, the presence of an ectodermal invagination, which is afterwards evaginated and exudes a cement attaching the planula to some foreign body (Mem. Boston Soc. Nat. Hist. iii. p. 402-3).

A typical or monoproniid Graptolite, belonging to the section *Graptoloidea*, consists of a hollow chitinoid coenosarc tube or perisarc, which bears along one of its aspects a row of tubular offsets, the cells or thecae. The tube is usually linear, rarely leaf-like; straight or curved; simple or branched; its walls composed of three (?) layers. A solid or hollow chitinoid rod (=virgula) is imbedded in its walls on the aspect opposite to the thecae. The proximal end of the coenosarc is connected to a pointed dagger-like germ or sicula, from which it appears to originate, the pointed end being imbedded in the coenosarc in some families, the broad in others. Two such organisms may be united back to back by their virgular aspects, as in the diproniid Graptolites, or even four, as in the *Phyllograptidae*. The virgula often projects in these compound forms, more rarely in the monoproniid, far beyond the distal end of the coenosarc; and it may project slightly, as the radicle, at its proximal or sicular end. Specimens of diproniid Graptolites have been found bearing large oval or triangular capsules, supposed to be gonangia. Oval or bell-shaped capsules—*Dawsonia*—are often found mingled with the Graptolites, and have been supposed to be detached ovarial capsules (Nicholson). In the *Retioloidea*, the second section of *Graptolithidae*, there is no sicula; the outer layer of the perisarc is thin, the two inner reduced to a network; there are two opposite rows of thecae, but the coenosarc tube is common to both; the two virgulae have either coalesced, or are opposed to each other, but in both instances situate in the perisarc. The colony is free in both sections.

There is no indication as to what the animal of the Graptolite was like. Allman has suggested that it resembled a Plumularian machopolype, inasmuch as the thecae, like those of machopolypes, are not constricted at their bases as are those of hydranths. This argument is not necessarily conclusive, for the thecae of *Cuspidella* (Hincks, op. cit. p. 209), or of *Trichydra* (Id. p. 216, Fig. 26) are simple tubes. The virgula is a structure unknown in any living Hydrozoan. The second stem, found by Jickeli in *Anisicola* (*Plumularia*) *Halecioides*, which bears no hydranths itself, but supports the main stem to which it is connected at intervals, is hardly comparable to it; see M. J. viii. p. 636. Another difficulty is the fact that the virgula extends far beyond the theca-bearing region of the coenosarc. Jickeli suggests (loc. cit. pp. 668-71) that the Graptolites are possibly Octactinians. There are no known Antipatharians with a chitinoid perisarc covering the outside of the organism; but, supposing there were, the virgula is not altogether unlike the chitinoid tubular skeleton of *Antipathes*; cf. p. 737. On the other hand no known Anthozoa possess special enlarged generative capsules; nor do the Polyzoa, a group to which the Graptolites have been sometimes assigned.

<sup>1</sup> Cf. note, p. 759, *ante*, and Haeckel, 'System,' pp. 101, 105.

The *Siphonophora*, the third order of *Craspedota*, are pelagic and colonial. The various parts which may enter into the composition of a colony<sup>1</sup> are as follows. (1) The polypite or gastrozoid, universally present, usually attached to the coenosarc of the colony by a longer or shorter pedicle, and consisting of three regions, a basal with thickened ciliated ectoderm containing cnidoblasts, a central somewhat dilated, and a terminal oral ciliated portion, extremely changeable in shape. Cnidoblasts are to be found round the mouth. The endoderm cells are vacuolate, and those of the middle region are pigmented, produced into longitudinal ridges<sup>2</sup> or villiform processes. (2) *Hydrocysts* or *feelers* (= Taster of German writers), absent in *Calycophoridae* and *Discoideae*. These structures are polypites in which the distal or oral extremity is imperforate and usually armed with cnidoblasts<sup>3</sup>. The pedicle is absent or short, and the three regions (*supra*) are not differentiated, no trace of the basal ectodermic thickening being even discernible. The endoderm is vacuolate and rarely elevated into ridges (*Apolemia*). The hydrocysts are represented in the *Discoideae* by small zooids (blastostyles) with mouths. (3) *Tentacles*. These structures in the *Discoideae* are simple and tubular; in *Porpita* dilated terminally and provided with a number of short capitate processes. The large tentacles of *Physalia* attain sometimes the length of many feet. Each tentacle, whether large or small, consists of a conical hollow sac (? = hydrocyst) covered with cnidoblasts, a long hollow filament attached to the base of the sac but connected by a membranous expansion with its side. The first section of the filament is coiled from side to side, but the greater portion of it hangs freely. One of its aspects is covered with transverse hollow reniform elevations in which cnidoblasts are aggregated. The tentacles of other *Siphonophora* are, with the partial exception of *Athorybia* and *Abyla*, attached to the pedicles of the polypites, on a special elevation of ciliated ectoderm containing cnidoblasts, from which new 'nettle batteries' are derived in growth. They are branched except in *Apolemia*, and each branch terminates in a single nettle battery, the structure of which is often extremely complicated and characteristic of a genus, or even species. The tentacles of the hydrocysts are unbranched. (4) The sexual zooids or gonozooids are medusiform. In the *Discoideae* they are medusae, and are borne in numbers upon blastostyles (gonoblastidia) which are disposed in a

<sup>1</sup> See p. 775, *post*, on the character of the colony.

<sup>2</sup> They are due to the contraction of endodermal circular muscles.

<sup>3</sup> An opening is present at the apex of the hydrocyst of *Halistemma tergestinum* (*pictum*) and of *Physalia* (?). So too in a young *Agalmopsis* (*Agalma*) *Sarsii*, where it afterwards closes. The apex of the hydrocyst is pigmented, and it has been observed that irritation of the animal in *Forskalia* causes this pigment to be shed into the water, giving the latter an opaque and red tint. The contained fluid is highly albuminous and dense, and probably serves to keep the walls of the hydrocyst tense, and thus render it more sensitive (Korotneff). Hydrocysts occur among the nectocalyces in *Apolemia* but not in other *Siphonophora*.



zone round the large central gastrozoid. The medusa of *Veleva* is known as *Chrysomitra striata*; it is a quarter of an inch in diameter, has a single tentacle, and its generative products are developed in four groups on the manubrium as in *Anthomedusae*<sup>1</sup>. The female zooid of *Physalia* is probably detached as a medusa. In all other instances the zooid is a medusoid: it has typically four radial canals, a circumferential canal, and an imperforate manubrium or spadix which bears the sexual products. The *Calycophoridae* have many ova, the *Physophoridae*<sup>2</sup> a single ovum. The spadix in the latter grows round the ovum, and its cavity becomes reduced to a system of branched canals, sometimes confounded with the radial canals. A velum is present in the sexual zooid of the Diphyzooid (p. 773) but not in other instances<sup>3</sup>. In the Calycophorids *Hippopodius* and *Epibulia* (= *Galeolaria*) and in *Physophoridae*, the bell itself consists only of three layers, an endodermal lamella bounded by two ectodermal, an outer and inner, and the bell cavity is small. The zooids are numerous in *Physalia*, *Physophoridae*, and the Calycophorid *Hippopodidae*, developed in grape-like bunches on the pedicle, or as in *Physalia* and *Physophora* extending up the sides, of the hydrocysts, male and female in connection with the same hydrocyst, or as in *Agalma rubrum* with different hydrocysts. In the *Diphyidae* they are developed successively one after another on the pedicles of the polypites. The zooids, male and female, are detached in *Hippopodius* and *Epibulia*, or the male only is so, e. g. in *Physophora*, *Halistemma*, *Forskalia*, swimming by means of the cilia covering the bell. The sexual zooid in a Diphyzooid discharges the sexual products, and is detached when its successor is ready to replace it. The colonies are usually hermaphrodite. *Abyla pentagona* and some species of *Diphyes*, however, are of separate sexes. (5) The *hydrophyllia* or *bracts* (= *Deckstücke*), absent in *Discoideae*, *Physalia* and *Hippopodidae*, are protective zooids of a leaf-like character but of various shapes, attached by a short pedicle either to the coenosarc (*Physophoridae*) or to the pedicles of the polypites (*Calycophoridae*). They consist of a lamina of mesoglaea covered by ectoderm, in which cnidoblasts are frequently to be found at the apex or projecting angles of the hydrophyllium. They contain a central endodermic canal from which, as in *Crystalloides* (*Agalma rigidum*), a process may extend to the lateral angles. (6) *Nectocalyces* absent in *Discoideae*, *Physalia*, *Athorybia*, and *Rhizophysa*. They resemble a craspedote Medusa with four radial canals, minus a manubrium, mouth and tentacles<sup>4</sup>. (7) The *pneumatophore* or *float*, an air-

<sup>1</sup> But see Metschnikoff, 'Medusologische Mittheilungen,' Arb. Zool. Inst. Wien, vi. p. 238 (p. 2 of paper). The female, according to him, only brings one ovum to maturity.

<sup>2</sup> This term is used in the text to denote the sub-order, not the family.

<sup>3</sup> Chun's genus *Lilyopsis* is no exception to this statement, for the groups of zooids are not detached; see note, p. 773, and SB. Akad. Berlin, 1886, p. 688.

<sup>4</sup> The absence of a manubrium is a great peculiarity; it has been observed by Mereschkowsky as a constant occurrence in certain species of *Bougainvillea*. See A. N. H. (5), iii. 1879.

vesicle distinctive of *Physophoridae*, *Physalidae*, and *Discoideae*. The float is in the last-named circular and slightly concavo-convex in *Porpita*, rhomboidal with a diagonal solid vertical crest in *Verella*; in both genera composed of a series of concentric chambers which communicate in *Verella*, have chitinous walls, and are covered by coenosarc. The chambers open externally on the upper surface by apertures, restricted in number in *Verella* and placed close to the base of the vertical crest, very numerous in *Porpita*, urn-like in shape, ranged upon the summits of radial ridges, and becoming closed in the central chambers by the deposition of fresh chitinous layers. The lower surface of the float in *Porpita* has hollow radiating ridges from which, and from the central chamber, innumerable pneumatic filaments depend, passing into the walls of the polypite and blastostyles. The corresponding filaments in *Verella* are few and branched (?). The float of *Physalia* is large and fusiform, one end long and drawn out, with an aperture into the contained chitinous saccule. In *Physophoridae* it is a small more or less globular body. It consists essentially of the expanded proximal portion of the coenosarc which has typically, e. g. in *Forskalia Ophiura*, a medusoid structure. The part corresponding to the manubrium forms an air-vesicle, and what should answer to the cavity of the bell is occupied by a brittle cuticular lamina formed on the surface of the manubrium, which is represented in the species named by two layers of cells. The cuticular structure in shape resembles a retort, mouth downwards. The mouth corresponds to the spot where the manubrium passes into the wall of the bell, which in this instance contains seven radial canals opening basally into the cavity of the coenosarc. The typical structure is more or less disguised in most cases. The cavity of the air-vesicle is said to open at its apex to the exterior in *Rhizophysa*<sup>1</sup>.

The coenosarc in the *Discoideae* and *Physalia* simply invests the float. The zooids in the former are spread over one, the ventral aspect, a large polypite s. gastrozooid in the centre surrounded by a zone of blastostyles, and these in turn by a zone of tentacles or dactylozooids. The coenosarc of *Physalia* is produced into a prominent crest, vertical and exposed above the water in the natural position. The zooids are aggregated in one or more ventral masses, and the float may in some species attain a length of eight inches. Among *Physophoridae* the coenosarc of *Athorybia* is almost globular, of *Physophora* somewhat elongated, but the portion bearing the zooids is short and saccular. In all other *Siphonophora* it is elongated and tubular. The float of *Physophoridae*, or the nectocalyces of *Calycophoridae*, occupy its proximal end,

<sup>1</sup> The development of the air-vesicle, which was first observed by Metschnikoff, corresponds, as he stated, with the view that the float is a Medusoid structure. A solid ingrowth of epiblast—an entocodon, takes place as in the development of a Medusa where it forms the ectoderm of the sub-umbrella and manubrium. In the case of the float it gives origin to the air-vesicle and its walls.

The nectocalyces of the *Physophoridae*, when present, come next to the float. The rest of the coenosarc carries the other zooids which are arranged in distinct groups in the Physophorid *Apolemia*, and in all *Calycophoridae*. Segments bearing several groups of zooids are detached in *Apolemia*, and single groups (bract, polypite, tentacle) are set free in some species of *Diphyes*, in *Abyla*, *Monophyes*, and *Muggiaea*. These single groups are known as Diphyozooids, and have received special names, e.g. *Diplophysa* (*Monophyes*), *Eudoxia*, &c. (*Diphyes*). The Diphyozooid develops a succession of sexual zooids. The nectocalyces and zooids are developed along one and the same aspect of the coenosarc tube; but, owing to the fact that it is spirally twisted in *Physophoridae*, they appear to be disposed in two or more rows, and the real arrangement is not evident. The twist of the nectocalycine region is in the opposite direction to that of the rest of the coenosarc. New nectocalyces in the *Physophoridae* appear distally to the float: the other zooids distally to the nectocalyces both in *Calycophoridae* and *Physophoridae*<sup>1</sup>. The coenosarc tube is eminently contractile. Its ectoderm develops a circular and a longitudinal layer of muscle cells, its endoderm a circular.

The colonies of *Physophoridae* are mostly of moderate size, but *Agalma elegans* attains a length of four feet, *Apolemia uvaria* of twenty to thirty feet. The *Calycophoridae* are small, the largest, e.g. *Diphyes*, is a few inches long, *Galeolaria* two feet or less. The colony is retractile within a furrow or canal formed at the side of the distal nectocalyx in *Diphyes* and *Abyla*; by the two nectocalyces in *Praya*; or into a pit in the side of the single nectocalyx in *Monophyidae*. The *Siphonophora* are found in the Mediterranean and the open seas, sometimes at considerable depths (eight hundred to fifteen hundred fathoms or even more). *Physalia* is brilliantly coloured: *Velella* and *Porpita* are greenish blue. The majority are hyaline with spots of colour on the float, the polypites, hydrocysts, and tentacles.

The ovum appears to be impregnated and to develop while floating freely. It is devoid of a membrane save in *Hippopodius*. Segmentation is regular, and results in the formation of a solid ciliated planula with large vacuolated central cells. The

<sup>1</sup> It appears that in the *Diphyidae* the functional nectocalyces are constantly replaced by others. The new nectocalyx is produced distally to the old, not proximally as in *Physophoridae*. See Chun, SB. Akad. Berlin, 1885, pp. 521 et seqq.; and Korotneff, Mitth. Zool. Stat. Naples, v. 1884, pp. 279 et seqq.

The *Hippopodidae* differ from other *Siphonophora* in the fact that the nectocalycine section of the coenosarc is bent parallel to the section bearing the remaining zooids, and the point at which the flexure takes place is also the one at which the rudiments of both nectocalyces and other zooids are formed. Other notable peculiarities in the Order are the presence of hydrocysts among the nectocalyces of *Apolemia*, and the addition of a nectocalyx to each group of zooids in certain species of *Praya*, hence erected by Chun into a genus, *Lilyopsis* (SB. Akad. Berlin (1), 1885).

permanent hypoblast is differentiated from this central mass of cells as a superficial layer of cells beneath the epiblast, the central cells undergoing gradual absorption. In the Calycophorid *Galeolaria filiformis* = *Epibulia aurantiaca*, a nectocalyx, a polypite, tentacle, hydrophyllium are formed. The second nectocalyx appears on the pedicle of the first group of zooids, i. e. on the developing coenosarc. The buds of a second polypite, tentacle, hydrophyllium, grow out, and the colony is established by the development of successive groups of zooids in the order named. The cavity of the first nectocalyx in *Hippopodius* is remarkably small, but its mesoglaea extends as a cap over one extremity of the planula. A provisional hydrophyllium is developed in the first instance in most *Physophoridae*,—*Athorybia*, *Physophora*, *Agalmopsis*, and *Crystallodes*, but not in *Halistemma*. The float appears next in succession; see note, p. 772, ante. *Agalmopsis* and *Crystallodes* have a set of provisional hydrophyllia (the so-called *Athorybia*-stage), and the tentacle knobs of the young Physophorid are different in character to those of the adult. *Halistemma* has a single provisional nectocalyx. A portion of the planula persists for some time as the yolk-sac of *Crystallodes*.

A well-developed diffuse system of ganglion cells has been detected in the *Discoideae*. Ganglion cells occur also in the tubular coenosarc of some other *Siphonophora*. The nervous elements are especially differentiated in *Physophora*. Remarkable branched cells, 'neuro-muscular cells,' in connection with the longitudinal musculature of the coenosarc, have been described in some forms by Korotneff; cf. Mitth. Zool. Stat. Naples, v. p. 235, Pl. 14, Fig. 13.

The Diphyozooid (*supra*) swims by means of the medusiform sexual zooid. If it is derived from a hermaphrodite colony, it is said nevertheless to be itself unisexual. But one derived from the unisexual *Abyla pentagona* has been observed by Chun to develop first a male and then a female zooid.

The sexual products of the Discoidean medusa are developed *after* the medusa is detached, probably from the ectoderm of the manubrium; in all other *Siphonophora* properly examined from the endoderm: in *Epibulia* (= *Galeolaria*) in the rudiment of the gonophore: in *Hippopodius* in the bud of the future peduncle of the bunch of gonophores: in *Forskalia* in the rudiment of the peduncle: and in *Agalma* in the rudiments subsequently differentiated into several gonophores. The young sexual cells are not sub-epithelial at first, as they are in those *Hydroidea* where they appear in the endoderm, but they project into the cavity of the bud: but whether or no they really originate in the first instance from endoderm cells is not known. The sexual cells in the male wander into the ectoderm of the manubrium: so too in the female of the Calycophores named, but the endoderm subsequently grows round each ovum, furnishing it with an incomplete follicle placed to the outer aspect. But in the Physophores *Forskalia* and *Agalma* the single ovum is arrested in the endoderm, and surrounded by the spadix as stated p. 771.

Chun has propounded a theory of cyclical development in *Monophyidae*; e. g. (1) a form called by him *Monophyes primordialis*, which has been shown by Claus to be a larva, gives origin to (2) a second form = *Muggiæa Kochii*, in which the swimming bell of the *Monophyes* is replaced by a second and differently shaped nectocalyx, and the coenosarc develops groups of zooids: and (3) one of these groups of zooids is detached as a Diphyozooid, the sexual *Eudoxia Eschscholtzii*. Cf. Chun, SB. Akad. Berlin (2), 1882, and A. N. H. (5), xi; Claus, Arb. Zool. Inst.

Wien, v. 1884. According to Chun, the nectocalyx of the genus *Monophyes* is a second nectocalyx; cf. op. cit. (1), 1885; and Claus, Z. A. viii. 1885.

A Siphonophoran has been variously regarded (1) as an assemblage of organs, or (2) as a colony of polymorphic zooids. The former view appears to have been based upon the idea that in any Hydrozoan colony the several factors represent organs of an individual, the individual being the colony itself. Such a view cannot be regarded as any longer tenable. There can be no reasonable doubt that a Hydroid colony is an assemblage of zooids which remain connected instead of separating after their formation by budding. It is no less certain that in a Siphonophoran, the nectocalyx, pneumatophore, sexual zooid, a polypite or hydrocyst, represent so many polymorphic individuals, and that structurally a Siphonophoran is as much a colonial organism as a *Sertularia*<sup>1</sup>.

As to the special character of the colony two views have found acceptance. One is, that the coenosarc, as it is called, is the homologue of the manubrium of a Medusa, the primitive hydrophyllium, present, e. g. in the larval *Physophora*, representing the umbrella: the other that it is a floating colony, the individuals of which are connected by a coenosarcial stem or stolon the equivalent of a hydrorhiza. The former theory is supported by the analogy of such a medusa as *Sarsia* or *Willia*, in which the manubrium produces medusae by budding. The following objections, however, appear fatal to it. (1) A primitive hydrophyllium is not present in all *Physophoridae*, and is not present at all in *Calycophoridae*, and to suppose that it has been aborted in these instances is the purest assumption; (2) that the hydrophyllium itself is probably the homologue of a medusa in its entirety; (3) that it is a lateral appendage invariably of the coenosarc, and there is no reason to suppose it is anything else in the planula; (4) taking such a form as *Epibulia* (Calycophore) or *Halistemma* (Physophore), it is clear that the coenosarc is attached to the aboral apex of the exumbrella of the first nectocalyx developed, and cannot possibly represent a manubrium. For these reasons the second view mentioned above is certainly to be preferred. The coenosarc of a Siphonophoran is then comparable to the aboral stolon of the young Narcomedusan *Cunina rhododactyla*, or of *Cunocantha octonaria*, which produces buds for a stated period<sup>2</sup>. The fact that the planula

<sup>1</sup> The hydrophyllium is usually regarded as the homologue of a nectocalyx. Its central endoderm canal is furnished with accessory canals such as occur in the nectocalyces of *Diphyes* and *Praya*. The homology of the tentacle is more difficult. In the *Discoideae* it probably represents a zooid, i. e. is a dactylozooid, but in *Physalia* it is possible that the sac represents a hydrocyst. The tentacle itself is in that case attached to this hydrocyst in the same position, i. e. at its base, as is the tentacle of most other *Siphonophora*. The position is a most unusual one, but Metschnikoff states that he has observed a single tentacle attached similarly to the base of the manubrium of a Medusa (*Dipurena*). The Siphonophoran tentacle, however, is sometimes attached directly to the coenosarc as in *Athorybia rosacea*. And it may be noted that in the Physophirid *Stephanospira insignis* the hydrocyst bearing the female zooids is prolonged apically into a tentacular process with lateral branches bearing nettle-batteries; see Gegenbaur, Nova Acta, xxvii. p. 399. It is quite possible that such a structure as the tentacle of *Porpita*, beset with capitate processes, represents a zooid form from which the more complicated tentacles of other *Siphonophora* have been derived. In determining such a question, much stress cannot be laid on the origin of the tentacles from separate buds. The tentacles of a *Hydra* originate in the same manner. The place of origin of the buds is however another matter.

<sup>2</sup> See Metschnikoff, Z. W. Z. xxiv. 1874, pp. 28 et seqq., Pl. V. Figs. 4-8; and Brooks, Mem. Boston Soc. Nat. Hist. iii. (12), 1886, pp. 362 et seqq.

gives rise to more than one zooid is simply an instance of precocious gemmation, to be paralleled by the fission of the embryo of *Lumbricus trapezoides*, and possibly of the Acrasped *Chrysaora*. It may be noted also that the Hydroid planula does not always form the hydranth directly; e.g. in *Eutima* it attaches itself and produces a hydranth by gemmation, itself becoming a hydrorhiza<sup>1</sup>.

The Craspedota are classified as follows—

I. Order *Trachymedusae* = *Trachylinae* (Haeckel). Tentacles solid, sometimes replaced in part in the adult by hollow; tentaculocysts or auditory organs with endodermal axis, containing one or more otoliths. Development by metamorphosis from free hydroid larvae.

(1) *Narcomedusae*: tentaculocysts always free; tentacles at some distance from margin of bell to which they are connected by peronia; margin of the bell lobed; radial pouches to the stomach sometimes present, sometimes absent; festoon canals generally present; genital organs on the subumbrellar aspect of stomach, extending beneath radial pouches or restricted to the latter. Four families, *Cunanthidae*, *Peganthidae*, *Aeginidae*, *Solmaridae*.

(2) *Trachomedusae*: tentaculocysts either free or inclosed in capsules, which may be sunk in the mesoglaea; radial canals (4, 6, 8) and a circumferential canal; caecal centripetal canals sometimes present; genital organs on the subumbrellar aspect of the radial canals. Four families, *Petasideae*, *Trachynemidae*, *Agauridae*, *Geryonidae*.

II. Order *Hydroidea*. Hydranth small as a rule; sexual only in *Hydra*; sometimes non-colonial, but usually giving origin by gemmation to a plant-like colony; often polymorphic. An exo-skeletal perisarc usually investing the coenosarc, chitinous, sometimes calcareous forming a coenosteum. Sexual zooid or Medusa craspedote with ocelli or entirely ectodermic otocysts, produced by gemmation from the coenosarc or a hydranth; frequently more or less degenerate, see p. 762, and p. 768.

(i) *Tubulariae* s. *Gymnoblastera*. Hydranth of very variable appearance, non-tentaculate in *Micro-* and *Proto-hydra*; its tentacles varying in character and arrangement; rarely specialised as a blastostyle; sometimes non-colonial (*ante*, p. 755), and in *Hydra* locomotive; usually colonial; coenosarc of colony invested by a perisarc which never forms hydro- or gono-thecae but generally extends on to the hydrocephalis, and in *Bimeria* even invests the bases of the tentacles; Medusa bell-like, ocellate, belonging to the *Anthomedusae*, see *ante*, p. 760. *Hydra*, *Clava*, *Cordylophora*, *Coryne*, *Syncoryne*, *Eudendrium*, *Tubularia*, *Corymorpha*, *Hydractinia*, *Podocoryne*, &c.

(ii) *Hydrocorallina*. Hydranth polymorphic, either a gastrozooid (pp. 758–9) or dactylozooid (p. 758); colonial; skeleton a calcareous coenosteum with gastro- and dactylo-pores (p. 756). (1) *Milleporidae*: coenosteum arborescent or encrusting composed of a superficial living and a number of deep dead layers; pores crossed by tabulae, either scattered or in systems with dactylo-pores grouped round a central gastropore; sexual products developed in capsules of the coenosarcular canals; *Millepora*. (2) *Stylasteridae*: coenosteum arborescent; either entirely living or with deeper dead layers; pores either scattered or grouped in systems

<sup>1</sup> Brooks, *op. cit.* *ante*, p. 403; and cf. pp. 764–5, *ante*.

sometimes confined to the margins or to one surface of the colony. Colonies of separate sexes; sexual zooid, a sporosac, developed on the coenosarc tubes and contained in a special cavity or ampulla of the coenosteum, several sporosacs in one ampulla in the male, a single one in the female. Many genera, e. g. *Pliobothrus*, *Stylaster*, *Cryptohelia*.

(iii) *Campanularia* s. *Calyptoblastea*. Hydranth furnished with a single circle of filiform tentacles with a solid axis; perisarc, as a rule, forming *hydrothecae* and *gonothecae*, structures absent in *Campanopsis* (= *Octorchis*), *Eutima*, *Zygodactyla* (= *Aequorea*); a specialised blastostyle in all cases where *gonothecae* are developed; Medusa disc-like, either ocellate or vesiculate, i.e. provided with otocysts, belonging to the *Leptomedusae* (pp. 760-1, ante). *Campanularidae* with pedunculate thecae, e.g. *Campanularia*, *Clytia*, *Obelia*, *Gonothyrea*, &c.; *Plumularidae*, thecae sessile, uniserial, with machopolypes, e.g. *Plumularia*, *Antennularia*, *Aglaophenia*, &c.; *Sertularidae*, thecae sessile, biserial, e.g. *Sertularia*, *Diphasia*, *Halectium*, &c.<sup>1</sup>.

III. Order *Siphonophora*: pelagic, colonial; zooids polymorphic.

(i) *Physophoridae*: coenosarc, either short and sac-like or long and tubular, spirally twisted; a flask-shaped pneumatophore; nectocalyces as a rule present, and distal to the pneumatophore, disposed in two or several rows. Hydrophyllia and hydrocysts nearly always present, alternating regularly with the polypites and sexual zooids. Female zooid produces but one ovum. *Athorybiadae*, *Physophoridae*, *Agalmidae*, *Apolemiadae*, *Rhizophysidae*.

(ii) *Physaliidae*: pneumatophore large, fusiform, with an aperture; no nectocalyces nor hydrophyllia. Female zooid a Medusa (?). *Physalia*.

(iii) *Discoideae*: coenosarc a disc; air-vesicle composed of concentric chambers, more or fewer of which open externally; a central polypite surrounded by a zone of blastostyles, the latter by a zone of tentacles<sup>2</sup>. Sexual zooid a free medusa. *Porpita*; a vertical crest, *Velella*, young known as *Rataria*.

(iv) *Calycophoridae*: a single nectocalyx (*Monophyiidae*), or two (*Diphyiidae*), or a double series (*Hippopodiidae*). No hydrocysts. Zooids in groups on an elongated tubular coenosarc, retractile into a groove or canal of the distal nectocalyx except in *Hippopodiidae*. The groups are detached as Diphyozooids in some species of *Diphyes*, in *Abyla*, and *Monophyiidae*. Female zooid produces many ova. *Hippopodiidae*, see note, p. 773, ante; *Diphyidae*; *Monophyiidae*, see pp. 774-5, ante.

I. *Trachymedusae*, Haeckel, System der Medusen, Jena, 1879, pp. 234-359; Id. Deep-sea Medusae, Challenger Reports, iv. 1882, pp. 9-48; *anatomy of various species*, see in O. and R. Hertwig, Das Nervensystem und die Sinnesorgane der Medusen, Leipzig, 1878; Id. Organismus der Medusen, Jena, 1878; *Nervous system, &c., of Carmarina*, Eimer, Die Medusen physiologisch, &c., auf ihr Nerven-

<sup>1</sup> For another classification cf. von Lendenfeld, Z. A. vii. 1884.

<sup>2</sup> Beneath the central gastrozooid of the *Discoideae* lies a mass of tissue often spoken of as 'liver.' Its structure has been worked out by Bedot, who terms it 'central organ.' It consists essentially of a mass of cnidoblasts and tubes. The latter are connected to the central zooid and the canals of the coenosarc, and form a dense layer beneath the pneumatophore, connected to a second but less dense superficial layer. The cells of the first layer contain coloured corpuscles in *Velella*, granules and crystals of guanine in *Porpita*. The blastostyles and tentacles (dactylozooids) are connected to the canal system.

system untersucht, Tübingen, 1878. Cf. on *Liriope eurybia* and *Carmarina hastata*, Haeckel, J. Z. ii. 1866; *critical notes on genera*, &c., Metschnikoff, Medusologische Mittheilungen, Arb. Zool. Inst. Wien, vi. 1886, p. 244 (pp. 8 et seqq. of paper).

*Freshwater Limnocoelium*, Allman, J. L. S. xv. 1881; E. Ray Lankester, Q. J. M. xx. 1880; *developing forms of*, Id. op. cit. xxi. 1881; *hydroid form* (?), A. G. Bourne, P. R. S. xxxviii. 1884. *Medusa in Lake Tanganyika*, Böhm and von Martens, SB. Ges. Natf. Freunde, Berlin, 1883, p. 197.

*Eggs, segmentation, formation of germinal layers*, Metschnikoff, Embryologische Studien an Medusen, Wien, 1886. *Delamination in Liriope eurybia and Carmarina fungiformis*, Id. Z. W. Z. xxxvi. 1882, p. 435.

*Development of Cunocanthia octonaria*, Brooks, Mem. Boston Soc. Nat. Hist. iii. 1886, p. 360, cf. Metschnikoff, Embryol. Studien, p. 123; *C. Köllikeri*, F. Müller, A. N. 27 (1), 1861; *Sporogony of Cunina proboscidea*, Metschnikoff, op. cit. p. 102; cf. also and on *C. rhododactyla*, Id. Z. W. Z. xxiv. p. 27; *C. parasitica*, Metschnikoff, Z. W. Z. xxxvi. 1882, p. 437, cf. Embryol. Studien, p. 122, Schulze, Mittheil. Vereins für Steiermark, Graz. 1875 (Archiv für Ges. Naturwissenschaften, 46, p. 494, or A. N. 41 (2), p. 404); *for figures*, Haeckel, J. Z. ii. Taf. ix. figs. 74-77, Fewkes, American Naturalist, xiv. 1880, p. 303, and F. Müller, A. N. 27, Taf. iv. fig. 30. *Development of Polyxenina leucostyla (Solmoneta flavescens) and Aeginopsis (Solmundella) mediterranea*, Metschnikoff, Embryol. Studien, and Z. W. Z. xxiv. 1874, p. 22.

*Development of Aglaura*, Metschnikoff, Embryol. Studien, *supra*, p. 93; *Liriope mucronata*, with remarks on *Geryonia proboscoidalis (Carmarina hastata)*, Id. *ibid.* p. 90; *on last-named*, also Z. W. Z. xxiv. p. 17; *Geryonia (Carmarina) fungiformis*, Fol, J. Z. vii. 1873; *Liriope scutigera*, Brooks, op. cit. *supra*, p. 373.

*Metamorphosis of Liriope (Glossocodon) eurybia*, Haeckel, J. Z. ii. 1866, p. 129; *of Carmarina hastata*, Id. *ibid.* p. 174; *of Liriope Catharinensis*, F. Müller, A. N. 25 (1), 1859.

## II. Hydroidea, see p. 249, *ante*.

Contributions to Nat. Hist. United States, L. Agassiz, iv. 1862, pp. 183 et seqq.; Wirbellosen des Weissen Meeres, Wagner, Leipzig, 1885, pp. 69-81; cf. Australian *Hydromedusae*, von Lendenfeld, Proc. Lin. Soc. New South Wales, ix; x. *Anthomedusae and Leptomedusae*, Haeckel, System der Medusen, Jena, 1879, pp. 3-233.

*Hydroid forms: Hydra*, pp. 328-9, *ante*; *Microhydra*, Ryder, American Naturalist, xix. 1885; *Protohydra*, Greeff, Z. W. Z. xx. 1870; *Polypodium*, p. 766, *ante*; *Tiarella*, Schulze, Z. W. Z. xxvii. 1876; *Lar Sabellarum*, Hincks, A. N. H. (4), x. 1872; *Amphibrachium Euplectellae*, Schulze, Trans. Royal. Soc. Edinburgh, xxix. 1880, p. 671; *Monobrachium*, Mereschkowsky, 'New genus,' &c., A. N. H. (4), xx. 1877; *Sarsia radiata and its flexor muscles*, von Lendenfeld, Z. A. vii. 1884; *Cladocoryne*, du Plessis, Mitth. Zool. Stat. Naples, ii. 1881; *Myriothele*, Allman, Ph. Tr. 165, 1875; *Podocoryne*, Grobben, SB. Akad. Wien, lxxi. Abth. 1. 1875, Hamann, J. Z. xv. 1882, p. 517; *Oorhiza*, Mereschkowsky, A. N. H. (5), i. 1878, p. 325, Wagner, op. cit. *supra*, p. 71; *various genera*, Jickeli, M. J. viii. 1883. *For various hydroids reared from Medusan ova*, see Metschnikoff, Embryol. Studien, *infra*; and *for Turritopsis and Eutima*, Brooks, *infra*.

*Deep-water Hydroidea from Norway and Iceland*, Hincks, A. N. H. (4), xiii. 1874; cf. Allman, *Hydroidea* of Porcupine, Tr. Z. S. viii. 1874; cf. Quelch,



A. N. H. (5), xvi. 1885. *Gigantic Monocaulus*, Nature, xii. 1875, p. 555. *Hydra and Cordylophora of Australia*, von Lendenfeld, Spengel's Zool. Jahrbücher, ii. 1886.

*Sarcothecae, or machopolytes*, von Lendenfeld, Z. W. Z. xxxviii. 1883, transl. A. N. H. (5), xii. 1883; Mereschkowsky, A. Z. Expt. x. 1882; cf. Metschnikoff, Q. J. M. xxiv. 1884, p. 91.

*Medusa. Laodice (Cosmetira) salinarum*, du Plessis, A. N. H. (5), iii. 1879; *Mnestra parasites*, Claus, Verhandl. z. b. Ges. Wien, xxv. 1876, Fewkes, American Naturalist, xviii. 1884, pp. 197-8; *Orchistoma*, Keller, 'Mittheilungen,' Recueil Zool. Suisse, i. 1884; *Aequorea and its development*, Claus, Untersuchungen über die Organisation, &c., der Medusen, Leipzig, 1883, pp. 61 et seqq.; *Octorchis with Campanopsis, Irene (=Tima), Phialidium*, Id. Arb. Zool. Inst. Wien, iv. 1882; *Gastroblasta timida*, Keller, Z. W. Z. xxxviii. 1883, p. 622; *history and development of Turritopsis and Eutima*, W. K. Brooks, Mem. Boston Soc. Nat. Hist. iii. 1886, pp. 386-404; 'Notes,' &c., Id. Studies Biol. Lab. Johns Hopkins University, ii. 1883; 'Notes,' Fewkes, Amer. Naturalist, xviii. 1884; *Eleutheria*, Hartlaub, Z. A. ix. 1886.

*Deep-sea forms*, Haeckel, Challenger Reports, iv. 1882, pp. 1-9.

*Fission in Medusae*, Lang on *Gastroblasta Raffaelei*, with lit. cited, J. Z. xix. 1886. *Gemmation in ditto*, see table in Böhm, J. Z. xii. 1879, p. 136; Brooks, American Naturalist, xiv. 1880, p. 670; Allman, Gymnoblasic Hydroids, Ray Soc. 1871, p. 82; Haeckel, 'System,' Pls. I and VI.

*Egg and development*, Metschnikoff, Embryologische Studien an Medusen, Wien, 1886; *of Hydra*, pp. 328-9, *ante*; *of Tubularia*, Ciamician, Z. W. Z. xxxii. 1879, Conn, Z. A. v. 1882; *of Myriothela*, Korotneff, Z. A. ii. 1879, cf. Allman, Ph. Tr. 1875; *of Obelia*, Mereschkowsky, Bull. Soc. Zool. France, viii. 1883; *of Turritopsis and Eutima*, Brooks, Mem. Boston Soc. Nat. Hist. iii. 1886, (*supra*).

*Migration of sexual cells in Obelia*, Hartlaub, Z. W. Z. xli. 1885.

*Origin of sexual cells*; with many facts relating to the structure of the colony, the development of the egg, and Medusa, as well as to the structure of the sexual zooid, Weismann's Entstehung der Sexualzellen bei den Hydromedusen, Jena, 1883.

*Hydrocorallina*, Moseley, Challenger Reports, ii. 1881 (cf. *Milleporidae*, Ph. Tr. 167, 1877, and *Stylasteridae*, Ph. Tr. 169, 1878). *Milleporidae*, Quelch, Reef Corals, Challenger Reports, xvi. 1886, p. 190; *ampullae in M. Murrayi*, Id. p. 192 of Reef Corals, or in Nature, xxx. p. 539; *generative capsules*, Hickson, P. R. S. xl. 1886, p. 325. *New Stylasteridae*, Quelch, A. N. H. (5), xiii. 1884; xvi. 1885.

*Graptolithidae s. Rhabdophora*, Zittel, Handbuch der Palaeontologie, Abth. 1, Palaeozoologie, i. p. 290, or Nicholson's Manual of Palaeontology, 1879, i. p. 162; Lapworth, Geological Magazine, x. 1873; Id. on the geological distribution of ditto, A. N. H. (5), iii. and iv. 1879; v. and vi. 1880. Cf. Allman's critical remarks in the Gymnoblasic Hydroids, pp. 176-186, and p. 769, *ante*. *Other fossil forms*, Zittel, op. cit.; and cf. note 1, p. 756, *ante*.

III. *Siphonophora*. Oceanic Hydrozoa (with lit. p. 139), Huxley, Ray Society, 1858; Neue Beiträge, &c., Gegenbaur, Nova Acta, xxvii. 1860. Zur Kenntniss der Siphonophoren von Nizza, Leuckart, A. N. xx. (1), 1854; Zool. Untersuchungen, Id. Giessen, 1853. Schwimmpolypen von Messina, Kölliker, Leipzig, 1853. *Siphonophora of deep waters*, Studer, Z. W. Z. xxxi. 1878. Cf. Fewkes, Bull. Mus. Harvard, ix. pp. 246, 302.

*Halistemma tergestinum*, Claus, Arb. Zool. Inst. Wien, 1, 1878; *Agalmopsis utricularia*, Id. op. cit. ii. 1879; *Porpitiidae and Velellidae*, Agassiz, Mem. Harvard Mus. viii. 1881-84; *Veleva and Rataria*, Bedot, Recueil Zool. Suisse, i. 1884; *the same and Porpita*, Id. op. cit. ii. 1885; *Notes on Rhizophysa and Physalia*, Chun, SB. Akad. Berlin, 1882, pp. 1168-70; *Diphyes subtilis*, Id. op. cit. 1886, p. 681; *Diphyozoids*, Id. ibid. p. 686; *Cyclical evolution and Monophyidae*, see p. 774, ante.

*Histology in general*, Korotneff, Mitth. Zool. Stat. Naples, v. 1884. *Nervous system of Porpita*, Conn and Beyer, Studies from Biol. Laboratory, Johns Hopkins Univ. iii. 1883; *of Veleva*, Chun, Z. A. iv. 1881.

*Origin of sexual cells*. Weismann, Entstehung der Sexualzellen bei den Hydromedusen, Jena, 1883, pp. 193-213; pp. 212, 265, 291.

*Development*. Entwicklungsgeschichte der Siphonophoren, Haeckel, Utrecht, 1869; Metschnikoff, Z. W. Z. xxiv. 1874; *of Agalma*, Fewkes, Bull. Mus. Harvard, xi. 1885.

## SUB-CLASS 2. ACRASPEDA<sup>1</sup>.

(*Acalephae, Phanerocarpa, Steganophthalmata, Scyphomedusae*).

*Hydroid form known in a few instances only; small and fixed, protected partially in some instances by a perisarcal tube; with a peristomial disc bordered by sixteen (or more) solid tentacles; mouth squarish and gastric cavity traversed by four vertical interradiial ridges; multiplying either by lateral buds which are detached, or by creeping stolons which throw up buds at intervals. The Medusa is derived from it by multiple transverse fission of the oral extremity of the body, giving rise to a temporary form known as Strobila.*

*The Medusa has a square-shaped manubrium, the oral angles of which are sometimes produced into four simple or branched arms; bifid marginal lobes to the bell rarely absent, either four perradiial or four perradiial and four interradiial, supporting as many sensory bodies, i.e. tentaculocysts, or rhopalialia; more or fewer gastral filaments disposed in rows or groups (phacelli) within the central gastric cavity at the sides of the manubrium; and genital organs similarly placed with a genital epithelium of endodermal origin. The sexes are separate: development is direct in Pelagia. There is no velum to the bell. Tentacles may be absent, or, if present, either situated on the exumbrella or subumbrella. The nervous centres are contained in the marginal sensory bodies. Marine.*

The non-sexual Hydroid form of the Acraspeda, the *Scyphostoma* or *Hydra tuba*, is only known in genera of the *Ephyroniae* or second division of the sub-class<sup>2</sup>. It is relatively small in size (half-an-inch or less), and its

<sup>1</sup> See p. 747, ante, for Götte's view as to the position of this sub-class.

<sup>2</sup> That is to say in *Nausithoe marginata*, *Chrysaora* (*C. isosceles*, *C. Mediterranea*), *Cyanea* (*C. arctica*, *C. capillata*, *C. Annaskala*), *Aurelia* (*A. aurita*, *A. flavidula*), *Pilema pulmo* = *Rhizo-*

special characters are as follows. The mouth is dilatible and somewhat squarish in outline, especially in early stages: its margin is thickened and armed with cnidoblasts: it is situate in the centre of a disc or peristome of great mobility. The margin of the peristome carries normally sixteen tentacles: the number may however be greater, e.g. twenty or thirty-two. The tentacles are contractile, and have a solid core of endoderm cells. Four of them, the *periradial* tentacles, which are first developed, correspond to the four angles of the mouth; four others, the *interradial* tentacles, second in development, to the centres of the square sides of the mouth, and the remaining eight *adradial* tentacles occupy the intervals between the per- and inter-radial. The body is somewhat elongated, but contracts below into a peduncle, by which the animal is affixed to some foreign object (stones, sea-weeds, &c.). This peduncle is slender in *Chrysaora* and *Cyanea*, and inclosed in a gelatinoid sheath secreted by the ectoderm<sup>1</sup>. The young *Nausithoe marginata* inhabits a perisarcal tube. The internal aspect of the gastric cavity is traversed by four vertical ridges, septa or *taeniolae*, which correspond one to each of the four interradial tentacles. They are projecting ridges of mesoglaea covered by endoderm cells and inclosing a tube of muscle cells of endodermal (Claus) or ectodermal and peristomial (Götte) origin. They have been compared to the mesenteries of Anthozoa. The tentacles especially are provided with nematocysts of two sizes, and the smaller (microcnidae) have extremely long cnidocils. Cilia occur upon the tentacles, in greatest numbers near their bases, as well as upon the peristome and margins of the body. The *Scyphostoma* multiplies in two ways, by means of lateral buds which are detached, and by two to three creeping basal stolons, from which buds are thrown up at intervals<sup>2</sup>.

*stoma Cuvieri*, *Pseudorhiza aurosa*, *Stylorhiza punctata*. As these genera represent several families, there can be little doubt that the *Scyphostoma* is of general occurrence.

<sup>1</sup> L. Agassiz states that the sheath is sometimes wanting in *Cyanea*, and the young animal may be seen creeping on its tentacles.

<sup>2</sup> F. E. Schulze has described (A. M. A. xiii. 1877), under the name *Spongicola fistularis*, a Hydroid which he observed inhabiting the canal-system of several marine sponges, e.g. *Reniera fibulata*, *Esperia Bauriana*, &c. It forms a colony of nearly vertical branching tubes invested by a chitinous perisarc. The Hydroid itself has the typical structure of the Acalephan Hydroid as given above. Its peristome measures about 1-1½ mm. in diameter. It has 16, 20, &c. up to 40 solid contractile tentacles, and the *taeniolae* extend across the peristome to the margin of the mouth. The peristome is bordered by a strong circular fold. The exposed part of the body and the tentacles are ciliated. The fore-part of the body bearing the tentacles can be invaginated. Allman has also described a sponge-inhabiting Hydroid, *Stephanoscyphus mirabilis*, which closely resembles *Spongicola*. It is colonial, has a perisarcal tube, &c. But its great peculiarity, according to its discoverer, is the presence of a circular and four longitudinal canals. It is probable that the structures in question are really four *taeniolae* and a circular fold such as are described above. See Allman, Tr. L. S. (2), i. 1879. Schulze's Hydroid is probably identical with the structures described by Eimer (Tageblatt der Natf. Versaml. in Leipzig, 1872, p. 62), and supposed by him to be integral parts of the sponge in which they occur.

Kowalewsky, quoted by Metschnikoff (Embryol. Studien an Medusen, 1886, p. 88) appears to have seen the strobila of *Spongicola* and the detachment of *Ephyrae*.

The *Scyphostoma* passes in late autumn into the *Strobila* stage. A circular furrow constricts the body on the aboral side of the tentacular circle, cutting off a disc. A series of similar furrows appear one after another, a basal pyriform portion of the body alone remaining undivided. The disc-like segments thus cut off increase in diameter and are detached as young Medusae or *Ephyrae* (= *Ephyryulae*, Haeckel). In the first-formed segment eight bifid marginal lobes grow out, each of which embraces the base of a per- or an inter-radial tentacle<sup>1</sup>. These tentacles shorten, and their basal portions are converted into the sensory bodies or rhopalia of the Medusa. The eight adradial tentacles undergo complete atrophy. The gastric cavity grows peripherally as four pouches separated by the four taeniolae, and a perforation then takes place through the base of attachment of each taeniola putting the pouches in communication. The gastric cavity extends outwards into each of the eight bifid lobes, which are much elongated. The portions of the four taeniolae cut off are usually converted into gastral filaments, and the taeniolar muscles are lost. The same eight bifid lobes and the rhopalia appear in each of the remaining segments of the *Strobila*. The basal pyriform portion of the *Scyphostoma* develops, sooner or later, a set of sixteen tentacles, and after the detachment of the last *Ephyra* grows in size. In spring it has been observed to pass again into the *Strobila* condition.

The *Ephyra* grows in size after its detachment. It may retain its external appearance (certain *Cannostomae*). But with few exceptions it undergoes changes of shape. The eight adradial intervals between the eight marginal lobes increase much in extent, and either remain simple, or are divided into a number of lobes, simple or bifid. The lobes in question are either independent outgrowths of the bell-margin, which may or may not divide, or are produced by fission (1) from the sides of the *Ephyra* lobes, and (2) of the lobes thus derived. The bell itself is somewhat flattened, of greater breadth than depth. It is sometimes divided into a central and peripheral portion by a circular furrow in the exumbrella, the *fossa coronaris*. Its margin never becomes inflected inwards: when it is thin and velum-like, as e. g. in *Aurelia*, it is termed by Haeckel 'velarium.' The mouth retains its square outline in *Cannostomae*, or its four angles are prolonged outwards into four oral arms, with a deep adoral furrow lined by endoderm and folded edges in *Semostomae*: and in *Rhizostomae* these four arms become bifid at their apex during growth; the edges of their furrows become much folded and produced into processes; the surfaces of the folds and processes condesce from place to place, leaving only funnel-shaped openings, which lead into the adoral furrows now converted into

<sup>1</sup> Haeckel in his System and elsewhere appears always to count the two divisions of these lobes as separate lobes. He terms them subradial, the tentacles intervening between successive pairs being adradial.

canals. At the same time the mouth is closed by the concrescence of the folds bordering it and by the fusion of the bases of the arms. Crustaceans, and even fish of fair size have been found within the funnel-shaped apertures, and a *Rhizostoma* (*Pilema*) has been captured with a semi-digested animal embraced by the arms. The ectoderm of the edges of the arm-grooves is raised into papillae with cnidoblasts in *Semostomae*. These papillae develop into short mobile processes or digitelli in all *Rhizostomae*, in the *Semostome Cyaneidae*, and to a certain extent in *Aurelia*. Some *Rhizostome* genera also possess 'nettle-bulbs,' stalked processes with or without a terminal opening, ending in a knob covered with cnidoblasts, and 'nettle-whips,' which are elongated funnel-shaped openings, sometimes closed except at their apices, and beset with digitelli<sup>1</sup>. The angles of the manubrium become thickened and the thickenings extend on to the subumbrella, giving rise to four pillars. The subumbrella itself is also more or less thickened, except at the base of the four sides of the manubrium, where it remains thin. These thin spots are the *gastro-genital membranes*. Tentacles, absent in all *Rhizostomae*, are, when present, either solid or hollow; situated one between each of the eight marginal lobes when the *Ephyra*-form is retained<sup>2</sup>; usually numerous, and then placed above the margin of the bell, e.g. in *Aurelia* between the lobes of the margin, or in groups towards the periphery of the bell on the surface of the subumbrella, as in *Cyanea*. The ectoderm of the exumbrella may contain pigment cells and groups of cnidoblasts. The ectoderm of the subumbrella develops ganglion cells and muscle-cells, the latter aggregated along certain lines. The principal muscular tracts are (1) a circular zone of striated muscles close to the margin of the bell, often broken up into sixteen sub-divisions, corresponding to the perradii, interradii, and adradii; (2) radial striated muscles corresponding to the pillars of the manubrium. There are also muscles in connection with the bases of the tentacles and the marginal lobes. The

<sup>1</sup> For an account of the structure of digitelli, nettle-bulbs, and whips, see Hamann, J. Z. xv. 1882; for the development of the first two, Claus, 'Untersuchungen,' pp. 44 and 55; and of the *Rhizostome* arms, the last-named, op. cit. pp. 43 et seqq. The arms of *Pilema*, e.g. *P. pulmo* (*Rhizostoma Cuvieri*), of *Mastigias papua*, &c. end in 'terminal knobs,' at first perforate, later imperforate; for their origin, cf. Claus, op. cit. p. 51, under 'Arm-kolben.' Two of the terminal arm-folds in the *Rhizostome*, *Pilemidae* and *Crambessidae*, pass during growth to the aboral aspect of the arms, which consequently appear in transverse section triangular, each angle carrying a folded ridge. The majority of *Pilemidae* possess 'scapulets,' eight in number, springing from the sides of the manubrium above the bases of the arms. Haeckel and Hamann regard them as dissociated arm-folds; Claus, however, has proved that they originate as eight hollow outgrowths which become perforate. The edges of their apertures become folded, concresce from place to place, and are beset with digitelli. See in his work, cited above, the account of the metamorphosis of *Rhizostoma*.

<sup>2</sup> Claus states ('Untersuchungen,' &c. p. 21) that in the young *Ephyrae* of *Chrysaora* and *Aurelia*, as well as of *Cyanea* (on Fewke's authority), there is a stage with only four tentacles, which he distinguishes as *Metephyra*. If the *Ephyra* be regarded from the dorsal, i. e. exumbrellar aspect, the four tentacles in question were in all specimens examined by him outgrowths of the adradius to the right of the four perradial marginal lobes when the perradius was directed forwards.

sense-bodies, tentaculocysts or rhopalia, are cylindrical, straight or curved organs, with the following structure. The endoderm at their apex forms a mass of nucleated cells or protoplasm, imbedding a variable number of calcareous otoliths, which do not however contain Lime Carbonate. The ectoderm cells of the apex are flattened (? ciliated), those of the sides are more or less columnar (1) supporting cells, (2) sense-cells, furnished with sense-hairs, and prolonged basally into filaments in connection with ganglion cells which lie among the sub-epithelial nerve-fibres (Claus, von Lendenfeld). A patch of visual pigment is commonly present on the dorsal aspect of the organ near its base, but in *Nausithoe* and its congeners there is a ventral eye provided with a lens, with sense-cells, pigmented supporting cells and ganglion cells (?). The sense-bodies are usually protected by a dorsal, i. e. exumbrellar covering-piece or hood, sometimes of large size, and by two lobes which curve round it below, and are developed from the inner edges of the bifid *Ephyra* lobes. There is often a depression in the exumbrella above the base of each sense-body. It is lined by ciliated cells, and is supposed to test the character of the sea-water, i. e. to exercise a gustatory or olfactory function<sup>1</sup>. The sense-bodies appear to be so many nerve-centres, and they are connected to a sub-ectodermic plexus of ganglion cells in the subumbrella, and control the movements of the animal.

The exumbrellar and subumbrellar walls of the peripheral part of the gastric cavity fuse from place to place with the formation of a gastral lamella, leaving pouches, simple or branched vessels, or retia, and there is very generally a circumferential canal<sup>2</sup>. The gastric filaments are motile cylindrical processes disposed in groups (phacelli) on the subumbrellar

<sup>1</sup> In *Aurelia* and *Cyanea Annaskala* the base of the marginal bodies is surrounded by sensory epithelium, nerve-fibrils and ganglion cells. There is also a similarly constituted elongated patch extending centripetally from near the base of the marginal body on the surface of the subumbrella. *C. Annaskala* and *C. capillata* possess sensory patches also upon the inner and outer faces of the two lateral protective lobes of the rhopalia. A layer of nerve-fibrils underlies the olfactory epithelium which in *C. Annaskala* at least is scarcely distinguishable from that of the sensory bodies themselves.

The number of rhopalia is more than 8 in a few instances; 19-22 occur in *Atolla*; 32 in *Collaspis* (*Cannostomae*); 12 are found in the Semostome genera *Phacellophora*, *Patera* and *Medusina*, and the Rhizostome genus *Polyclonia*; 16 in the Rhizostome *Cassiopeia*. Von Lendenfeld has observed that the young *Ephyra* of the Rhizostome *Stylorhiza punctata* has 24; reduced in an older *Ephyra* to 16, and finally to 8; see Z. A. vii. pp. 430-31. He does not mention that its *Scyphostoma* shows any peculiarity: cf. Proc. Lin. Soc. N. S. Wales, ix. p. 297, under *Phyllorhiza punctata*; and for figures of the bell-margin of the *Ephyra*, *ibid.* Pl. V.

<sup>2</sup> The gastral lamella formed by the cohesion of the exumbrellar and subumbrellar walls of the gastric cavity consists of a single layer of cells in the fully formed central region of the bell, and sometimes, if not always, of a double in the peripheral growing parts. It appears to extend at its edges as the bell grows in size, and vessels are excavated between its two layers. See von Lendenfeld, Z. W. Z. xxxvii. p. 490, and Haeckel, 'Deep-sea Medusae,' Challenger Reports, iv. Pl. XXV. Figs. 8 and 10. Indications of its double nature are always to be discerned in the Cubomedusan *Charybdata*, according to Claus.

wall of the gastric cavity centrally to the genital organs. Four single filaments only are present in the genus *Ephyra*. The endoderm covering them consists of ciliated cells, gland cells, muscle cells, and cnidoblasts. The genital organs are either ridge-like or lamellate, and project into the gastric cavity. They are situated on the inner aspect of the thin gastro-genital membranes (p. 783); and the genital products are derived from the endodermal cells of the peripheral or lower face of the ridges or lamellae. The original shape of the ridge is that of a horseshoe, with the concavity turned to the margin of the bell, but in the majority of *Semostomae* and *Rhizostomae* the curvature is reversed. The ridge is rarely divided into two parts, as in a few *Cannostomae*, but it is very generally converted into a lamella which may become lobed<sup>1</sup>. The gastrogenital membrane may increase in size, become folded and hang down into the cavity of the bell in some *Semostomae*, e.g. *Pelagia*, *Cyanea*; or be invaginated into the gastric cavity, e.g. in *Aurelia*, most *Rhizostomae*. The walls of the subumbrella surrounding the four membranes may be much thickened, and consequently the membranes come to lie at the bottom of *subgenital cavities* or *lemnia*, as in *Aureliadae* and most *Rhizostomae*. The aperture into the cavities may, in the last-named, be greatly reduced, or covered by an axial and abaxial process of the subumbrellar wall, so that each of them acquires the appearance of a double cavity. In the Rhizostome *Versuridae* and *Crambessidae* the four gastrogenital membranes meet in the centre of the bell. The basal portion of the manubrium is consequently resolved into four hollow pillars which correspond to its four angles. The cavity thus formed is the 'sub-genital portico' or *syndemnum*<sup>2</sup>. The Semostome *Chrysaora* is hermaphrodite. Sperm sacs occur upon its genital lamellae, which produce ova in a normal manner, as well as upon the subumbrellar wall of the gastric cavity, in the gastric pouches, and on the arms<sup>3</sup>.

Variations in the number of the radial segments sometimes occur. *Aurelia aurita* is particularly liable to such malformations, and in it the number may be increased from eight to twelve, or diminished to three or four. The bell may be affected alone or the manubrium, and the genitalia

<sup>1</sup> The primitive ridge is converted into a lamella by the growth of endoderm cells from its margin into the mesoglaea of the gastrogenital membrane. Connecting pillars of cells, or of mesoglaea covered by cells, are often left between the genital lamella and the gastrogenital membrane. See von Lendenfeld, Z. W. Z. xxxvii. p. 536 et seqq.; and Claus, Untersuchungen, p. 33 et seqq. and p. 38.

<sup>2</sup> Von Lendenfeld appears to have observed the formation of this chamber in *Stylorhiza punctata*. He states that it occurs as Haeckel supposed, i.e. by the encroachment of the gastrogenital membranes on the base of the manubrium until they meet and fuse. See Proc. Lin. Soc. New South Wales, ix. p. 307, or Z. A. vii. p. 431. In the first-named paper the author describes the Medusa in question under the generic name of *Phyllorhiza*. This is an error, because *Phyllorhiza* is a Pilemid genus, and there is no subgenital portico in *Pilemididae*.

<sup>3</sup> The subumbrellar sacculs of certain *Linergidae* (*Cannostomae*) are perhaps testes. See Haeckel, System, p. 493.

as well. Sexual individuals of this species occur in autumn half to a quarter the normal size, i. e. four inches.

The characters above given apply to the second division of Acraspeda, the *Ephyroniae* of Haeckel. A large number of Medusae belong to it, and it contains three orders, the *Cannostomae*, *Semostomae*, and *Rhizostomae*.

The first division of Acraspeda, the *Tesseroniae*, contains relatively few forms. The bell is of great depth; and in the *Depastridae* and *Lucernaridae* it is produced into a hollow peduncle by which the animal attaches itself at will. Its cavity is prolonged aborally into four interradial 'funnel cavities' of variable extent, corresponding to the four sides of the manubrium. The angles of the latter are consequently attached by four perradial septa, 'mesogonia,' to the subumbrellar wall. Rhopalia are absent in the *Stauromedusae* and their place may be taken in *Lucernaridae* by adhesive tentacles, sometimes lost, or by simple tentacles in *Tesseridae*. They are four in number when present, interradial in *Peromedusae*, perradial in *Cubomedusae*. They bear one or two dorsal eyes in the former, sometimes also a ventral: in the Cubomedusan *Charybdaea marsupialis* three pairs, a large central and two lateral pairs. In the last-named the retinal layer is cup-shaped; the cup filled by a vitreous body, to which is added in each of the large eyes a lens formed by elongate ectoderm cells much as in Vertebrata. *Charybdaea* has also a continuous nerve-ring, in position corresponding to the inner nerve ring of Craspedota. It consists of fibres and ganglion cells, the latter especially aggregated at the bases of the rhopalia, with an overlying ectoderm of sense and supporting cells. Tentacles are usually limited in number, and are rarely solid. In the fixed forms they are capitate, ranged round the bell-margin in *Depastridae*, grouped at the end of eight short hollow adradial arms in *Lucernaridae*. The mouth is square. The main gastric cavity consists of four pouches communicating peripherally by apertures of varying size, depending on the length of the septa that separate them<sup>1</sup>. Processes from the cavity pass into the marginal lobes of *Peromedusae*, and the velarium, when present, of *Cubomedusae*, e.g. in *Charybdaea*. The taeniolae are greatly

<sup>1</sup> Claus points out (Untersuchungen, p. 14) that the starting-point of the *Tesseroniae* is conceivably the stage in the formation of the *Ephyra* from the *Scyphostoma* at which the taeniolae are perforated by passages putting the four gastric pouches into communication. The gastric cavity becomes much complicated in the *Peromedusae*: see Haeckel, System, p. 402 et seqq. There seems to be some confusion as to the character of the septa dividing the gastric pouches. In *Charybdaea marsupialis* each septum is traversed by a layer of endoderm cells, showing that there has been a fusion of the two walls of the gastric cavity. On the contrary, the septa of *Lucernaridae*, as may be seen from Claus' figures (Untersuchungen, Pl. IX. Fig. 62; Pl. X. Figs. 71, 72), contain no such layer, and are probably taeniolar growths. The distinction is certainly one of importance. Haeckel appears to think that the septa in question, whether nodes, lines or lamellae, are always formed in the same way: see Deep-sea Medusae, Challenger Reports, iv. pp. lxxix.-lxxx.

The *Depastridae* and *Lucernaridae* are probably to be regarded as specialised *Scyphostomae*, and as standing apart from other Acraspeda.



developed in most *Stauro-* and *Peromedusae*, extending along the exumbrellar wall of the gastric cavity to a greater or less extent. The funnel cavities penetrate them in some *Lucernaridae* and the *Peromedusae*. The gastral filaments may be only four, as in *Tessera*, but are generally, especially in the *Peromedusae*, extremely numerous, and in *Cubomedusae* aggregated into a single or double group at the axial ends of the gastric septa. In *Stauro-* and *Pero-medusae* they frequently extend along the exumbrellar wall of the gastric cavity even to its centre. The genital organs are situated on the subumbrellar walls, but in one section of *Lucernaridae*, the *Halicynthidae* or *Cleistocarpidae*, are contained in special mesogonial or gastrogenital pouches opening into the central gastric cavity and placed perradially in the cavity of the bell. The organs are either horseshoe shaped, the convexity of the curve being adcentral, or the two limbs of the horseshoe are separate (*Lucernaridae*, *Peromedusae*). In the *Cubomedusae* there are eight genital lamellae, attached two to each gastral septum, one on either side<sup>1</sup>.

The development of the *Tesseroniae* is unknown save to a certain extent in a *Lucernaria*. In it segmentation is equal and results in the formation of a morula. The endoderm is formed either by delamination from the ectoderm cells at one pole or by an immigration(?) of ectoderm cells at all points into the centre of the morula (Götte). The larva is non-ciliated (? in all cases) and creeps about; it is elongated; one pole is beset with cnidoblasts, by the other it fixes itself<sup>2</sup>. The ovum of *Ephyroniae* is either set free from the ovary and has then a vitelline membrane, or in *Nausithoe marginata* a mucous coat with cnidoblasts, or, as in *Chrysaora*, remains enclosed in an envelope of follicle cells. In the first case it may pass into the planula condition while attached to the oral arms of the female (*Aurelia*, *Cassiopeia*), and it may even nearly attain the *Scyphostoma* stage in this position (*Cyanea Annaskala*, *Stylorhiza punctata*), or the embryos are contained in pouches of the radial canals (*Pseudorhiza aurosa*). Segmentation is regular: the blastocoele is large in *Pelagia* and *Chrysaora*, small in other cases. The endoderm is formed by an invagination the cavity of which is linear: the gastrula mouth closes but the pole which corresponds to it is denoted by the development of cnidoblasts, and is the one at which the mouth of the adult is formed later on. The planula (=two-layered blastula) is sometimes ciliated and free-swimming (*Aurelia*, *Chrysaora*). When it fixes itself the mouth is formed: two perradial tentacles first

<sup>1</sup> On the nature of these genital lamellae, see O. and R. Hertwig, J. Z. xiii. p. 599; Claus, Arb. Zool. Inst. Wien, i. 1878, p. 269 et seq., and his Untersuchungen, p. 37. Their accounts differ.

<sup>2</sup> Haeckel believes that the *Tesseroniae* possess a *Scyphostoma* stage; Claus that they develop direct. The former is supported by Haacke, who has observed a young *Charybdaea Rastonii* in which a canal was prolonged aborally from the gastric cavity and closed at the apex of the exumbrella by a thin lamella. See Z. A. ix. 1886.

make their appearance opposite to one another, then the remaining two, finally the interradial tentacles and taeniolae simultaneously. The planula of *Pelagia* develops direct into an *Ephyra*<sup>1</sup>.

Most Acraspeda are pelagic; a few deep-sea forms are known. The *Depastridae* and *Lucernaridae* attach themselves by their peduncle to algae, &c. In some instances the Medusa frequents the surface of mud-banks and coral reefs, and often rests reversed, i. e. upon the convexity of the bell<sup>2</sup>. *Cassiopeia polyoides* from the coral banks of the Red Sea has an exumbrellar groove which acts as a sucker. The ectoderm cells of the groove secrete a plentiful mucus which cements the coral sand, and there is also an exumbrellar radial musculature. The *Tesseroniae* are for the most part small: the Cubomedusan *Tamoya* attains, however, a diameter of eight inches. Many *Ephyroniae* are large, e. g. *Aurelia aurita* four inches, and the Rhizostome *Pilema pulmo* (= *Rhizostoma Cuvieri*) two feet: but the Semostome family *Cyaneidae* contains the largest known Medusae. An old example of *Cyanea arctica* has been measured with a bell seven and-a-half feet across and tentacles a hundred and twenty feet long. Many Acraspeda are brilliantly coloured, and some of them, e. g. *Cotylorhiza*, are inhabited by the symbiotic alga *Zooxanthella* (see pp. 242-4). Most of the fossil Medusae mentioned above, p. 746, belong to this sub-class.

Haeckel classifies the Acraspeda as follows in his System:—

I. *Tesseroniae*: rhopalia four or none; stomach surrounded by four wide per-radial gastric pouches separated by longer or shorter septa; genital organs lodged either in the subumbrellar wall or in the cavity of the gastric pouches. Bell of great depth, usually conical. There are three orders.

(1) *Stauromedusae*: no rhopalia; includes *Tesseridae* with *Depastridae*, and *Lucernaridae*. (2) *Peromedusae* with four interradial rhopalia. (3) *Cubomedusae* with four perradial rhopalia and lamellate genitalia, e. g. *Charybdaea*.

II. *Ephyroniae*: rhopalia eight, i. e. four per- and four inter-radial, rarely more numerous; stomach surrounded by 8, 16, or 32 gastric pouches or radial canals; genitalia attached to the subumbrellar wall of the central gastric cavity. Bell flat; for the most part disc-like. One order, *Discomedusae*, with the above-detailed characters; three sub-orders as follows:—

(1) *Cannostomae*: mouth simple, square; tentacles solid and usually short; the *Ephyridae* and *Linergidae*. (2) *Semostomae*: mouth a cross, the four oral angles prolonged into long arms; without a circumferential canal, *Pelagiidae*, e. g. *Chrysaora*, and *Cyaneidae*; with one, *Flosculidae* and *Ulmaridae*; the last-named

<sup>1</sup> It is possible that the planula of *Chrysaora* may multiply by fission or gemmation: cf. Claus, Untersuchungen, p. 5, and Dk. Wien. Akad. xxxviii. p. 7. Haeckel has described such phenomena together with remarkable forms of *Scyphostoma*, and even a direct development similar to that of *Pelagia* in his 'Metagenesis und Hypogenesis von *Aurelia aurita*,' Jena, 1881. Claus in his Untersuchungen criticises (*passim*) Haeckel's statements unfavourably. Note his corrigendum, p. 90.

<sup>2</sup> The young *Cotylorhiza* may attach itself in the same fashion, according to Keller.

includes *Aurelia*. (3) *Rhizostomae*: mouth obliterated; four oral arms divided into eight; edges of their grooves united, leaving funnel-shaped apertures; four subgenital cavities separate, *Toreumidae*, e.g. *Cassiopeia*, and *Pilemidae*, e.g. *Pilema*, or united to form a syndemnum, *Versuridae*, e.g. *Cotylorhiza*, and *Crambessidae*.

Claus, in the Arb. Zool. Inst. Wien, vii. p. 109, divides the sub-class as follows:—

I. *Tetrameralia*: with four radial sectors.

Orders (1) *Calycozoa* = *Depastridae* and *Lucernaridae*: (2) *Marsupialida*, including *Charybdaea* and its allies.

II. *Octomeralia*: with eight sectors. Order *Discophora* with two sub-orders:—

(1) *Catammnata*, with persistent septal unions<sup>1</sup> including Haeckel's *Peromedusae* and *Cannostomae*: (2) *Acatammnia*, with no septal unions, but with a gastral lamella and the oral angles prolonged into arms, subdivided into (a) *Mono-stomeae* (= *Semostomae*) and (b) *Rhizostomeae*.

For the families he refers to his Untersuchungen, pp. 24 and 60.

Haeckel, System der Medusen, Dk. med. wiss. Gesellschaft, Jena, i. pt. 2 and Atlas, 1879; Id. Deep-sea Medusae, Challenger Reports, iv. 1882, p. 48; Claus, Untersuchungen über die Organ. und Entwick. der Medusen, Leipzig, 1883; Id. Dk. Wien. Akad. xxxviii. 1878; cf. for points of Anatomy, O. and R. Hertwig, Organismus der Medusen, Jena, 1878, and Nervensystem und Sinnesorgane der Medusen, Leipzig, 1878; L. Agassiz, Contributions to the Nat. Hist. of U. S., iv. pt. 3, Boston, 1862.

*Lucernariae and their allies*, Clark, Smithsonian Contributions to Knowledge, 1878; *Craterolophus Tethys*, Kling, M. J. v. 1879. *Charybdaea marsupialis*, Claus, Arb. Zool. Inst. Wien, i. 1878. *Nausithoe*, Claus, Untersuchungen, &c., (*supra*), p. 24; *Aurelia*, (= *Medusa aurita*), Ehrenberg, Akalephen des Rothen Meeres, Phys. Abhandl. Akad. Berlin, 1835; *ditto*, *Chrysaora*, &c. (and development), Claus, Dk. Akad. Wien, xxxviii; *Aurelia*, *Cyanea*, *Pelagia*, *Stomolophus*, *Polyclonia*, L. Agassiz, Contributions, &c. (*supra*); *Cyanea Annaskala*, von Lendenfeld, Z. W. Z. xxxvii. 1882; *C. arctica*, Wagner, Wirbellosen des Weissen-Meeres, Leipzig, 1885, p. 83. *Cassiopeia polyoides*, Keller, Z. W. Z. xxxviii. 1883, p. 632; *Rhizostoma Cuvieri*, = *Pilema pulmo*, Brandt, Mem. Imp. Acad. St. Petersburg (7), xvi. 1871 *metamorphosis of ditto and of Cotylorhiza*, Claus, Untersuchungen, &c. (*supra*), p. 43, and Arb. Zool. Inst. Wien, v. 1884; *Pseudorhiza aurosa*, von Lendenfeld, Z. A. v. 1882, p. 380; *Ps. Haeckelii*, Haacke, Biol. Centralblatt, iv. 1884-85, p. 291; *Crambessa Tagi*, Grenacher and Noll, Abhandl. Senckenberg Ges. x. 1876, and Greeff, Z. A. iv. 1881.

*Oral arms of Rhizostomae*, Hamann, J. Z. xv. 1882.

*Monstrous forms of Aurelia*, Romanes, J. L. S. xii. 1876, p. 527; xiii. 1878, p. 191, with two plates; Ehrenberg, op. cit. *supra*, p. 199, and Pl. II.

*Development of genitalia in Lucernaria, Craterolophus, Charybdaea, Aurelia, Discomedusa, Chrysaora*, Claus, Untersuchungen, &c. (*supra*), p. 39 et seqq.; cf. p. 88; cf. also O. and R. Hertwig, J. Z. xiii. 1879, p. 599 et seqq. *Formation of sperm in Cassiopeia borbonica* (= *Cotylorhiza tuberculata*), Merejkowski, A. Z. Expt. x. 1882.

<sup>1</sup> By septal unions (Septalknoten) Claus appears to mean from p. 27 of the Untersuchungen, four interradial spots to the outer or abaxial side of the gastral filaments where the exumbrellar and subumbrellar layers of endoderm have fused: cf. note 2, p. 784, and note, p. 786, *ante*.

*Development of Lucernaria*, Korotneff, Z. A. vii. 1884. *Young stage of a Charybdaea*, Haacke, Z. A. ix. 1886. *Egg and Scyphostoma of Nausithoe marginata*, Metschnikoff, Embryol. Studien an Medusen, Wien, 1886, pp. 28 and 86; *ditto and Strobila of Aurelia and Chrysaora*, Claus, Untersuchungen, &c., and Dk. Akad. Wien, xxxviii. (*supra*), with lit. cited; cf. *on Aurelia and Cetylrorhiza*, Götte, Abhandl. zur Entwicklungsgeschichte der Thiere, pt. iv. 1886; and pp. 747-8, *ante*. Cf. Haeckel, System (*supra*), p. 474; also von Lendenfeld, Proc. Lin. Soc. N. S. Wales, ix. 1885, *for ontogeny of Cyanea Annaskala*, p. 275, *of Pseudorhiza aurosa*, p. 293, and *Stylorhiza punctata*, p. 297. *Ontogeny of Pelagia*, Krohn, Archiv f. Anat. und Physiol. 1855, p. 491; Kowalewsky, in Hoffmann and Schwalbe's Jahresbericht, ii. 1873, p. 280; and L. Agassiz, Contributions (*supra*), p. 128. *Scyphostoma of Rhizostoma (= Pilema)*, Claus, Z. A. iv. 1881, p. 79.

*Medusa in reversed position*, Guppy, Nature, xxvii. 1882-83, p. 31 (with ref.); Keller *on Cassiopeia (supra)*; Id. *on Cetylrorhiza*, Recueil Zool. Suisse, i. 1884, p. 405.

*Local colour varieties of Scyphomedusae*, von Lendenfeld, A. N. H. (5), xiv. 1884. *Colouring matter of Jellyfish*, McKendrick, Journal of Anat. and Physiol. xv. 1881; *of Rhizostoma (= Cyanein)*, Blanchard, Z. A. vi. 1883; Krukenberg, *ibid.* *Zooxanthellae in Cetylrorhiza*, Keller, Recueil Zool. Suisse, i. 1884, p. 413.

*Locomotor system of Medusae*, Romanes, Ph. Tr. 166, 1876; 167, 1877; 171, 1880; Eimer, Die Medusen physiologisch und morphologisch auf ihr Nervensystem untersucht, Tübingen, 1878. Cf. Wagner, Wirbellosen des Weissen Meeres, 1885, pp. 81-2.

## CLASS (?) PORIFERA.

### (*Spongida, Spongiae, Spongiariae*).

*Coelenterata of very varied and often inconstant shape; frequently massive; devoid of tentacles. Concrescence between parts of the same individual or of different individuals of the same species is very general. The body-wall is perforated by innumerable minute inhalent pores, and as a rule by one or more larger exhalent apertures—the oscula. The epithelia are unilaminar, the endoderm cells typically collared and flagellate, or in certain regions only, flattened and either flagellate or non-flagellate. The gastric cavity is (1) simple and either tubular or vasiform; or (2) tubular with radial outgrowths or cones, a system of inhalent canals more or less complex leading to it, and the tubular central cavity sometimes partially replaced by a system of exhalent canals; or (3) it is represented by sac-like, pyriform, or spherical ampullae with inhalent and exhalent canal systems as in (2), the central cavity being as a rule much restricted in extent. Skeletal structures are rarely absent, and consist of either variously shaped spicules hardened by calcite or silica, or of horny spongin fibres with or without siliceous spicules or foreign inclosures. Unisexual or hermaphrodite. The sexual cells are mesoglaeal: the ovum develops into a ciliated larva within the mesoglaea*

except in *Clione* (? *Clionidae*). *Discontinuous gemmation occurs in two forms. Colonial* (?). *Marine with the exception of the freshwater Spongillidae.*

The external outline of the body even when most constant and characteristic, e. g. in some *Calcarea*, many *Hyalospongiae*, is not uniform as it is in other Metazoa. Indeed, it is extremely variable in most instances, the variability amounting to Polymorphosis, or change of form without a corresponding physiological division of labour; see p. 238. The variability in question depends chiefly on two factors:—(1) an irregular mode of growth; and (2) on concrescence or a fusion of parts belonging to the same sponge, the same colony (?), or to sponges of the same species growing hard by one another. Such fusion frequently leads to the enclosure of spaces really external to the sponge-body, which form a false gastric cavity (pseudogaster) opening by a false osculum (pseudosculum s. pseudostome) and false pores (pseudopores). Anatomy, especially that of the gastric and skeletal systems, affords at present the only characters of classificatory value.

The primitive Poriferan, as seen in the simple form (*Olynthus*) of the Asconid *Leucosolenia* (*Ascetta*) *primordialis*, is a vasiform individual with an osculum or aperture at one end and a peduncle of attachment at the other; with thin body-walls perforated by numerous pores, and a gastric cavity of the same shape as the body, lined throughout by collared and flagellate endoderm cells. Such simple forms are few, and the external shapes assumed by Poriferans are very numerous and may differ at various stages of growth. A radial symmetry may be acquired by the development of conular outgrowths from the body or by the arrangement of the skeleton. But a sponge may be a shapeless or sub-spherical mass, tubular, cup or saucer-shaped, columnar, leaf or fan-like, branched or dendriform. It is very rarely, if ever naturally, free; but either adherent to some foreign object or rooted in sand or mud by basal processes or by spicules as in many *Hyalospongiae*. The Calcarean *Homodermis* is an exceptional instance of the union of individuals by a creeping tubular stolon. The *Clionidae* bore into shells or stones<sup>1</sup>. The thickness of the body-wall undergoes great increase, and its consistence is variable, both depending largely on the character of the mesoglaea and the skeleton. And the gastric cavity undergoes at the same time great changes.

The ecto- and endo-derm are unilaminar. The former consists as a rule of flattened, rarely cubical, polygonal cells, with clear contents

<sup>1</sup> Nassonow states that the larval *Clione* commences to bore into a shell as soon as it fixes itself, and before any skeletal structures are developed. It throws out slender processes, which perforate the shell-substance and cut out small semi-ellipsoidal pieces, which are taken up and then cast out by the sponge. The penetration of the shell-substance is effected beyond doubt by chemical means. See Z. W. Z. xxxix. pp. 297-300.

except immediately round the nucleus. Each cell bears a flagellum in *Oscarella (Halisarca) lobularis*, *Plakina monolopha*, *Aplysilla violacea*, and *Dendrilla*<sup>1</sup>; and in *Halisarca Dujardini* the cells appear to change into a slimy layer. The pavement epithelium lining the inhalent cavities and canals (pp. 793-5) is probably always, in some cases certainly, of ectodermic origin. The endoderm cells are typically flagellate, the base of the flagellum surrounded by a clear collar—an extension of the exoplasm of the cell. The endoplasm is variably granular and pigmented: it generally contains vacuoles (? contractile). The cells are large in the *Calcarea* (.012 mm.), small in *Non-Calcarea*. Their shape is not the same in all sponges: they are as a rule closely apposed, but in *Euplectella* are planted apart in diagonal lines, connected, however, by slender cords of protoplasm. This typical endoderm is restricted, except in *Calcarea Homocoela*, to limited portions of the gastric cavity, and is reduced in the oscular tube and exhalent cavities and canals (*post*) to a pavement epithelium, flagellate in *Oscarella lobularis*, *Plakina monolopha*, and *Aplysilla violacea* (at least in part), but usually non-flagellate<sup>2</sup>. Columnar cells are sometimes found where the two epithelia pass into one another. The mesoglaea is scanty in *Calcarea*, especially in *Homocoela*, and most particularly so in the Hyalospongian *Euplectella*. It is soft or firm, hyaline or granular; it imbeds the skeleton, and contains cells of many kinds, some of which are contractile or muscular, whilst others have lately been regarded as sensory and nervous (pp. 806-7).

The gastral system is one of the most characteristic features of the Porifera; it opens externally by pores and oscula. The pores are very numerous, round or oval in shape; minute as a rule, e. g. in *Asconidae*, .01—02 mm. as a mean; sometimes large and small (macro-, micro-pores) in the same sponge; and in many instances capable of being closed either partially or completely. They are either scattered or aggregated in areae, and in

<sup>1</sup> Judging from von Lendenfeld's figures, the ectoderm is also ciliated in *Homoderma*, *Leucandra maeandrina* (*Calcarea*); in *Bajalus*, *Aulena villosa* and two species of *Euspongia*; see Proc. Lin. Soc. New South Wales, ix. Pl. 65, Fig. 33; Pl. 67, Fig. 43; *ibid.* x. Pl. 2, Fig. 4; Pl. 34; Pl. 37; Pl. 38, Fig. 2. The ectoderm cells are said to be sometimes not traceable, a fact due, perhaps, to faulty modes of preparation; see Harmer, On silver staining of marine objects, Mitth. Zool. Stat. Naples, v. 1884, p. 445. A cuticula has been described in some sponges, e. g. by Schulze, in some specimens of *Euspongia officinalis* (*Z. W. Z.* xxxii. p. 626), and on spots of the surface in *Aplysina aerophobia* where the ectoderm had been accidentally removed (*Z. W. Z.* xxx. p. 392). Von Lendenfeld traced the formation of a similar structure in *Aplysilla violacea* when the ectoderm was destroyed, derived from the superficial gland cells of the mesoglaea (*Z. W. Z.* xxxviii. pp. 255-6). *Ianthella* (*Darwinellidae*) has a distinct cuticle according to Poléjaeff, *Keratosa*, Challenger Reports, xi. p. 37.

<sup>2</sup> It is figured by von Lendenfeld as flagellate in *Leucandra maeandrina*, *op. cit. supra*, ix. Pl. 67, Fig. 43. Haeckel states (*Kalkschwämme*, i. p. 144) that the endoderm is multilaminar in certain *Asconidae*. No such arrangement has been found in any sponge examined by modern methods. An amoeboid condition of the endoderm cells has been observed in some *Calcarea*; cf. Metschnikoff, *Z. W. Z.* xxxii. p. 362.

the latter case generally perforate a thin pore-membrane stretched across a larger canal or aperture. False pores may be similarly aggregated. The whole pore-system is, properly speaking, inhalent, i.e. gives entrance to currents of water, but when there is no osculum certain pores are large and exhalent<sup>1</sup>. The osculum or proper exhalent vent is usually considered as the homologue of the mouth, a view beyond a doubt incorrect. (pp. 801-2). It is at first single, but during growth the number undergoes increase; and then the new oscula may be either scattered or grouped together. In leaf-shaped sponges they are more or less confined to one surface, the pores to the other (Poléjaeff)—a separation which is complete in the Calcarean family *Teichonidae*. The aperture may be superficial, at the apex of a papilla, depressed, or surrounded by a corona of spicules, as in *Homoderma* and some other *Calcarea*. It is often limited by a contractile membranous sphincter. Its size depends on that of the sponge in great measure. In the Calcarean *Asconidae* it has approximately the same diameter as the body, i.e. 1-2mm.: in *Heterocoela* it ranges from 1-2mm. or even more. The *Non-Calcareae* show great differences in this respect, and oscula of 8-10 mm. ( $\frac{3}{8}$  in. *circa*) have been observed. The absence of an osculum is known as lipostomy<sup>2</sup>.

The gastric cavity conforms to one of four types, all of which occur in *Calcarea*, only the third and fourth in *Non-Calcareae*. (1) The cavity is lined throughout by collared flagellate endoderm—*Calcarea Homocoela*. It is simple and more or less tubular in *Asconidae* and *Leucopsidae*; in *Homoderma* produced into a number of radial cones, thus forming a transition to the next type. (2) The cavity is divided into a central oscular tube lined by non-flagellate pavement cells, and a set of radial cones to which the collared flagellate endoderm is confined. The cones have a wide aperture into the oscular tube<sup>3</sup>; the pores open on their surfaces, and the spaces between them constitute an inhalent or 'intercanal' system of channels. This type characterises the family *Syconidae* among *Calcarea Heterocoela*. The cones may remain separate and independent, *Syconinae*; their walls may coalesce from place to place owing to the growth of mesoglaea converting the inhalent canals into irregular branched

<sup>1</sup> See von Lendenfeld's figure of a section of *Ascetta (Leucosolenia) Macleayi* (op. cit. ante, ix. Pl. 62, Fig. 12, cf. p. 1147), where small pores open externally, and large into a pseudogaster: so too in *Leucopsis* (ibid. p. 1089). He sometimes speaks of the inhalent canal closed by a pore-membrane as *the pore*; cf. Z. W. Z. xxxviii. p. 240-1. In *Euplectella* there are pores of large size (= oscula?) in the body-wall which open direct into the central cavity of the sponge, and have no connection to the gastric ampullae.

<sup>2</sup> The cause of lipostomy is generally assumed to be the obliteration of the osculum in growth. It is possibly never formed in some instances. *Euplectella* is often quoted as an example, but the sieve plate at the summit of the body contains ampullae identical with those of the body-wall.

<sup>3</sup> Haeckel terms these apertures 'gastral ostia.' He supposed the cones to possess also distal or 'dermal ostia,' non-existent according to more recent researches.

channels, and the surface of the sponge is smooth, *Uteinae*; and with the same coalescence the cones themselves may become branched, *Grantinae*<sup>1</sup>. Two sets of pores are to be distinguished in consequence of the establishment of the branched inhalent set of canals: the pores at the surface of the sponge, and the pores by which the canals open into the cones. A transition to the next type is indicated in the Uteine *Amphoriscus elongatus*, where a certain number of cones may have a common aperture into the oscular tube. (3) The collared flagellate endoderm is confined to sac-like chambers or ampullae of large size, which have a single wide aperture of about the same diameter as the ampullae themselves, into an exhalent canal. The ampullae are also set radially or vertically to the cavity of the canal. This type is seen in the Sylleibid genus *Polejna* (*Calcarea Heterocoela*)<sup>2</sup>; in *Euplectella*; in *Halisarca Dujardini*, where the ampullae are often branched, and *Bajalus*; in *Spongelia*, *Velinea*, *Aplysilla*, and to a less marked degree in *Dendrilla*<sup>3</sup>. The differences depend on the degree of complication observable in the inhalent and exhalent canal-systems which are present universally in this and the following type. The exhalent canals are short wide tubes, *Polejna* (*Leucilla*) *connexiva*; short tubes somewhat branched, *P. (L.) uter*; long tubes, simple in *Bajalus*, branched in *Halisarca Dujardini*, in *Aplysilla*, *Dendrilla*, *Velinea*, and *Spongelia*. The inhalent canals are more or less branched, wide in *Halisarca*, with pore membranes and subdermal cavities (*post*) in *Bajalus* and the Ceratine genera (? *Velinea*). Both systems of spaces are remarkably large, and the mesoglaea is reduced to mere anastomosing strands in *Euplectella*. The ampullae communicate with the inhalent canals as a rule by many pores, scattered over their surface, *Polejna*, *Euplectella*, *Spongelia*, or aggregated at the end opposed to the exhalent aperture, e.g. *Bajalus*, *Aplysilla*. The *Plakinidae* are transitional to the next type, the ampullae frequently communicating with the exhalent canals by a short tube (*Vosmaer*). In other respects they offer various degrees of complication, e.g. in *Plakina monolopha* the ampullae may open outwards by a superficial pore, whilst *Plakortis simplex* has subdermal cavities. (4) The ampullae are small, either pyriform with a funnel-shaped exhalent pore-canal, or spherical with a tubular canal. When the inhalent canals are

<sup>1</sup> The subfamilies named have been established by von Lendenfeld, Proc. Lin. Soc. New South Wales, ix. pp. 1090-1110.

<sup>2</sup> The family Sylleibidae, with two genera, *Vosmaera* and *Polejna*, is due to the same authority (op. cit. p. 1110). *Polejna* corresponds to Poléjaeff's genus *Leucilla* (*Calcarea*, Challenger Reports, viii. p. 51). *Vosmaera* is a peculiar type. The ampullae are disposed in a radial fashion round the oscular tube, but communicate with a branched inhalent and exhalent canal system. The genus corresponds to Poléjaeff's *Leucetta* in part, i.e. to *L. imperfecta* and *L. vera*. *L. Haeckeliana* is included by von Lendenfeld through apparently a mistake, as may be seen on comparing his definition, p. 1110, with Poléjaeff's figures, op. cit. Pl. VIII.

<sup>3</sup> *Darwinella* and *Ianthella* are stated by Poléjaeff to agree with *Aplysilla* (*Keratosa*, op. cit. xi. pp. 22, 23).



wide, the ampullae have many inhalent pores; when fine and tubular, several tubes may open into the same ampulla. This fourth type is found among *Calcarea Heterocoela* in the *Leuconidae*, and so far as is known also in the *Teichonidae* and in all thoroughly investigated *Non-Calcarea* except those under (3) *supra*<sup>1</sup>. The inhalent and exhalent canal systems are branched and of considerable extent. The superficial pores may lead either directly into ampullae or into canals which branch only slightly, e.g. *Oscarella lobularis*; into canals which first unite and then branch, e.g. *Chondrosidaë*; through pore-membranes either directly or indirectly by a narrow canal into a more or less extensive system of subdermal spaces, from which branching canals take origin—a very general mode. In the *Geodidae* and several *Ancorinidae* the pores may open each into a cortical funnel (*Isops*), or into narrow canals which unite, or into subdermal spaces, from which in either case cortical funnels lead into a system of anastomosing subcortical crypts, and these in their turn into the inhalent canals. The exhalent canals may be wide spaces, or slender canals, uniting together to form larger and larger spaces or canals, which open finally into an oscular tube. The length of the latter varies; when very short it is often termed cloaca. *Isops* has exhalent cortical funnels comparable in all respects to the inhalent<sup>2</sup>.

The subdermal spaces and subcortical crypts are not to be confounded. The former lie immediately beneath the outer surface, covered by a thin layer of sponge substance: they are large simple cavities usually communicating one with another<sup>3</sup>. The subcortical crypts form a set of anastomosing cavities between the cortex and medulla, i. e. at a deeper level than the subdermal spaces. The funnels or chonae (*supra*) are divided by a constriction into an outer part, the ectochone, long and cylindrical, and an inner part, the endochone, short and more or less hemispherical<sup>4</sup>. Other structures to be noted are the endogastric septa of Haeckel, cords or membranes extending into or across the oscular tube and anastomosing together. They are of secondary origin and occur in both divisions of Porifera<sup>5</sup>.

<sup>1</sup> Poléjaeff states that pore-canals to the ampullae are wanting sometimes in *Spongidae*; *Keratosia*, op. cit. p. 17. Transitional or variable forms between types (3) and (4) are certain to occur, and probably not infrequently.

<sup>2</sup> In the *Auleninae*, the sponge appears to have a very irregular mode of growth into processes or lamellae. The intervals between the lamellae, &c., are generally traversed or protected by perforated membranes, thus becoming lacuniform. The lacunae are common both to the pores and oscula. Von Lendenfeld, Proc. Lin. Soc. New South Wales, x. p. 283; cf. his table, p. 490.

<sup>3</sup> The spaces in question are traversed in *Bajalus* by anastomosing filaments, in *Dendrilla* by slender vertical filaments, in both cases composed of mesoglaea covered by epithelium.

<sup>4</sup> For the subcortical crypts and funnels, see Sollas, A. N. H. (5), v. pp. 135, 140, 252; and on *Isops*, pp. 396, 402.

<sup>5</sup> See Haeckel, Kalkschwämme, i. p. 252; Vosmaer, Mitth. Zool. Stat. Naples, v. p. 489, and Porifera, Bronn's Thierreich, &c., ii. p. 128.

The skeletal structures are either inorganic or organic, separate or in union, or partially, very rarely completely, represented by foreign inorganic bodies. They are rarely absent entirely, as in *Oscarella*, *Halisarca*, *Bajalus*, and *Chondrosia*, and are always lodged in the mesoglaea. The proper inorganic skeleton is made up of spicules. A spicule consists of a very scanty organic basis or spiculin, laminated, hardened by Calcium carbonate as Calcite in the *Calcarea*, by colloidal silica in the *Non-Calcarea*, and inclosing an axial thread of organic matter, the so-called canal, said to be absent sometimes. It is formed in the first instance within a cell<sup>1</sup>, beyond which it soon projects. It continues to increase in length and thickness. The calcareous spicule is covered by a sheath or cuticle, by the calcification of which the spicule grows, and outside the cuticle by a layer of mesoglaeal cells except when it projects freely, the covering cells in this case being derived from the ectoderm (or in the gastric cavity from the endoderm?). The siliceous spicule appears to remain in close connection with a cell until it is of full size. When it projects above the surface it is, so far as is known, naked. It sometimes attains a great length, especially in the rooting spicules of *Hyalospongiae*, e. g. of *Hyalonema*, which reach even two feet or more. As to shape, four leading types are recognised in accordance with the number of axes traceable. (1) Monaxile; straight and then pointed, blunt, or knobbed, smooth or spinulose; curved, and then of very various shapes—hook, anchor, bow, &c.: (2) triaxile, characteristic of *Hyalospongiae* and only present in rudiment elsewhere; the three axes are those of an octohedron, equal or unequal in length, one even suppressed in some instances: (3) tetraxile; the four axes are lines drawn from the centre to the vertices of a tetrahedron; of equal or unequal length; becoming triaxile by the suppression

<sup>1</sup> For the origin of the calcareous spicule within a cell, see Metschnikoff, Z. W. Z. xxxii. pp. 361, 369, and Balfour's Comp. Embryology, i. note p. 117; similarly for the siliceous, Keller, Z. W. Z. xxxiii. p. 334; Schulze, Z. W. Z. xxxiv. p. 421; Deszö, A. M. A. xvi. p. 640; Goette, Abhandl. Entwick. der Thiere, pt. 3, Leipzig, 1886, p. 16; Sollas, *infra*. Poléjaeff has described cells (calcoblasts) lying upon the calcareous spicules of *Ute argentea* and *Leuconia multiformis*, which, he suggests, may be concerned in their growth (*Calcarea*, Challenger Reports, viii. p. 32, Pl. VI. Fig. 3 c.). The statements in the text relative to the calcareous spicule are derived from von Lendenfeld's paper on the 'Histology of the *Calcispongiae*' in Proc. Lin. Soc. New South Wales, ix. pp. 979-80. Sollas states (A. N. H. (5), ix. p. 159), that he not only observed the origin of siliceous spicules within cells in the young *Craniella* s. *Tetilla cranium*, but that he found in this and some other sponges an association of a cell with 'all not fully developed spicules.' The relative proportions of silicified and organic layers to one another is variable, and the spicules may even be bendable; see Bowerbank, British Spongiadae, Ray Soc. i. p. 7 et seqq. The calcareous spicule is doubly refractile according to Haeckel. Max Schultze found that the organic layers of the spicules in *Hyalonema* were so: Die Hyalonemen, Bonn, 1860, pp. 17-18. For the proofs of the statement that the silica is in a colloidal condition, and the lime carbonate in the crystalline form of Calcite, see Sollas, Sci. Proc. Royal Dublin Soc. iv. 1885, p. 374. The siliceous spicule is often attacked by a minute vegetable parasite, the *Spongiophagus Carteri* of Martin Duncan (A. N. H. (5), viii. p. 120), and sometimes, perhaps, by *Achlya penetrans* so common in corals; see Id. Journ. Royal Micr. Soc. (2), i. 1881, p. 557.

of an axis, as appears to be the case with the triaxiles of *Calcarea* and some other Porifera: (4) polyaxile; as in the stellate, or the globular, spicule; the stellate globule, &c. The ends of the axes may be pointed, knobbed, or branched. Most sponges possess a variety of spicules when they are present: some *Calcarea*, *Renieridae*, and *Suberitidae*, have needle-shaped monaxiles alone. Structures may occur which fall under none of the four types, e.g. the amphidiscs of the gemmules of *Spongilla* (p. 250)<sup>1</sup>.

The siliceous spicules may be united in one of three ways; (1) by interlocking processes as in *Lithistidae*; (2) by a deposit of silica involving the bundles as a whole or only their ends as in most *Hyalospongiae*; and (3) by spongin or pseudo-keratose<sup>2</sup>, variable in amount, e.g. in *Halichondridae*, completely surrounding them as in many *Desmacidonidae*, or completely surrounding some, and only one end of others forming a hispid fibre as in *Ectyonidae*. Spicules united together are often termed 'skeleton' spicules, whilst the loose spicules which occur in the same sponge are known as 'flesh' spicules. When the spicules are all loose, they may lie in a confused manner, or disposed in regular bundles as in many *Tetractina*, or in a definite order as in *Calcarea*.

The organic skeleton, especially characteristic of the *Ceratina* (= *Keratos*), is composed of spongin, a substance close akin chemically to silk. It takes the form of triaxile spicules in *Darwinella*, side by side however with fibrous structures, the usual shape in which it occurs. The fibrous skeleton may consist of isolated and slightly branched stems, rooted to some foreign object, *Aplysilla*; of a much branched tree, *Dendrilla*; of a regular network in which the fibres are nearly equal in size, *Velinea*; or of principal radial or vertical fibres connected by more slender transverse fibres, e.g. *Spongidae*. The free extremities of the principal fibres lie immediately beneath the surface of the sponge which they raise into conuli (Fig. 12, A. c. p. 251). The fibre has a cortex and a medulla; the former laminated, yellowish, clear, refractile, polarising light to a variable degree (note 2, *infra*), the latter more or less granular and opaque. The relative proportions to one another of the two parts is not the same in all sponges, nor even in fibres of the same diameter in the same sponge. The medulla is plentiful in the *Darwinellidae* (= *Aplysillidae*) and *Aplysinidae*; so scanty in some *Spongidae* that the fibre appears homogeneous, though it is doubtful if it is ever really so. The formation and growth of the fibre are due to spongoblasts; see Fig. 12, C, p. 251. The apex of the fibre is capped by a mass of polygonal cells: its surface clothed with pyriform cells, placed

<sup>1</sup> For a shorthand mode of describing the spicular skeleton, see Vosmaer, *Tidschrift Nederl. Dierk. Vereen.* v. p. 197.

<sup>2</sup> The term 'pseudokeratose' has been proposed by Ridley (*J. L. S.* xv. p. 481) for a sponge-like material which does not polarise light. Vosmaer found great variability in the polarising power of spongin; sometimes none at all, as in *Aplysilla sulfurea* and *Siphonochalina coriacea* (*Mitth. Zool. Stat. Naples*, v. p. 491-2).

radially to it, and the two sets of cells are in continuity. The cortex increases by the addition to the apex of the fibre of caps of spongin prolonged laterally into lamellae. A certain proportion of medulla, derived probably by the metamorphosis of some of the polygonal cells in the apical cap, is inclosed between successive caps of spongin. The medulla becomes as a rule continuous throughout the system of fibres. A structure closely resembling that of the fresh formed fibre is retained in *Aplysilla*, *Aplysina*, and *Dendrilla*<sup>1</sup>.

Foreign inorganic bodies, such as grains of sand, spicules of other sponges, &c., commonly occur in the medulla of the fibres, either of the principal alone, or of all without distinction, in the *Spongidae* and *Spongelidae*. They are probably taken up by the caps of polygonal cells from the mesoglaea. Their amount may be trifling or considerable, and the connecting spongin much reduced and of soft consistence, e. g. in *Dysidea*, *Psammoclema*: or it may even disappear altogether as in *Psammopemma*. Foreign bodies frequently occur scattered through the mesoglaea, taken up from the surface of the sponge, and it has been supposed that a given sponge exercises a selective action on the material imbedded<sup>2</sup>. The peculiar 'skipping rope' fibres, i. e. filaments with a knob at each end, which occur dispersed in variable quantities in the mesoglaea of certain Ceratine sponges, are supposed to be either parasitic organisms or pathological formations caused by the presence of parasitic algae. They attain some length, e. g. 8—10 mm. ( $\frac{2}{5}$  in. *circa*) in *Hircinia variabilis*, and were at one time thought to be characteristic of a family *Hircinidae*<sup>3</sup>.

<sup>1</sup> Cells, probably imbedded spongioblasts, are found between the lamellae of the cortex in *Ianthella* (*Darwinellidae*) and in the medulla of *Dendrilla*. According to von Lendenfeld, who has studied the fibres of *Dendrilla*, these cells, which form layers between the caps of spongin, are destructive in nature,—hence spongioclasts. They destroy the caps of spongin and the inner layers of the cortex, and grow centrifugally, retaining their cap-like disposition. They also bore through the cortex at a spot where a branch is forming, and give origin to its medulla. Their powers become exhausted at last, and then they give origin to caps of spongin. Hence though the structure of the fibre resembles that which it has when first formed, it is not absolutely identical with it. *Aplysilla violacea* and *Aplysina* resemble *Dendrilla* in the structure of their fibres. The exact mode of formation of the medulla, how it becomes continuous throughout the fibres, how it increases, if it does increase in other sponges, are points unknown. See on the subject, von Lendenfeld, *Z. W. Z.* xxxviii. pp. 267, 285, 304; *Id. Z. A.* viii. p. 469; Poléjaeff, *Keratoso*, op. cit. pp. 4—12.

<sup>2</sup> On the inclusion of foreign bodies, see Schulze's remarks, *Z. W. Z.* xxxiii. p. 14. In *Halmenidus Vesparum* (*Auleninae*) the cortex of the sponge is filled with sand grains, large on the exposed portions, small in the sheltered or internal, cemented into a crust by spongin. *Dysidea*, *Psammoclema*, *Psammopemma* are described by Marshall, *Z. W. Z.* xxxv, together with *Phoriospongia*. The last-named affords an instance of a skeleton of foreign bodies, plus proper siliceous spicules. Some true horny sponges possess spicules; see von Lendenfeld, *Proc. Lin. Soc. New South Wales*, ix. p. 493; x. p. 490. Hence it is possible that *Phoriospongia* is a Ceratine in which the spongin is lost, as in *Psammopemma*. The relationship of the horny to other sponges is a vexed question. See Poléjaeff, *Keratoso*, op. cit. p. 76 et seqq.; Vosmaer, *Biol. Centralblatt*, vi. p. 187; von Lendenfeld, op. cit. *supra*, x. p. 483; *Id. Z. A.* vii. p. 201; *ibid.* viii. p. 484.

<sup>3</sup> See Schulze, *Z. W. Z.* xxxiii. p. 19; Poléjaeff, *Keratoso*, op. cit. pp. 12—16; and for the second view mentioned, von Lendenfeld, *Z. A.* viii. p. 483. Carter maintained, in 1878, the view

Many sponges have been found unisexual, others hermaphrodite, e.g. *Sycandra* (*Sycon*) *raphanus*, *Aplysilla violacea*, *Dendrilla*; others sometimes in one, sometimes in the other condition, e.g. *Oscarella lobularis*, *Halisarca Dujardini*<sup>1</sup>. The male element in hermaphrodite species usually ripens first. A coloration indicative of sex has been observed in *Chalinula fertilis* by Keller though not by Vosmaer, and the male and female *Spongilla lacustris* are said to differ structurally by Marshall. The sexual cells are wandering mesoglaeal cells which ripen in the mesoglaea. The spermato-spore of the *Calcarea* and *Verongia* (*Aplysinidae*)<sup>2</sup> becomes binucleate: its protoplasm so divides that one portion becomes a covering or enveloping cell, whilst the nucleus of the other multiplies and the nucleated mass gives origin to the spermatozoa. The whole spermato-spore in other sponges divides into spermatoblasts. The ovum of the *Calcarea* remains during growth an amoeboid wandering cell, but in other sponges it becomes spherical and acquires a fixed outline. Both spermato-spore and ovum in the *Non-Calcarea* are invested by a capsule of flat epithelium derived from mesoglaeal cells and generally arranged in a single layer, but in *Aplysilla violacea* and *Dendrilla* in several layers. And in the two exceptions named both sexual products collect in small masses, each mass invested by a common epithelial capsule with processes separating the individual spermato-spores or ova one from another<sup>3</sup>. The ripe ovum is naked<sup>4</sup>, more or less granular, with a clear exoplasm, sometimes pigmented. It undergoes impregnation, segmentation, and development into a ciliated embryo *in situ*, except in the burrowing sponge *Clione*, where it is expelled as soon as it is ripe enough to undergo development (Nassonow). Segmentation is total and as a rule regular; variably but slightly irregular in *Oscarella lobularis*; somewhat irregular in *Halisarca*

that the filaments in question, to which he gave the name of *Spongiophaga communis*, were vegetable parasites; see his paper on 'Parasites of the Spongida,' A. N. H. (5), ii. p. 165.

<sup>1</sup> The male or female element predominates in a given specimen of *Sycandra raphanus*. Unisexual individuals of *Oscarella*, &c., may have shed one or the other element. It is possible that all sponges may produce at one time sperm, at another ova. The sexual products ripen in the walls of the cones in *Syconidae*, among the ampullae of other sponges, in the base of incrusting sponges, or in the endogastric septa, e.g. in *Oscarella*.

<sup>2</sup> Poléjaeff, *Keratosa*, op. cit. p. 72. In the Calcarean *Asconidae* the ripe sperm-balls may frequently be found projecting into the gastric cavity. Hence Haeckel thought they were derived from endoderm cells. See Poléjaeff, *Calcarea*, op. cit. p. 33, and Vosmaer, *Porifera*, p. 413.

<sup>3</sup> In *A. violacea* the number of ova in each mass appears to increase by fission (?) to about forty, and subsequently to dwindle to four. The ovum of the same sponge is separated by a space from the walls of its capsule to which, however, it is suspended by a single peduncle cell. The contents of each mass of capsules ripen simultaneously in *Aplysilla* but not in *Dendrilla*. The ova of *Euspongia* are aggregated 10-30 in number within a small area near an exhalant canal, and the mesoglaea in which they lie is surrounded by a richly anastomosing network of canals. Poléjaeff states that the epithelial cells of the capsule of an ovum grow in volume during the formation of the embryo (*Keratosa*, op. cit. pp. 52-3).

<sup>4</sup> There is an egg membrane in *A. violacea* (von Lendenfeld), and a calcareous shell in *Sycaltis* (*Amphoriscus*) *testipara* and *S. (A.) ovipara* (Haeckel, *Kalkschwämme*, i. p. 157).

*Dujardini*, extremely so in *Chalinula fertilis*. The diameter of the embryo increases during segmentation, and when fully grown it passes into the gastric cavity and escapes by the osculum or by the inhalent canals. The parent sponge may then perish (*Chalinula fertilis*).

The free larva has one of three forms. (1) It is an oval blastula with a large blastocoele. The cells are all similar, and the blastocoele is soon filled by the immigration of cells at all points as in *Ascetta* (*Leucosolenia primordialis*), or at one pole as in *A. (L.) blanca* and *A. (L.) clathrus* among *Calcarea Homocoela*. The cells are collared and flagellate, and one pole is invaginated to form a gastrula in *Oscarella lobularis*. Or the posterior pole is a patch of rose-coloured non-ciliated cells as in *Verongia* (*Aplysilla?*) *rosea*<sup>1</sup>. (2) It is an oval amphiblastula, one half composed of large granular ectoderm cells, the other of columnar ciliated endoderm cells<sup>2</sup>, jointly inclosing a blastocoele. This larva occurs in all *Calcarea* save the three above-named and in the horny sponge *Gumminea* (*Halisarca?*) *mimosa*. In *Sycandra* (*Sycon*) *raphanus* the granular cells are derived by the growth of a circle of eight cells at one pole of the embryo after it has reached an advanced stage of segmentation (48 blastomeres): and the columnar cells are invaginated after a period of free larval existence, giving rise to a gastrula<sup>3</sup>. (3) It is solid, either oval or conical, with a posterior flattened or concave pole: its superficial cells are columnar, ciliated, disposed in a single layer, and form the ectoderm of the sponge. They inclose (i) a mass of cells projecting posteriorly as in *Chalinula fertilis*, *Esperia Lorenzii*, *Clione stationis* (?); (ii) a mesoglaea with cells, all stellate as in *Aplysilla sulfurea*, stellate in the centre, hour-glass shaped at the periphery as in *Spongelia pallescens*; (iii) cells each contained in a clear capsule, the protoplasm reduced to a stellate figure by an accumulation of a clear liquid as in *Euspongia*; (iv) a granular material (coenoblastem of Marshall) with a few nuclei and subsequently many cells as in *Plakina monolopha*, or many nuclei as in *Reniera filigrana* and apparently many other allied sponges. The origin of the contained nuclei or cells is not known except in *Euspongia*, where cells immigrate inwards during the

<sup>1</sup> *Halisarca Dujardini* is said by Barrois to have a blastula; by Metschnikoff to have a solid larva with cells arranged in rosettes, and perhaps derived by immigration. *H. pontica* has solid larvae, and two or three of them may fuse to form a zygoplanna.

<sup>2</sup> These ciliated cells are said to be collared: O. Schmidt, Z. W. Z. xxv. Suppl. pp. 129-30; cf. Haeckel, Kalkschwämme, i. p. 335.

<sup>3</sup> The opposite, i. e. invagination of the granular non-flagellate cells, was said by Keller to happen in *Ascandra* (*Leucosolenia*) *Lieberkühnii* and *Leucandra* (*Leuconia*) *aspera*, but the latter agrees with *Sycandra* (*Sycon*) *raphanus*, according to Metschnikoff. Barrois concluded that the granular cells gave rise to the endoderm in *Ascandra* (*Leucosolenia*) *contorta*, *Sycandra* (*Grantia*) *compressa*, *S. coronata* (*Sycon coronatum*) and *S. ciliata* (*Sycon ciliatum*), but he observed neither invagination nor the act of fixation. Schulze states that abnormal or transitory invaginations of the granular cells, giving rise to a pseudo-gastrula, may occur in *Sycandra* (*Sycon*) *raphanus*: they are occasionally of great extent but have no significance in development. See Z. W. Z. xxxi. p. 266.

progress of segmentation<sup>1</sup>. The posterior pole or the anterior (*Reniera*), sometimes both poles, are marked by a pigment patch. The larva is very sensitive to light, and as a rule attracted by it, more seldom repelled (*Reniera*). In *Chalinula fertilis* mesoglaea appears among the cells of the anterior and middle portions of the inclosed mass, and spicules, as is commonly the case, are formed in some of the cells near the periphery.

Fixation takes place by the gastrula mouth, which is subsequently closed in *Sycandra* (*Sycon*) *raphanus* and *Oscarella lobularis*<sup>2</sup>; by the projecting cell-mass at first in *Chalinula fertilis*, afterwards by one of the two sides of the larva which has now become flattened; by the posterior pole in *Plakina*; by the central mass protruding at the posterior pole in *Reniera filigrana*. The ectoderm cells throw out short pseudopodial processes for the purpose of fixation, which are retracted as development progresses; they lose their columnar form and are gradually flattened. The stages subsequent to the larval have as yet been accurately observed only in a few instances. *Sycandra* (*Sycon*) *raphanus* becomes cylindrical with a flattened free pole, in the centre of which the osculum is formed.—Before it appears, however, spicules are developed in mesoglaeal cells, and then protrude at the sides of the cylinder, which are pierced by pores. At the same time the endoderm cells, which lost their collars and flagella by absorption immediately after invagination, acquire them again. *S. ciliata* (*Sycon ciliatum*) may attain a height of 1 mm. before the radial cones begin to form as evaginations of the wall. The endoderm cells of the central tube flatten out and lose their flagella at a later period. In *Oscarella lobularis* the gastric cavity or archenteron develops a peripheral circle of diverticula, some large, some small, parallel to the surface of the sponge, and directed aborally. These diverticula are in the course of growth thrown first into radial, i. e. zig-zag folds; the folds are then divided by constrictions into an outer and inner circle of chambers or ampullae, and the outer circle is doubled in number by the radial division of each ampulla. A cross section, however, shows that the ampullae form a single superficial layer, a condition which persists in the adult, and is seen also in some *Plakinidae*. The ampullae open into the central gastric cavity, the cells of which are now cubical and flagellate but no longer collared, by wide mouths subsequently

<sup>1</sup> The anterior pointed pole and the posterior concave pole of the conical larva are said to be sometimes non-ciliate, and the latter to be girdled by cilia of exceptional length. But Schulze found the concave pole ciliated in *Spongelia* and *Euspongia*, and Keller states that in *Chalinula fertilis* it is non-ciliate before the escape of the larva, that it then acquires cilia but loses them just before fixation. In *Reniera filigrana*, according to Marshall, the central mass forces its way out at each pole of the oval larva when it is mature, and the anterior bare patch is surrounded by very long cilia.

<sup>2</sup> *Oscarella* is attached in later stages by one or two foot-like processes (=tentacles?), and here and there by the base of the sponge, i. e. by the surface formed on the closure of the gastrula mouth. Heider states that the ectoderm covering the feet is columnar and secretes a clear cement.

narrowed, and they acquire an opening to the exterior either by the fusion of the superficial ectoderm with the endoderm of an ampulla, and the perforation of the fused spot, or by ectodermic invaginations which communicate with two adjoining ampullae. The osculum is formed by the growth of a solid aboral mesoglaeal cone, the invasion of this cone by a diverticulum of the gastric cavity, and the fusion and perforation of the ecto- and endo-derm at its apex. Mesoglaea appears between the ecto- and endo-derm after fixation in both sponges alike; its cells are derived in *Sycandra* (*Sycon*) from the ectoderm, in *Oscarella* from the endoderm<sup>1</sup>. The attached larvae of *Chalinula fertilis*, *Plakina monolopha*, and *Reniera filigrana* become flattened, but of the first-named subsequently raised into an eminence. The gastric cavity makes its appearance as an incomplete or complete ring, afterwards widening into a simple central space in *Plakina*, as a simple space in the other two named. The spaces are lined by a single layer of columnar cells delaminated from the common cell-mass. The ampullae originate in *Chalinula* from groups of deeply coloured cells, which acquire a cavity and open into the central space; in *Reniera* as outgrowths of the central space. In *Plakina* they are oval chambers lined by collared cells, opening as in *Chalinula*, but their mode of origin is not known. The cells of the central mass remaining after the differentiation of the endoderm become mesoglaeal cells, a gelatinous substance appearing between them. The osculum of *Chalinula* is central, of *Plakina* marginal, but in both formed seemingly as a simple perforation. In *Reniera* the central space extends towards the surface and opens in the anterior protruded portion of the central mass of the larva. The pores and inhalent canals of *Plakina* are believed by Schulze to be of ectodermic origin. The outgrowths of the central space in *Reniera* not only give origin to ampullae and the exhalent canals, but outgrowths from the ampullae to other ampullae and to the inhalent canals. The latter open outwards through the ectoderm in protrusions of the mesoglaea (Marshall)<sup>2</sup>.

The development of the freshwater *Meyenia* (*Spongilla fluvialis*) is, if Goette's results are to be trusted, extremely peculiar in some respects. The primitive ovum divides; one of the cells thus produced grows into the

<sup>1</sup> The ectoderm cells in question of *Sycandra* (*Sycon*) may be differentiated in part before fixation (Metschnikoff). Heider thinks that the blastocoele of *Oscarella* is filled by a gelatinous fluid from which the first-formed mesoglaea is derived. The growth of the mesoglaea probably causes the formation of the diverticula and their resolution into ampullae, above described. It is possible that new ampullae may develop as evaginations of the endoderm at or near the base of the young *Oscarella*.

<sup>2</sup> In *Halisarca Dujardini* certain of the cells in the newly attached larva, which is solid, become grouped; within each group is formed a canal; the canals are at first independent, but afterwards fuse into a system with a central space. So, too, in *Ascetta* (*Leucosolenia*) *primordialis* and *A. blanca*, a portion of the cells lengthen and are radiately arranged round a common centre, where a space has been observed in the latter of the two sponges named. A delamination of the contained cell-mass into endoderm and mesoglaeal cells is probably characteristic of all solid larvae.



definitive ovum, and of the remainder some perhaps take part in forming the follicle, whilst others are nutritive, and either atrophy or fuse with the ovum. Segmentation is total; the blastomeres are irregularly massed; a cap of cubical cells, the ectoderm, is differentiated and grows round the remaining cells, which inclose an 'endodermal' cavity excentrically placed near one—the apical—pole, but of no significance. The ectoderm becomes ciliated. The metamorphosis of the ovate larva may be accomplished after fixation, which takes place by the apical pole, during its free life or within the egg-follicle. Its two principal features are the loss of the ectoderm and the obliteration of the endodermal cavity. The cell-mass inclosed by the ectoderm forms the sponge. Its most superficial cells become epidermis. Spaces or gaps between the cells give rise to the pores and oscula. The ampullae are formed independently of one another from large cells which bud, a cavity appearing in the cell-mass. Several such may fuse together. The subdermal cavities, the in- and ex-halent canals, are developed from intercellular spaces, their epithelium from amoeboid cells<sup>1</sup>.

As to asexual reproduction, fission does not occur among Porifera, but the washing Sponge (*Euspongia*) may be propagated artificially from fragments. It is generally said that many sponges are colonial. Where individuals conresce, or where there is, as in *Homoderma*, a creeping tubular stolon connecting the individuals, there can be no doubt about the question<sup>2</sup>. And in those instances where a given sponge consists of columnar or cylindrical masses united by a common base or stem, and furnished each with its own osculum, it is natural to regard it as a colony. But oscula cannot be considered as the equivalents of mouths; they are often absent; and though a young sponge just developed from a larva possesses but one osculum, it is doubtful if an increase in the number of such apertures as the sponge grows in size necessarily indicates the occurrence of continuous gemmation<sup>3</sup>. Discontinuous gemmation, however, occurs, and falls under two types. (I) In the Calcarean *Ascandra variabilis* = *Leucosolenia botryoides* tubular outgrowths of the body-walls are developed and set free, the aperture formed by detachment becoming the osculum of the new

<sup>1</sup> According to Ganin, the larval ectoderm persists; the endodermal cavity becomes the internal cavity, and outgrowths of it give rise to the ampullae, but the subdermal cavities originate independently as spaces between the ectoderm and mesoglaeal cells.

<sup>2</sup> Whether or no buds are formed by the solid branching stolons of *Esperia stolonifera* from the White Sea, described by Merejkowsky (Mem. Imp. Acad. St. Petersburg (7), xxvi. No. 7, p. 23), seems uncertain.

<sup>3</sup> The ampullae probably multiply by division, or by the separation of a small part: see Keller on *Reniera semitubulosa*, Z. W. Z. xxx. p. 579. Schulze states that isolated ampullae are met with on the walls of the oscular tube where they are very thin in *Oscarella lobularis*: see Z. W. Z. xxviii. p. 23, Pl. II. Fig. 9. The view held by some authorities that the ampulla represents an individual, is negated by the facts of embryology and the undoubted homology existing between ampullae and radial cones.

sponge. (2) In *Tetilla radiata*, *T. euplocamus* (*Ancorinidae*), and *Tethya maza* (*Tethyadae*) mesoglaeal cells multiply and form a mass near the surface of the sponge. They surround in the *Tetillae* in question 12-20 ampullae, but in the *Tethya* ampullae grow out among the cells and then multiply in number. The bud-mass is gradually extruded either along a fascicle of spicules belonging to the parent, or by an outward movement of the fascicle. It has an ectoderm; spicules develop in it and in the *Tethya* named subcortical spaces. In *Tetilla japonica* the mass of cells contains no ampullae, nor does it in *Tethya lyncurium*, where it originates by the division of a single cell. Buds of a similar external character, the histology of which is not known, occur also in two or three other species of *Tethya*, in a *Suberites*, and in *Rinalda* (= *Polymastia*?) *arctica*. They are developed in the last-named at the apex of hollow conular processes of the sponge, the walls of which are perforated by pores<sup>1</sup>; and there are usually two or three buds in a line, one beyond the other, connected by spicules, and a small quantity of sponge-substance, a phenomenon seen also occasionally in a *Tethya* from the White Sea. In *Craniella Mülleri* (= *Tethya* s. *Tetilla cranium*) buds of the same kind develop into sponges within the parent. The freshwater *Spongillidae*, with one or two exceptions, develop resting buds, the seeds or gemmules, at the commencement of the winter in cold regions, of the hot season in tropical. They possess a protective envelope or case, an organic membrane hardened, at least in some instances, by silica, generally strengthened by siliceous spicules as well, often complex in structure and provided with a single aperture, or with a principal and several secondary apertures. A hydrostatic apparatus, or vesicular dilatation of the special membrane or cuticle, which immediately invests the contents of the case, closes the aperture in two instances. The envelope is said to be formed by the outer layer of cells of the gemmule in *Meyenia* (*Spongilla*) *fluviatilis*, by mesoglaeal cells in *Spongilla lacustris*. Its contents are granular cells, closely packed, derived from mesoglaeal and transformed endodermal cells. When climatic conditions are favourable, they escape and reproduce the sponge. See p. 250<sup>2</sup>. The production of gemmules brings about the death of the sponge.

A peculiar mode of propagation has been observed in *Oscarella*

<sup>1</sup> Merejkowsky thinks that these conular processes are converted into oscular tubes, after having served as supports for the buds: Mem. Imp. Acad. St. Petersburg, (7), xxvi. No. 7, p. 10.

<sup>2</sup> Goette, Wierzejski, and Marshall do not quite agree in their accounts of the mode in which the gemmule and its case are formed. See the summary by Vosmaer, Porifera, Bronn's Thierreich, ii. pp. 428-9; Goette, Abhandl. Entwicklungsgeschichte der Thiere, Leipzig, pt. 3, 1886, p. 21; Wierzejski, Archives Slaves de Biologie, i. 1886; Marshall, SB. Naturf. Ges. Leipzig, 1884, pp. 22-9, or Journ. Royal Micr. Soc. (2), v. 1885, p. 1011.

Gemmules were said by O. Schmidt to occur in a marine *Reniera* (Z. W. Z. xxv. Suppl. p. 139): but Keller states that he observed similar structures in a dead *Chalinula fertilis*, and that they proved to be the egg-masses of a *Dinophilus* (Z. W. Z. xxxiii. p. 341).

*lobularis*. The papillae of the surface, or the whole sponge, if small, may be converted into globular vesicles or brood-buds, 2-3 mm. in diameter. The wall of such a bud is composed of ectoderm, mesoglaea and endoderm. It contains semi-globular ampullae, which open externally by narrow pore-canals, internally by a single aperture. Its internal cavity is the dilated exhalent canal system of the papilla or sponge, as the case may be. These brood-buds float about, but finally settle down, flatten out, and give rise each to a new sponge.

With the exception of *Spongillidae*, the Porifera are marine. They are found in all seas. The *Calcarea* are cosmopolitan. The majority of *Hyalospongiae* live at depths greater than 150 fathoms, often descending below 400, as do the *Lithistina* below 100. Most *Halichondrina* and *Ceratina* are restricted by a zone of 50 fathoms, the *Calcarea* of 100, but *Ascetta* (*Leucosolenia*) *blanca* has been dredged at 450. Sponges frequently shelter animals of other groups, especially Crustacea, within their canal systems. As to size, they vary extremely, some attaining a maximum limit, others differing much. The *Calcarea* are small; e.g. the mean size of the *Asconidae* is 1-3 mm., of the *Syconidae* and *Leuconidae* 15-20 mm. (i.e.  $\frac{3-4}{5}$  in.). The goblet sponges, *Poterion*, are the largest known. *P. Amphitritae* may attain a height of  $3\frac{1}{2}$  ft., and its cup a diameter of  $2\frac{1}{2}$  ft. The *Calcarea* are colourless; other sponges are variously tinted, but usually of one colour. The *Spongillidae* possess chlorophyll; see pp. 242-4, 251. The yellow pigment Aplysinofulvin turns blue, then black on exposure to air. In some instances coloration is due solely to algae living in the mesoglaea<sup>1</sup>. Many sponges exhale a strong and peculiar odour somewhat resembling oxydising phosphorus or ozone<sup>2</sup>. Fossil forms are numerous. As to *Calcarea*, a Syconidan, *Protosycon*, has been found in Jurassic strata, and an extinct group, the *Pharetrones* of Zittel, represented by a single species in the Devonian, is greatly developed in the Mesozoic period, and dies out in the Eocene<sup>3</sup>. Of the *Non-Calcarea*, the *Hyalospongiae* and *Lithistina* appear in the Silurian, and attain their maximum development

<sup>1</sup> See the table in Vosmaer, Porifera, p. 458; Brandt, Mittheil. Zool. Stat. Naples, iv. p. 223, and Carter, A. N. H. (5), ii. 1878. According to Brandt, *Zooxanthella* (see p. 243, ante) is found in *Hircinia variabilis* and *Reniera cratera*.

<sup>2</sup> See Krukenberg, Vergleich. Physiol. Studien (1), 2, p. 37, and cf. p. 44. The smell is probably due to an ethereal oil.

<sup>3</sup> Inasmuch as lime often replaces silica and *vice versa* in the fossil spicules of sponges, the position of the *Pharetrones* has been much debated. But the complete accordance of their spicules with those of living *Calcarea*, the fact that they may be oval or rhomboidal in section, whilst true siliceous spicules are round, has led the most recent authorities to support Zittel's view. See von Dunikowski, Palaeontographica, xxix. 1882-3; Hinde, A. N. H. (5), x. 1882, and Catalogue of Fossil Sponges, Brit. Mus. 1883, p. 157; Sollas, Sci. Proc. Royal Dublin Soc. iv. 1885, p. 387, and cf. pp. 389-90. Calcarean spicules occur in Pleiocene beds (Hinde, Quart. Journ. Geol. Soc. xlii. 1886, p. 214). For lime replacing silica, see Sollas, A. N. H. (5), vi. p. 437 et seqq., and *vice versa*, Id. Quart. Journ. Geol. Soc. xxxiii. pp. 252-4, 813-19, 835; cf. Hinde, Ph. Tr. 176, pp. 425-33.

in the Upper Chalk; the *Tetragonina* are sparingly represented in Carboniferous strata and the Chalk. Shells, bored, as it is supposed, by a *Clione*, occur in Jurassic, Cretaceous and Tertiary formations, and the spicules of a *Spongilla* (*Sp. Purbeckensis*) have been detected in freshwater limestones of the Purbeck series (Jurassic).

The mesoglea is soft or firm, hyaline or granular; it contains cells of various kinds, and sometimes fibres. The cells are either naked or provided with a delicate membrane. They fall under the following heads:—(1) fusiform or stellate cells, the latter sometimes connected by their processes; (2) pigment cells; (3) vacuolated cells; (4) amoeboid cells of variable shape and wandering habit, sometimes becoming granular and then vacuolate, or converted into hyaline, refractile, lumpy bodies of irregular shape with fat-like contents (*Chondrosia*), or partially filled by a starch-vacuole<sup>1</sup>. Fibres or fibrils united in bundles or lamellae, and apparently non-nucleated, occur in some instances, e. g. in *Chondrosia*, but never in *Calcarea*. Other forms of cells are the spongioblasts, the spicule-bearing cells, gland-cells, contractile fibre cells and nervous cells. The gland-cells are saccular or pear-shaped, disposed in a single layer below the ectoderm, towards which one or more granular processes extend. They are found in many *Non-Calcarea* and some *Leucone Calcarea*, and have been most completely investigated in *Aplysilla violacea* and *Dendrilla* by von Lendenfeld (Z. W. Z. xxxviii. pp. 254-6; 278-80). He found that if the ectoderm were injured, the cells in question secreted a slimy substance (? spongin), hardening under water in about twenty-four hours into a cuticle, beneath which a new ectoderm and layer of gland cells were developed. The contractile fibre cells are fusiform, nucleated, and in *Euspongia canaliculata* (= *anfractuosa*) showing traces of transverse striae, more or less regular<sup>2</sup>. They are found sparingly in *Calcarea Heterocoela*, but are very common in the *Non-Calcarea*, round the pores and oscula, accompanying the inhalent canals or the bundles of spicules, e. g. in *Tethya*, or in the cortex (p. 807), or surrounding the fibres of the skeleton in *Aplysilla violacea* and *Dendrilla*. Nervous elements have only been detected recently: their character and position leave little doubt as to their real nature. There are two forms of them, the palpcil and synocil. The former is a delicate

<sup>1</sup> The granules in the granular cells appear to be albuminoid; cf. Keller, Z. W. Z. xxx. pp. 570-2; fat-like bodies are described in *Chondrosia* by Schulze, Z. W. Z. xxix. p. 104; starch-containing or amyllum cells in various sponges by Keller, op. cit. pp. 572-6. Brandt considers that the starch is due to the presence of algae: see Mitth. Zool. Stat. Naples, iv. pp. 232, 296. For starch vacuoles and granules in *Spongilla*, see Ray Lankester, Q. J. M. xxii. p. 241. Carter states that starch is met with in the ova of marine sponges as well as in the gemmules of *Spongilla* (A. N. H. (5), xii. 1883). Krukenberg has found an ethereal oil in *Chondrosia* and some other sponges (Vergl. Physiol. Studien, (1), ii. p. 42 et seqq.).

<sup>2</sup> These cells resemble in form the smooth or non-striped muscle-cells of many Metazoa. They are certainly endowed with contractility, and the closure, whether complete or incomplete of the pores, &c., or movements of the surface of a sponge, are, beyond doubt, due to their action. They are called contractile fibre cells because they have no connection with a nervous system; but, if recent discoveries are correct, and there is connection between the sense, ganglion, and fibre-cells of the pores or canal system, as von Lendenfeld supposes in some instances, then they may be termed muscle-cells. It is difficult to say what their function may be when they surround the skeletal fibres as in *Dendrilla*.

free process, springing from a mesoglaeal cell with one or more basal outrunners, near to which cells apparently ganglionic have been detected occasionally. A syncil, as yet observed only in a *Sycandra*, is a process of mesoglaea, 1 mm. long, containing a number of fine filaments derived from as many cells situate at its base<sup>1</sup>. Palpocils have hitherto not been found in *Calcarea Homocoela*: but in other sponges they occur round or near the pores of the inhalent canals (various *Syconidae*, *Vosmaera gracilis*); on the outer surface in groups or singly (various *Leuconidae*); upon the vestibular membranes (*Aulena villosa*); upon the membranes of the lacunar inhalent system (*Halme globosa*); or bordering the margins of the lacunar extensions of the exhalent system (*Euspongia canaliculata* = *anfractuosa*).

There is in some *Non-Calcarea* a marked structural difference between the superficial and deep portions of the mesoglaea, constituting a cortex and medulla. This is especially the case in *Chondrosidae*, where the cortex is fibrillate; in *Corticium*, where it contains lacunae, each lodging a cell which fills it partially; in *Weberella*, *Polymastia*, &c., where it has a plentiful mesoglaea, imbedding stellate and fusiform cells and fibrils; in *Tethyadae* and *Geodidae*, where its structure is complex, due partly to layers of peculiar spicules, of cells, of contractile fibre cells. The mesoglaea round the ampullae is generally granular, but not in *Spongelidae*.

The mode in which nutrition is effected has given rise to much debate. A living sponge is traversed by currents of water passing in at the pores and out of the oscula, or, if oscula are absent, out of other pores (see p. 793, and note 1). The currents may be suspended, but probably not reversed: they may be swift (? nutritive) or slow (? respiratory). Nutritive substances, whether animal or vegetable, alive or dead, are carried into the sponge suspended in the currents; and they have been observed in the mesoglaeal cells; see Metschnikoff, Z. W. Z. xxxii. pp. 372, 374; von Lendenfeld, Z. W. Z. xxxviii. p. 254. Particles of carmine suspended in water are taken up solely by the collared cells in the young *Spongilla* (Carter) and *Oscarella* (Heider). Metschnikoff found (loc. cit.) that in *Ascetta* (*Leucosolenia*) *primordialis* and *Spongilla* carmine particles were taken up by the collared and mesoglaeal cells; so too in *Haliscarca Dujardini* and *H. pontica*. Over-feeding the latter caused obliteration of the canals. On the other hand, no carmine was discoverable in the ampullae of *Reniera aquaeductus* and *Siphonochalina coriacea*, though present in the mesoglaeal cells. Von Lendenfeld experimented on *Aplysilla violacea*. Carmine particles were taken up by the epithelia of all parts if the sponge were kept for a sufficiently long time in water containing them in suspension; but the particles absorbed by the ectoderm of the subdermal cavities soon passed into the amoeboid wandering cells which were present in numbers in that part of the sponge; by them they were conveyed to the ampullae, and then excreted by the collared cells in a few days' time. Their angles were rounded off. Particles absorbed by the collared cells themselves were expelled unchanged. Whilst the epithelia of the subdermal cavities and ampullae, and the mesoglaeal cells were thus freed from carmine, this was not the case with the epithelia of other parts, even after the lapse of two months. The obvious conclusion is that absorption takes place by the ectoderm of the subdermal cavities, digestion by the mesoglaeal cells, excretion by the collared cells. Poléjaeff thinks (*Calcarea*, p. 15) that a nutritive function must be assigned also to the endodermic

<sup>1</sup> The syncils probably shrink at death; hence their cells may become separated.

pavement cells. He finds (op. cit. p. 16) that the pavement cells here and there in the inhalent canals, in the exhalent, or in both alike, may be swollen and more granular than usual, facts very well seen in *Leucetta vera*<sup>1</sup>. The mechanical objections he urges (op. cit. p. 15) against the view that the collared cells are the chief agents in the absorption of food, do not seem well founded, especially if the flagella may be supposed to act in a manner similar to that in which they act in the *Choanoflagellata*. It may be noted that Krukenberg has extracted a diastatic and peptic ferment from many sponges: the peptic ferment is replaced by a tryptic in very few instances (*Sycon* = *Sycandra*, *Reniera porosa*, &c.). A piece of raw fibrin laid upon the surface of *Suberites massa*, *S. domuncula*, *Chondrosia reniformis*, underwent resorption: so too in the osculum of *S. domuncula*. Surface digestion did not take place, however, in *Hircinia variabilis*, *Spongelia elegans*, and *Euspongia adriatica*. Fibrin was also digested when inserted into the mesoglaea of *Suberites massa*, but not of *S. domuncula*. See Krukenberg, Vergleich. Physiol. Studien (1), i. 1881, pp. 65-75; and on reserve material in sponges, ibid. ii. p. 42 et seqq. p. 57; cf. ibid. iii. p. 113.

Vosmaer and Heider regard the Porifera as a type in value coordinate with Coelenterata, Poléjaeff, Schulze, and others as a sub-type, agreeing with a sub-type represented by the three other Coelenterate classes as far as the gastrula-stage, and then diverging. The group is retained here among Coelenterata for reasons given pp. 715-16; but in the present uncertain state of opinion the value of a class assigned to it must be deemed provisional only. Both Vosmaer and Poléjaeff term the *Calcarea* and *Non-Calcarea* classes, but it may be doubted whether the essential distinction between them, viz. the hardening of the spicules by calcite or colloidal silica respectively, is a sufficient basis for so great a classificatory distinction. The differences that obtain between some of the orders of Insecta are quite as great. As to the subdivisions of *Calcarea* and *Non Calcarea*, they constitute in the former a well-defined series, but in the latter their mutual relations, and in the *Spiculispongiae* and *Cornacuspongiae* their limits, are by no means established.

The points to be borne in mind in determining the position of the Porifera seem to be as follows:—(1) There are various forms of larvae, the one known as amphigastrula being probably a modified and not a primitive one; (2) the gastrula is formed either by invagination, or by delamination from cells the common rudiment of both endoderm and mesoglaeal cells; (3) the invaginate gastrula is fixed by its mouth, and the osculum is a secondary formation; but the gastrula cavity is a true archenteron, and there is no reason for withholding the term 'gastric cavity,' used in a morphological sense, from the various forms assumed by the archenteron in the adults; (4) the inhalent system of canals is primitively formed by foldings of the surface of the body, and the pores are probably structural adaptations to the mode of fixation; (5) the increase of the mesoglaea, and the consequent irregularity of form are possibly dependent on the presence of pores; (6) the skeleton is formed entirely by the mesoglaeal cells as in some *Anthozoa Alcyonaria*, and is much

<sup>1</sup> It is possible that there are sponges in which there are no ampullae. At least Vosmaer has been unable to detect them in the thin fan-shaped *Phakellia*: see Bijdrag tot de Dierkunde, pt. 3, No. 12, Sponges of the Willem Barents Expedition, 1885, p. 24, Fig. 12. Canals pass from one side of the body to the other in these instances.

specialised; (7) the typical collared character of the endoderm cells is a unique feature; but it must not be forgotten that in the planula or larva of *Oscarella lobularis* the ectoderm cells are also collared; (8) the group is one of extreme antiquity.

A small group, the *Gastreae* of Haeckel, of doubtful affinities may be mentioned here. They are marine sponge-like organisms with a body-wall composed of an ectodermal syncytium (? mesoglea + ectoderm) and a ciliated collared endoderm, supported by a skeleton of sponge-spicules, Radiolarian shells, &c., according to habitat. Pores are absent. There are two sub-groups: (1) *Physemaria*, body-wall thin, solid, a single osculum, with four genera, two solitary, *Haliphysema*, *Gastrophysema*, and two colonial (?), *Dendrophysema*, *Clathrophysema*; (2) *Caementaria*, body-wall thick, traversed by gastral tubes lined wholly or in part by ciliated endoderm, mostly deep sea, with four genera, *Caementascus* with a single osculum, *Caementoncus*, *Caementissa* and *Caementura* with several. Ova have been seen in several instances: filiform spermatozoa and an invaginate gastrula in *Gastrophysema dithalamium*.

The group requires a careful re-examination. *Haliphysema Tumanowiczii*, which was originally described as a sponge by Bowerbank, has been proved to be one of the Protozoan *Reticularia* by Kent, Lankester and Möbius, as it was surmised to be by Carter. Moreover, it is identical with Carter's *Squamulina scopula* = *Gastrophysema scopula* according to Norman, which Carter supposed originally to be a Reticularian. Haeckel, however, states that he has himself never seen the *Squamulina* in question, and classes it among *Physemaria* on the strength of his own views relative to Carter's observations. A fate similar to that of *H. Tumanowiczii* has betaken *Wagnerella borealis* from the White Sea, described by Merejkowsky as a sponge, but now held to be one of the Protozoan *Heliozoa*.

*Neue Gastraeaden*, Haeckel, SB. Jen. Ges. 1883, pp. 84-9. *Physemaria*, Id., J. Z. xi. 1877. *Haliphysema Tumanowiczii*, Saville Kent, A. N. H. (5), ii. 1878; Ray Lankester, Q. J. M. xix 1879; Möbius, Beiträge zur Meeresfauna der Insel Mauritius, etc., Berlin, 1880, pp. 72-5, Pls. i, ii, 1. On *Haliphysema* and allied forms, Norman, A. N. H. (5), i. 1878.

The Porifera are classified as follows:—

I. *Calcarea* = *Calcispongiae*: skeleton composed of calcareous spicules.

1. *Homocoela*: gastric cavity lined in all parts by collared cells; three families.

(i) *Asconidae* = *Ascones*: gastric cavity flask-shaped and body-wall plain, *Leucosolenia* = *Ascetta*, *Ascandra*, &c.; (ii) *Homodermidae*: body-wall produced into radial tubes similar to those of *Syconinae* (*infra*), *Homoderma Sycandra*; (iii) *Leucopsidae*: a large amount of mesoglea imbedding 'mouthless Ascon-persons,' a large pseudogaster and pseudostome, *Leucopsis pedunculata*.

2. *Heterocoela*: endoderm differentiated into two forms of cells, pavement epithelium cells lining a central portion of the gastric cavity, and collared flagellate cells restricted to limited regions either radial tubes or ampullae; four families. (i) *Syconidae* = *Sycones*, body-wall produced into radial tubes or cones with sensory cells round the orifices of the inhalent canals, with three sub-families (pp. 793-4), *Syconinae*, *Sycon* = *Sycetta*, *Sycandra*, *Sycortis*, *Sycaltis* in part, *Uteinae*, e. g. *Ute*, *Grantessa*, &c., *Grantinae*, e. g. *Grantia*; (ii) *Sylleibidae*, with a complicated inhalent canal-system, and sac-like ampullae either placed radially to main axis of the sponge and con-

nected to central cavity by a complicated exhalent canal-system, *Vosmaera* = *Leucetta* in part, or placed radially to the wide exhalent canals, the layer of ampullae being thrown into folds, *Polejna* = *Leucilla*; (iii) *Leuconidae*: a ramified inhalent and exhalent canal-system, and spherical ampullae, *Leucetta* in part, *Leuconia* (= *Leucetta*, *Leucaltis*, *Leucandra* in part), *Pericharax* (= *Leucandra* in part); (iv) *Teichonidae*, external surface differentiated into two planes, one pore-bearing, the other with oscula, *Teichonella*, *Eilhardia*; the internal organisation of the latter does not differ from that of *Leuconidae* (Poléjaeff)<sup>1</sup>.

Extinct group, *Pharetrones* of Zittel, probably a sub-group of *Leuconidae*.

II. *Porifera Non-Calcareae* = *Fibrospongiae*: skeleton rarely absent, composed of either siliceous spicules or spongin fibres; the spicules are either isolated, or united by silica or spongin; gastric system belonging to either type (3) or (4); see p. 794.

1. *Hyalospongiae* = *Hexactinellidae*: skeleton wholly siliceous, spicules triaxile, either isolated or united by silica into a trellis-work; canal-system known only in *Euplectella*, belonging to type (3), see p. 794; marine, and for the most part deep-sea forms; extend from the Silurian to the present epoch; two sub-orders, (i) *Dictyonina*: spicules united by the tips of their arms; skeleton a trellis-work with square or irregular meshes; flesh-spicules present or absent, e. g. *Farrea*, *Aphrocalistes*, *Dactylocalyx*, and a large number of fossil forms, including the *Ventriculitidae*; (ii) *Lyssakina*: spicules united only by protoplasm, or a small quantity of silica; flesh-spicules usually numerous and of very various forms, e. g. *Hyalonema*, *Euplectella*, *Holtenia*, *Pheronema*, and fossil forms including the *Receptaculitidae*.

2. *Spiculispongiae*: skeleton very rarely absent; spicules generally independent, united either by interlocking processes or into bundles by organic material, with five sub-orders: (i) *Lithistina*: body strong and massive, a central cloaca, or scattered oscula; cloaca frequently replaced by vertical tubes; spicules tetraxile or branched regularly, often covered entirely or at their extremities with knobs, or much divided, for the most part firmly interlocked; monaxile needles frequent; flesh-spicules often present; extend from the Silurian to the present epoch, the majority extinct; (ii) *Tetractina*: spicules to a great extent tetraxile; large monaxiles common; both forms frequently disposed radially; stellates and globules almost always present; *Geodidae*, e. g. *Geodia*, *Pachymatisma*, &c.; *Ancorinidae*, e. g. *Stelletta*, *Tetilla*, *Craniella*; *Plakinidae*; *Corticidae*; (iii) *Oligosilicina*: skeleton, if present, composed of isolated stellates, canal-system belonging to type (3) or (4); *Chondrosidae*; *Halisarcidae* (= *Myxospongiae*), no skeleton, *Halisarca*, *Oscarella*; (iv) *Pseudotetraxonia*: body with a radial structure, a cortex usually well-defined, spicules for the most part monaxiles; stellates may also be present, canal-system belonging to type (4); *Tethyadae*, e. g. *Tethya*; (v) *Clavulina*, firm in consistence; a cortex common; a radial character sometimes visible in skeleton; spicules frequently knobbed; canal-system belonging to type (4), occasionally to (3); *Polymastidae*, e. g. *Polymastia*, *Rinalda*; *Suberitidae*, e. g. *Poterion*, *Suberites*; ? *Clionidae*.

3. *Cornacuspongiae*: skeleton consists either of principally monaxile spicules, which are united by more or less spongin, or of spongin fibres with or without

<sup>1</sup> For classification and genera, see the works of Poléjaeff and von Lendenfeld cited in the literature; for a table showing the correspondence of Poléjaeff's genera with Haeckel's genera and species, Vosmaer's *Porifera*, p. 389.



foreign inclosures; inhabitants of the sea, of brackish or fresh water; extend from the Carboniferous to the present epoch, with two sub-orders: (i) *Halichondrina*: skeleton for the most part spicular; spongin often almost if not quite absent; *Halichondridae*, e. g. *Reniera*, *Halichondria*; *Spongillidae*, spicules smooth or spinose, no spongin, asexual gemmae, cosmopolitan and freshwater, e. g. *Spongilla*, *Meyenia*, &c., see pp. 249-53; *Desmacidonidae*; *Ectyonidae*, spiculose and hispid spongin fibres; (ii) *Ceratina*, = *Keratosa*, = *Ceratospongiae*: skeleton of spongin fibres, proper spicules never present (but see note 2, p. 798); foreign inclosures, e. g. sand, spicules, &c., often taken up, and present both in mesoglaea and spongin fibres; canal-system belonging to type (3) or (4); *Spongelidae*, *Spongelia*, *Velinea*, *Psammoclema*, *Psammopemma*; *Spongidae*, e. g. *Euspongia*, *Hippospongia*, &c.; *Aplysinidae*; *Darwinellidae*, *Aplysilla*, *Dendrilla*, *Darwinella*.

See p. 253<sup>1</sup>.

I. *Calcarea*, Poléjaeff, 'Report on the Calcarea,' Challenger Reports, viii. 1883; von Lendenfeld, Proc. Lin. Soc. New South Wales, ix. 1885, pp. 896, 1083; cf. Id. Z. A. viii. 1885; Haeckel, Die Kalkschwämme, 3 vols. Berlin, 1872.

*Ascetta* = *Leucosolenia*, Metschnikoff, Z. W. Z. xxxii. 1879, p. 358; *Homoderma*, von Lendenfeld, op. cit. p. 903; *Sycandra* (= *Sycon*) *raphanus*, Schulze, Z. W. Z. xxv. Suppl. 1875; *Leucandra* (= *Leuconia*) *aspera*, Vosmaer, Tijdschrift Nederl. Dierk. Vereen, v. 1881; cf. Id. Mitth. Zool. Stat. Naples, v. 1884, p. 483.

*Histology and nervous system*, von Lendenfeld, op. cit. p. 977; Z. A. viii. 1885, p. 47, p. 448, and A. N. H. (5), xvii. p. 376; *Synocils*, Id. Z. A. x. 1887.

*Sperm formation in Sycandra (Sycon) raphanus*, Poléjaeff, SB. Akad. Wien, lxxxvi. Abth. i. 1883; Id. op. cit. *supra*, p. 33.

*Development of Ascetta and later stages of Sycandra*, Metschnikoff, op. cit. p. 362; of *Sycandra raphanus*, Schulze, op. cit. and Z. W. Z. xxvii. 1876; xxxi. 1878; cf. Keller, Z. W. Z. xxx. 1878, p. 585. *Amphigastrula in various Calcarea*, Poléjaeff, op. cit. p. 32.

*Gemmation of Leucosolenia botryoides*, Vasseur, A. Z. Expt. viii. 1879-80.

## II. Non-Calcarea.

*Hyalospongiae*. *Structure, classification*, Schulze, Abhandl. Akad. Wiss. Berlin, 1887 (1); *Euplectella*, Id. Trans. Royal Soc. Edinburgh, xxix. 1880; Max Schultze, Die Hyalonemen, Bonn, 1860; *Hexactinellidae*, Marshall, Z. W. Z. xxv. Suppl. 1875; xxvii. 1876.

*Spiculispongiae*. *Stelletta*, *Geodia*, *Isops*, *Pachymatisma*, *Tetilla cranium* = *Craniella*, *Thenea*, Sollas, 'Sponge fauna of Norway,' A. N. H. (5), v. 1880; ix. 1882; *Tetilla*, *Tethya*, Selenka, Z. W. Z. xxxiii. 1880; *Tetilla japonica*, Lampe, A. N. 52, (1), 1886; *Tethya lyncurium*, Deszö, A. M. A. xvi. 1879; xvii. 1880; \**Plakinidae*<sup>2</sup>, Schulze, Z. W. Z. xxxiv. 1880; \**Corticium*, Id. op. cit. xxxv. 1881; *Chondrosidae*, Schulze, Z. W. Z. xxxix. 1877, von Lendenfeld, Proc. Lin. Soc. New South Wales, x. 1886, p. 10; \**Halisarcidae* (= *Oscarella lobularis*, *Halisarca Dujardini*), Schulze, Z. W. Z. xxviii. 1877; *Bajalus*, von Lendenfeld, op. cit. x. p. 5; cf. Id. on affinities of *Myxospongiae*, Z. A. viii. 1885; \**Clione*, Nassonow, Z. W. Z. xxxix. 1885.

<sup>1</sup> A paper by von Lendenfeld on the classification and systematic position of Sponges is just published in the P. Z. S. for 1886; cf. Z. A. ix. p. 335, and Spengel's Zool. Jahrbücher, ii. (2), 1887.

<sup>2</sup> A single star before a name indicates that the larval form is described partially or completely, a double star that further stages of development have been investigated.

*Cornacuspongiae*. *Reniera*, Keller, Z. W. Z. xxx. 1878; \**Chalinidae*, Id. op. cit. xxxiii. 1880; *Spongillidae*, see p. 253; add Potts, A. N. H. (5), xviii. 1886; Noll, Vejdowsky, Z. A. ix. 1886; of *Australia*, von Lendenfeld, Spengel's Zool. Jahrbücher, ii. 1886, p. 88; 'Report on *Keratosa*,' Poléjaeff, Challenger Reports, xi. 1884; \**Spongelia*, Schulze, Z. W. Z. xxxii. 1879; *Dysideidae*, *Phoriospongia*, Marshall, Z. W. Z. xxxv. 1881; cf. von Lendenfeld, Proc. Lin. Soc. New South Wales, x. 1886, p. 81; *Velinea*, Vosmaer, Mitth. Zool. Stat. Naples, iv. 1883; \**Spongidae* (= *Euspongia*, &c.), Schulze, Z. W. Z. xxxii. 1879; von Lendenfeld, op. cit. x. p. 481; *Hircinia*, *Oligoceras*, Schulze, Z. W. Z. xxxiii. 1880; *Auleninae* (= *Halme*, *Aulena*), von Lendenfeld, op. cit. x. pp. 283, 568, 845; \**Aplysinidae* (*Aplysina*, *Aplysilla sulfurea*), Schulze, Z. W. Z. xxx. 1878; *Darwinellidae*, *Darwinella*, F. Müller, A. M. A. i. 1865; \**Aplysilla violacea*, \**Dendrilla* (= *Aplysillidae*), von Lendenfeld, Z. W. Z. xxxviii. 1883.

*Radial structure*, see Selenka and Lampe on *Tetilla*, under *Spiculispongiae*, *supra*.

*Nervous system*, von Lendenfeld, SB. Akad. Berlin, 1885 (2); cf. A. N. H. (5), xvii. 1886, and Z. A. viii. p. 466; also Id. Proc. Lin. Soc. New South Wales, x. pp. 315, 515.

*Sexual conditions*; of *Oscarella*, Braun, Z. A. iv. 1881; cf. Vosmaer, Biol. Centralblatt, i. 1881-82, p. 103.

*Development*; see under names marked with single and double stars, *supra*, the latter indicating post-embryonic development; see also on *Oscarella lobularis*, Heider, Arb. Zool. Inst. Wien, vi. 1886; cf. Sollas (under *Halisarca*), Q. J. M. xxiv. 1884, and Z. A. ix. 1886; *Halisarca Dujardini*, Metschnikoff, Z. W. Z. xxxii. 1879, p. 349; of *Reniera*, Marshall, Z. W. Z. xxxvii. 1882; cf. Vosmaer, Biol. Centralblatt, iii. 1883-84.

*Gemmation*. *Summary*, and in a *Tethya*, Merejkowsky, A. Z. Expt. viii. 1879-80; in *Tetilla* and *Tethya*, Salensky, Z. W. Z. xxxiii. 1880, pp. 470, 473; Lampe, A. N. 52 (1), p. 17; in *Craniella*, Vosmaer, 'Porifera,' p. 428, and Sollas, A. N. H. (5), ix. p. 158; in *Tethya lyncurium*, Deszö, A. M. A. xiv. 1879, pp. 633, 641; in *Rinalda arctica*, Merejkowsky, Mem. Imp. Akad. St. Petersburg, (7), xxvi. 1879, No. 7, p. 4. Cf. Keller, Z. W. Z. xxxiii. p. 341, and Schulze, Z. W. Z. xxx. p. 403.

*Gemmules of Spongillidae*, see p. 253; add Wierzejski, Archives Slaves de Biologie, i. 1886.

*Brood buds of Oscarella (Halisarca) lobularis*, Schulze, Z. A. ii. 1879; Id. SB. Ges. Natforsch. Freunde, Berlin, 1885, p. 183.

*Artificial propagation of Euspongia*, Marenzeller, Verhandl. z. b. Ges. Wien, xxviii. 1878.

*Colours of sponges*, Krukenberg, Vergleich. Physiol. Studien (1), ii. p. 67; iii. p. 3; (2), iii. pp. 30, 36, 108; of *Spongilla*, pp. 251, 253, *ante*. *Due to parasitic algae*, Schulze, Z. W. Z. xxxiii. p. 25; Carter, A. N. H. (5), ii. pp. 163-5; Brandt, Mitth. Zool. Stat. Naples, iv. 1883, pp. 224-31.

*Parasites of sponges*, Carter, A. N. H. (5), ii. 1878; cf. Vosmaer, 'Porifera,' pp. 457-8.

*Fossil Sponges*, Zittel, Handbuch der Palaeontologie, Abth. i, Palaeozoologie, i. 1876-80, pp. 128-202; Hinde, Catalogue of the Fossil Sponges in the British Museum, 1883; with a good bibliography on p. 231; Id. Ph. Tr. 176, 1885.

*Affinities of Porifera* ; see for most recent discussion, Heider on *Oscarella*, Arb. Zool. Inst. Wien, vi. p. 41 of paper or p. 215 of vol. ; Vosmaer, 'Porifera,' pp. 472-481 ; and for the late Prof. Balfour's views, his Comp. Embryology, i. p. 122 ; ii. p. 285 ; of the *Myxospongiae (Oligosilicina)*, von Lendenfeld, Z. A. viii. 1884 ; of the *Monactinellidae* (e. g. *Suberitidae*, &c.), Id. Z. A. vii. 1884 ; cf. viii. p. 484 ; of *Keratosa = Ceratina*, Poléjaeff, Challenger Reports, xi. p. 75 et seqq.

### MESOZOA (*E. van Beneden*).

Multicellular animals, in which there is only an ectoderm and endoderm or epi- and hypo-blast.

The ectoderm is composed of a single layer of cells, totally or partially ciliated, the endoderm of a single cell or of several cells. There is no mesoglaea nor meso-blast. The sexes are separate, and the sexual products originate from the endoderm. *E. van Beneden* adds that 'there are two forms of female, one producing females alone, the other males ;' and that 'the Mesozoa actually known are all parasites.' The first of these two assertions does not apply to the *Rhombozoa*, according to Whitman ; the second points to the possibility of the known Mesozoa being degenerate Metazoa.

There are two subdivisions of Mesozoa, according to the Belgian naturalist, the *Orthonectida* and *Rhombozoa*.

The *Orthonectida* are defined as follows by *E. van Beneden* : 'Body composed of several annuli ; endoderm formed of several cells, some of which are epithelio-muscle cells, and give origin to muscular fibres, whilst the remainder are converted into sexual products. - The male is elongated, annulated, and one of its anterior rings is papillate. Females oviparous' and, it may be added, dimorphic.

There is a single genus, *Rhopalura*, with two species ; one, *Rh. Giardi*, parasitic in the genital bursae of the Ophiurid *Amphiura squamata* (= *Ophiocoma neglecta*) ; the other, *Rh. Intoshii*, in the Nemertean *Lineus lacteus*. Both species are therefore marine.

*Rh. Giardi* has been recently investigated by *Julin*. The males and females are usually to be found in different individuals of the Ophiurid. The parasites cause an atrophy of their host's genitalia. The males are contained in saccules, apparently produced by the host, in which they swim freely, and are, when adult, about .104 mm. long. Their body is fusiform and divided usually by five furrows into six annuli. Each annulus is composed of a single layer of ectoderm cells. The first or head is constituted by 4 or 8 cells : the second of five rows of small cells, the so-called papillae, all of which are non-ciliate. The third annulus is usually the longest, and contains one row of cells. The last or caudal annulus has two rows of 4 cells, and when the rows are very distinct, it may be considered as split into two annuli. The cilia of the head are directed forwards ; of the third and following annuli backwards. The caudal cilia are long and stout. At the level of the third

annulus is contained the testis formed from the central endoderm cells. The spermatozoa possess a head and tail. Fibrils stretch from either end of the body beneath the ectoderm over the testis; nuclei have been detected in them. The ripe sperm ruptures the testis: the fibrils (*supra*) thereupon become collected into bundles, the ectoderm disorganised, its cells swelling and separating, while the sperm escapes into the water. The females occur in two forms, one cylindrical which produces only male embryos, the other flattened but pointed at each end, from which only female embryos originate. Both forms occur side by side. The first-mentioned is .280 mm. long. It has eight annuli: the second annulus which, like the third and fifth, contains only one row of cells, is non-ciliate in the adult. The remaining annuli vary in the number of their rows of cells. There is a sub-ectodermic fibrillar layer. The central mass consists of ova, polyhedric from mutual pressure, but free from one another when they are discharged into the water by the rupture of the body in the furrow behind the second annulus. The flattened female is .250 mm. long. It is completely ciliated, and the cilia of the anterior and posterior regions are directed as in the male and cylindrical female. Furrows are usually wanting, and the ectoderm cells are not distinguishable during life. Sub-ectodermic fibrillae are present, and near the anterior extremity of the body there is a uni-nucleate granular mass (the sub-polar cells of Metschnikoff) projecting inwards from the ectoderm. The ova are held together by an intervening granular substance. This female appears to break into segments, the Plasmodiumschräuche of Metschnikoff, which swim about and contain the developing and developed female offspring.

The male ovum divides into two blastomeres; one large, the endoderm cell; the other small, which divides in turn repeatedly, grows round the endoderm cell, and forms the ectoderm. The endoderm cell divides into three, a central and two polar, one anterior, the other posterior. The two polar cells divide in their turn and form small 'intermediate cell-masses,' from which the muscle-fibrils are derived. The central cell also divides and gives origin to the sperm. The youngest female observed consists of a mass of endoderm cells, at first partially, then wholly surrounded by ectoderm cells. The muscle-fibrils are produced from a superficial layer of endoderm cells. It may be observed that in both sexes there is an epibolic Gastrula. The young *Rhopalura* is at first entirely ciliated, and the cilia are subsequently lost from the second annulus. The five rows of papillae in the male are produced by the division of two rows of ectoderm cells.

*Rh. Intoshii* is very similar to *Rh. Giardi*, but it is smaller. The male has no papillate annulus, nor has either sex a non-ciliated annulus. The cilia of the head are directed forwards, of the other annuli backwards. This species is found in saccules (Plasmodiumschräuche) between the body-walls and digestive tract of its Nemertean host. They are probably formed by the host, in which the genitalia, owing to the presence of the parasite, appear either to remain undeveloped, or to atrophy. The saccules may contain only males, or females, or both together, and in variable numbers. Metschnikoff does not seem to have observed a second form of female. It is uncertain whether *Rh. Intoshii* is or is not identical with the Orthonectidan observed by McIntosh in the same Nemertean, or by Keferstein in the Polyclad Turbellarian *Leptoplana tremellaris*.

The *Rhombozoa* are defined as follows by E. van Beneden:—'Body never annulated; endoderm a single cell; no muscular fibres; the germs originate and

develop within an axial cell. The male has the form of a top; certain non-ciliated cells at its anterior extremity inclose refractile bodies; females viviparous. There are two families, *Dicyemidae* and *Heterocyemidae*.

Van Beneden considers that there are five genera of *Dicyemidae*, each genus confined to a genus of Cuttlefish, and a given species of each genus confined in turn to a given species of the corresponding genus of Cuttlefish<sup>1</sup>. Whitman has however proved (1) that the same Cuttlefish may harbour two Dicyemids belonging to different genera; (2) that the same species of Dicyemid may be found in different species of the same genus of Cuttlefish, or even in different but closely allied genera (*Sepia* and *Rossia*); (3) that two closely allied species of Dicyemids occur in Cuttlefish belonging to different families, while two remotely allied species occur in two closely related genera of Cuttlefish (*Sepia* and *Rossia*). Whitman consequently proposes to range the known species of Dicyemids under two genera, *Dicyema* and *Dicyemenea*, characterised solely by anatomical differences. The largest species described by Whitman (*Dicyema macrocephalum*) attains a length of 5-7 mm. : the smallest (*D. truncatum*) only .50-.75 mm.

Every Dicyemid consists of a head or calotte, and a more or less elongated body. The calotte is composed of two circlets of ectoderm cells, an anterior circlet of four propolar cells, a posterior of four metapolar cells in *Dicyema*, or of five, three dorsal and two ventral, in *Dicyemenea*. In the first-named the calotte is always symmetrical in the young animal; its cells arranged round an axis continuous with that of the body, hence orthotropical; but in the adult it becomes oblique and bent towards the ventral aspect, hence plagiotropical. The calotte is followed by two parapolar ectoderm cells, always lateral in position, one on the right, the other on the left. The remaining ectoderm cells cover the body: their number varies in the different species. The caudal extremity is formed by two cells, of which one is usually dorsal, the other ventral. The ectoderm cells are ciliated on their external faces, are uninucleate, and contain granules of different kinds. Certain of them, always few in number, often have their centres or posterior extremities swollen into a wart, hence verruciform cells; and in these warts are collected numbers of refractile globules. The edges of the cells fit one with another. The axis of the body is occupied by a single huge endoderm cell which extends from the propolar cells to the caudal extremity, covered at every point by the ectoderm. It is in shape a cylinder pointed at each end. Its protoplasm is largely vacuolated; the vacuoles contain a hyaline liquid, immiscible with water. Its nucleus is large, with a tough membrane, and contains a nuclear network.

Every Dicyemid, according to Whitman, is either *monogenic* or *diphygenic*. The first-named produces only vermiform embryos, and is hence a primary Nematogen. The second produces (1) infusoriform embryos (or males, E. v. B.), and then (2) vermiform embryos; it is consequently first a Rhombogen (E. v. B.), and next a secondary Nematogen<sup>2</sup>. On this view the Rhombogen and secondary Nematogen are successive phases in the life-history of one and the same individual,

<sup>1</sup> Van Beneden's names are as follows: *Dicyema*, confined to the Cephalopod genus *Octopus*; *Dicyemella* to *Eledone*; *Dicyemina* to *Sepia*; and *Dicyemopsis* to *Sepiola*. See the historical section in Whitman's paper, Mitth. Zool. Stat. Naples, iv. 1883, p. 3.

<sup>2</sup> Rhombogen = individual producing infusoriform embryos, Nematogen = individual producing vermiform embryos, according to E. van Beneden's nomenclature.

but it is not known whether the monogenic and diphygenic individuals are or are not different forms. The distinction between them, which was not recognised by E. van Beneden, depends solely on the different modes in which their germs develop. The primary Nematogen is most common in young Cuttlefish, the Rhombogen in adult.

In a young Dicyemid the axial endoderm cell contains in addition to its nucleus several germ-cells. The first and second germ-cells are derived by division of the nucleus of the axial endoderm cell and a separation of a part of its protoplasm round each of the nuclei thus formed. The remaining germ-cells are derived by binary fission of the two first formed. In a Rhombogen each germ-cell present develops as follows. First of all it divides: one half consists of a nucleus *plus* a very small portion of protoplasm, if any at all. This half is clear, and remains *in statu quo* as a 'paranucleus.' The other half consists of nucleus and protoplasm, and it proceeds to divide into a number of cells surrounding a single central cell. The whole group is called by Whitman Infusorigen, a term used by E. van Beneden as synonymous with Rhombogen. The central cell of the group, or germogen, produces fresh cells endogenously, i. e. by division of the nucleus within the germogen. The cells of the group are set free, one or two at a time; they are large with large nuclei. The endogenously produced cells are similarly detached. All of them develop into infusoriform embryos. Finally, the germogen gives rise to a number of small cells with small nuclei, which lie loose, i. e. not coherent in a group, multiply by division, and fill the axial endoderm cell in great measure. From them originate the vermiform embryos, but the development of the latter rarely occurs before all the infusoriform embryos have escaped. The germogen cell, exhausted by the work of fission, is finally reduced to a 'residual nucleus.'

The axial endoderm cell of a primary Nematogen contains only its own nucleus and germ-cells developing into vermiform embryos; of a Rhombogen its own nucleus + one or more paranuclei equal in number to the Infusorigens present; of a secondary Nematogen, its own nucleus + a number of paranuclei + a number of residual nuclei equal in number to the Infusorigens that have been resolved, + many germ-cells developing or about to develop into vermiform embryos. The maximum number of Infusorigens produced is generally eight. Whitman is inclined to believe that an Infusorigen is an individual equivalent to the Gastrula of the vermiform embryo.

The infusoriform embryo has the form of a top or pear; the broad end is the head, the conical portion the tail. The head is non-ciliated, the tail ciliated. The former consists of two dorsally-placed bodies, the refractile organs, which are two modified ectoderm cells, and a single ventral organ, the urn. The urn consists of a cover formed by four modified ectoderm cells, of a floor and sides formed by two modified cells (? ectodermic), and of contents. The latter are four bodies, or at first cells, containing granules which sometimes show ciliary motion, and hence are probably spermatozoa (E. v. B.). They are produced by division of the nuclei of the four cells, which in their turn are said to be derived from the two cells modified to form the sides and floor of the urn. The tail of the embryo is composed of ciliated cells. It swims head foremost. Two views are possible as to its nature: (1) That it spreads the race from one Cuttlefish to another. This view is supported by van Beneden's assertion that it lives longer in sea-water than a fully-formed Dicyemid, a fact denied however by Whitman. (2) That it is a male organism, a

view supported by the observation that it sometimes occurs in a degenerative condition in the axial endoderm cell, and by its resemblance (not very close) to a male *Orthonectid* (*supra*).

The vermiform embryo is produced by the division of a germ-cell first into two, then into four, cells. Of the latter, one remains passive, and eventually grows into the axial endoderm cell of the adult; the other three divide and give origin to the ectoderm cells. At the time of birth the vermiform embryo resembles its parent, and contains germs, sometimes even embryos. Birth, as in the case of the infusoriform embryo, takes place by simple perforation of the endoderm and ectoderm cells.

The *Heterocyemidae* differ from the *Dicyemidae* by the absence of a calotte, and in some minor points. There are two species, *Conocyema polymorphus* from *Octopus vulgaris*, and *Microcyema Vespa* from *Sepia officinalis*.

As to the first-named, the Nematogenous individual varies somewhat in shape. Four apical cells at one extremity (the head) tend to become verruciform, and sometimes throw out processes carrying stiff cilia. The remaining ectoderm consists of relatively few cells; their cilia are lost with age, and the cells themselves either flatten out and their limits become indistinguishable, or they may even be lost altogether. There is a single vacuolated endoderm cell. The vermiform embryo is formed as in *Dicyema*, but is conical in shape, the point of the cone being formed solely by the apical cells; the endoderm cell is spherical. The Rhombogen possess a more or less spherical endoderm cell, and an ectoderm consisting of a very few cells, non-ciliated and capable of throwing out pseudopodia; by their means the individuals are often united into colonies. The infusoriform embryo resembles that of *Dicyema*.

The adult *Microcyema Vespa* is cylindrical in shape, slightly enlarged at one end, and composed of a single endoderm cell covered by a thin non-ciliated cortical layer (=modified ectoderm?). The embryo in profile resembles closely a Wasp. Its anterior half is truncated, and consists of two ciliated ectoderm cells and a granular mass (? cell or cells), which bears long stout cilia; its posterior half is fusiform, and consists of two ciliated ectoderm cells inclosing a single endoderm cell.

It has been asked, is the establishment of a group, Mesozoa, for the reception of the *Orthonectida* and *Rhombozoa* justifiable? Do the organisms themselves really possess the exceedingly primitive structure assigned to them, or are traces of simplification of organisation observable?

It is self-evident that a great gap intervenes between the most highly differentiated unicellular Protozoon and the most lowly Metazoon, with ectoderm and endoderm, and mesoblast or mesoglaea. In every ontogeny a morula or blastula stage, and, except in certain parasites, a gastrula stage of some kind is to be traced; and it is of course to be concluded that they represent ancestral forms of development. None such are, however, known to exist as independent and perfected organisms, unless the *Orthonectida* and *Rhombozoa* are to be considered as modified gastrulae. The syncytium of Haeckel's *Gastreae* (p. 809) is doubtless an ectoderm *plus* mesoglaea as it has proved to be in the calcareous sponges: and the disc-like organism, *Trichoplax*, (Schulze, Z. A. vi. 1883) has a cellular mesoglaea. They are therefore Metazoa.

The fact that the Mesozoa so-called are parasitic organisms naturally raises a presumption that they are in some way degenerate. Parasitism must in all cases be

an acquired mode of life, and it invariably produces a change in the parasite, which is shown either by the simplification of some structures which have been evidently well developed in an ancestor, or by their total loss in the course of development. The gastrula of both *Orthonectida* and *Rhombozoa* is epibolic, a form which is usually not considered primitive. The most difficult point, however, is the question what character is to be assigned (1) to the 'intermediate endodermic cell masses' of the male *Orthonectid* and to the superficial layer of endoderm cells in the female respectively which give origin to muscular fibrils; and (2) to the two primitive germ-cells contained within the parent endoderm-cell of a *Dicyemid*, one at each pole? Are these endodermic derivatives to be considered as mesodermic cells originating, as mesodermic cells sometimes do in higher forms, from the endoderm; or are they to be compared with differentiated ectoderm cells which are still part and parcel of the ectoderm, as occurs with the epithelio-muscle-cells of some *Coelenterata*? The *Mesozoa* will or will not be considered as a rightly established section of the Animal Kingdom, according to which of these two alternatives be chosen. The first points to an origin from some higher form; the second alternative naturally makes in favour of E. van Beneden's views. Further research may throw light on what it must be confessed is no easy problem.

The questions touched on above are discussed by the authorities cited below.

*Orthonectida*, Julin, Archives de Biologie, iii. 1882; Metschnikoff, Z. W. Z. xxxv. 1881.

*Rhombozoa. Dicyemidae*, Whitman, Mitth. Zool. Stat. Naples, iv. 1883; E. van Beneden, Bull. Ac. Roy. Belg. (2), xli. xlii. 1876; cf. D'Arcy Power, Q. J. M. xvii. 1876. *Heterocyemidae*, E. van Beneden, Archives de Biologie, iii. 1882.

## PROTOZOA.

Unicellular animals, i. e. animals in which the organism is a single cell physiologically complete in itself.

An apparent exception to the above given definition is met with in the fusion-plasmodium of *Mycetozoa*, or the temporary fused state of some *Heliozoa*. The compound individual, however, comports itself in every way like a simple one, and there is no differentiation of function. The same statement is true of those colonial Protozoa in which individuals remain in organic connection. The sole example of physiological specialisation among Protozoa appears to be the Flagellate genus *Volvox*, where the power of reproduction is limited to a few individuals in each colony.

Notwithstanding their unicellular character, many Protozoa attain a high grade of complexity. The cell may be naked: it may protect itself by a superficial coagulated pellicle of protoplasm, or by differentiated cuticular structures. The latter may remain in close connection with the cell, or be completely detached from it. They may be gelatinous, formed of cellulose or a cellulose-like material, chitinoid, or composed mainly of calcium carbonate or silica. In other instances they consist of foreign bodies of very various character held together by a cement organic or inorganic. As a rule, the skeleton is a continuous whole, but in some *Heliozoa* and



*Radiolaria* it is discontinuous, i. e. spicular. During the growth of the cell, the first-formed portions of the skeleton may become inclosed in its substance; a few *Heliozoa* and *Radiolaria*, however, possess a special organic internal skeleton.

The protoplasm of the body exhibits much variety: it may be of a similar character throughout, or a more or less permanent distinction may exist between the exterior and central parts. It is often described as having a reticulate structure, or more correctly a vesicular, i. e. with more fluid and less refractile particles imbedded in a denser and more refractile matrix. It is sometimes coloured, and the colour may be proper to it, or derived from the food. Pigment may be present, either coloured vacuoles, granules, or corpuscles. Among the last-named, special interest attaches to the chlorophyl bodies which occur in many freshwater forms: whether they are to be considered as proper to the organism, or instances of an association or symbiosis of a green *Alga* with an animal, similar to that of a yellow *Alga* with an animal, e. g. an Infusorian (note 3, p. 833), Radiolarian (p. 881). See the account of Symbiosis given pp. 242-4, the authorities quoted p. 245, and the notes on the occurrence of chlorophyl in the account of the different classes (pp. 833, 842, 843, 868, 901).

In the structure of the cell itself attention must be paid to the density of the protoplasm, to the mode of locomotion, of ingestion and digestion of food, to reserve and excretory products, and the nucleus.

Though the protoplasm is throughout the body of the organism of the same essential structure, yet its density varies, and the products of digestion, foreign bodies, etc., may when it is very fluid be distributed throughout it evenly; or when its density is greater they may be restricted to a central region (endoplasm), leaving a more or less pronounced clear border (exoplasm) in which contractility is very marked. Some *Infusoria* indeed possess special fibrils of contractile protoplasm (p. 834), and distinct muscular connections between individuals are met with in some Vorticellids (p. 834). Locomotion is effected by flowing or vibratile extensions of the protoplasm. As to the former, when the protoplasm is not confined by a rigid envelope and is very fluid or very dense, there may be an even flow of the protoplasm as a whole. But as a rule the flow is restricted to partial and changeable extensions or pseudopodia, which become more and more specialised in form, more and more stable as the protoplasm increases in density. The pseudopodia may even lose their locomotor function and be vibratile (Bütschli, Z. W. Z. xxx. p. 271; Gruber, Z. W. Z. xxxvi. pp. 461, 462; Id. ibid. xli. p. 212; Bütschli, 'Protozoa,' pp. 123, 672-3, 440). A very large section of Protozoa move solely by vibratile processes, fine cilia or cilia-bundles, stouter and longer flagella, or vibratile membranes (membranellae s. pectinellae). Sometimes both modes of motion may be found in the same individual at different times, e. g. some *Flagellata* (p. 841; cf. p. 845) or in different stages of the life-history, e. g. *Radiolaria*.

As to the ingestion of food, it is procured either by a flow of protoplasm inclosing it, by means of pseudopodia, or by the action of vibratile processes, more rarely by special organs like the suctorial tentacles of *Acinetaria*. When it is carried out by vibratile processes, there is either a special spot, frequently a depression or tube, at which it is taken into the body, or a special organ to retain it like the collar of *Choanoflagellata* or the vacuolar process of a few *Flagellata* (p. 842). The pseudopodia in many instances exercise an instantaneously paralysing effect on motile organisms, e. g. *Infusoria*. Only a few Protozoa possess special weapons of

offence such as the rods discharged from the oesophagus in some *Infusoria*, the trichocysts or miniature thread cells of others (p. 834), a Flagellate (p. 484), and Dinoflagellate (p. 851) of some *Sporozoa* (p. 864). But it is not certain that the trichocysts in all cases are of use in entrapping prey. The food-material consists either of living or dead animals or plants, and the Protozoon is then said to be holozoic; or it is organic food-material in solution, and the Protozoon is saprophytic; or finally, in some instances where chlorophyl is present, nutrition appears to take place as in plants, in other words the Protozoon is holophytic. But the presence of chlorophyl need not necessarily lead to holophytic nutrition; how far it does so, is at present a moot point. The digestion of solid food is effected by contact with the protoplasm, or by a food-vacuole which may be formed either by the inclosure of some water with the food, or by the secretion of a liquid drop round it. There can be little doubt that whenever water is inclosed, the drop is modified by a secretion of the protoplasm; indeed it may be absorbed and a food-vacuole subsequently secreted. See Krukenberg, Vergleich. Physiol. Vorträge, i. p. 48; Greenwood, 'Digestion in Rhizopods,' Journal of Physiology, vii. 1886. The undigested residue is expelled at any spot when the cell is little differentiated, at a special spot or even by a special aperture when it is highly differentiated (some *Infusoria*). Excess of nutrition gives rise to reserve material, fat, albumen bodies, starch in some instances, especially in the presence of chlorophyl, glycogen (Barfurth, A. M. A. xxv. 1885, p. 314), or a starch-like substance known as paramylum (p. 843). Special excretory granules or crystals are sometimes found.

Water may collect in the protoplasm rendering it vacuolate. In most Protozoa its excess is got rid of by the formation of drops or vacuoles, which either collapse slowly or are rhythmically pulsatile, appearing at or near the same spot in rapid succession, and arising either by the increase in size of a single drop, or by the fusion of separate droplets, occasionally irregular in outline, but often disposed in a rosette. The pulsation is slower in marine than in freshwater forms, and it is quickened or the size of the vacuole increased by want of oxygen (Fischer, Journal R. Micr. Soc. (2), vi. p. 463). The pulsation indeed may take place so suddenly and with such force as to propel the animal onwards (Engelmann, Z. A. i. p. 121). The water expelled may contain granules in suspension, and it has been observed that colouring stains, such as Bismarck brown or aniline blue which do not kill the organism, accumulate in it and are thus removed (Ray Lankester, Encyclopaedia Brit. (ed. ix), xix. p. 836; Q. J. M. xxiv. p. 378). A special vacuolar duct exists in a few instances (some *Acinetaria*, *Vorticellidae*).

A nucleus is seemingly absent in some *Proteomyxa*, and occasionally in other Protozoa where it is normally present (Gruber, Biol. Centralblatt, iii. p. 580; cf. *infra*, p. 821). In structure it presents great variety. It may be homogeneous, or vesicular, i. e. with a membrane, occasionally much specialised, as in *Radiolaria*, inclosing a nuclear fluid and variously arranged chromatin. Its division may or may not be accompanied by mitosis. There may be one, or several, or many. If more than one, the increase may be normal to the organism (Gruber, Biol. Centralblatt, iv. p. 710), e. g. in some *Infusoria*, *Actinosphaerium*, some *Amoebae*, and be limited, e. g. to two, or unlimited; or it is connected directly or remotely with a reproductive phase. Furthermore the many nuclei may be alike in structure and size, or markedly dissimilar, as in the paranuclei of some *Acinetaria*, the *Infusoria* and the Dinoflagellate *Polykrikos*. Occasionally the Infusorian nucleus undergoes

pulverisation, i. e. is disseminated in a minutely divided state through the protoplasm. See on the forms of nuclei R. Hertwig, M. J. ii. 1876, and on the same with their modes of fission Gruber, Z. W. Z. xxxviii. 1883, and pp. 834-5 *infra*, on the Infusorian nuclei.

Reproduction takes place by fission, gemmation and spore-formation. The distinction between the two modes first named depends solely on the relative size of the parts: if they are equal or sub-equal then the process is termed fission; if markedly unequal, it is gemmation. Where axes are distinguishable in the organism, fission is termed transverse, longitudinal or oblique with reference to the longest axis. It is usually binary, i. e. the organism divides into two; it is very rarely multiple, i. e. the organism is resolved simultaneously into several parts; but it is frequently repeated without a pause of any length, leading to a more or less rapid diminution of size. Gemmation may be external, i. e. the bud projects freely, or internal, i. e. the bud is developed within a closed or nearly closed depression (some *Acinetaria*). One bud may be formed at a time or several. The term spore is applied to two different classes of structures: to bodies which are produced by the condensation of the protoplasm accompanied or not by fission, and which pass through a resting phase: or to bodies produced by the progressive or simultaneous total or partial resolution of the protoplasm into ultimately small portions, which are not set free until the process is complete, which do not resemble the parent organism when they are set free, and which as a rule pass through a quiescent period. The spores, however produced, may be naked, or protected by a special spore-membrane and may then be distinguished as chlamydo-spores. They may when they become motile be amoeboid or flagellate, and to these two states respectively the terms *amoebula*, or *zoospore s. flagellula* may be applied. In fission the nucleus divides before or after the commencement of division in the body of the cell; the same is true of gemmation. Indeed it has been shown experimentally in *Infusoria* by means of artificial section, that the presence of a part of the nucleus is indispensable to the progress of normal life. Non-nucleated fragments may increase in size and heal a wound, and if an organ such as the peristome in an Infusorian be in process of development at the time of section, it undergoes complete evolution; but such fragments cannot start the formation of an organ themselves; their life is limited, nor are they capable of reproduction. See on this subject Gruber, A. N. H. (5), xvii. 1886, p. 473; Nussbaum, A. M. A. xxvi. 1886, p. 509. As to spore-formation or sporulation, in some instances, e. g. *Radiolaria*, *Foraminifera*, it has been clearly proved that a multiplication of the nucleus precedes the resolution of the protoplasm.

A spontaneous breaking up of the body which is independent of the nucleus occurs in some *Infusoria*. It is of normal occurrence in the multinucleate *Opalina*, where it leads to the formation of new individuals. This, however, is probably not invariably the case; and the process is one of destruction. See Gruber, op. cit. *supra*, p. 481; Saville Kent, Manual of the Infusoria, p. 84; Parker, on *Amphileptus*, A. N. H. (5), xiii. 1884, p. 416.

Inasmuch as a Protozoon multiplies itself solely by some mode of cell-division, and the process continues under normal circumstances in a recurrent manner, it follows that there is no loss of substance at any time similar to the physical destruction or death which inevitably overtakes multicellular animals, i. e. all parts save the generative products, by which the race is perpetuated. For the discussions

to which this point has given rise, see Bütschli, Cholodkowski and Weismann, *Z. A. v.* 1882: Götte, 'Über den Ursprung des Todes,' Hamburg, 1883; Weismann, 'Über Leben und Tod,' Jena, 1884; Möbius, 'Das Sterben,' etc., *Biol. Centralblatt.* iv. p. 389.

There is a process known as conjugation which is generally if not universally connected with reproductive activity in some Protozoan classes (*Acinetaria*, *Infusoria*, many *Mastigophora*); whilst in others it is either of fortuitous occurrence, e. g. in *Gregarinida*, or it does not so far as is known occur at all, e. g. in *Radio-laria*, *Foraminifera*. It consists of a temporary or permanent union of two or rarely more individuals. When it is permanent, the two individuals may be similar so far as external signs are concerned, but they are sometimes totally unlike and with a different life-history, as in the Infusorian *Vorticellidae* and many *Flagellata*. When it is temporary, the two are alike, and during its progress they may or may not undergo as in some *Infusoria* a loss of their locomotor organs. In either case, one result attained is a mingling of two different protoplasms. When temporary, an interchange of nuclear bodies has been observed (note 2, p. 835); and whether temporary or permanent, disruption and reconstruction of the nucleus may take place. If temporary, the process is followed by growth (rejuvenescence) and growth in turn by fission: so too if permanent in some instances, with or without an intervening period of quiescence, but in others the fusion is followed by a formation of many spores, e. g. some *Flagellata*. There can be no doubt that the process is essentially a sexual one and that it inaugurates a new departure in the history of the individual. Indeed when the conjugating individuals are invariably different there is no reason why the terms male and female should not be applied to them. If conjugation fails to take place, where it is of normal occurrence, it has been noticed that the race becomes extinct, e. g. in some saprophytic *Flagellata*. The rapid decrease of size brought about by repeated fission in *Infusoria* is always followed by an epidemic of conjugation. The absence and origin of the process are alike difficult to explain. It is of course impossible to say that it *never occurs* in any given case: it has simply *not been observed*. As to origin, it is possible but not likely that it has come from associations of individuals united apparently for the better procuring of food, as is seen in some Rhizopoda, e. g. *Actinophrys*, *Microgromia*. Such unions do not appear to take place in Protozoa with a dominant ciliated or flagellate phase. For a recent theoretical discussion of the significance of the act, see Plate, *Z. W. Z.* xliii. p. 215 et seqq., p. 239<sup>1</sup>.

Encystation is a process universal among Protozoa. It is invariably protective, but the protection subserves different ends, either against unfavourable conditions of life (the hypn cyst as it is termed), for the purposes of digestion or reproduction, or for a necessary period of quiescence. The appearance and structure of the cyst may vary in accordance with the object to be attained in the same individual. It may be single, double or multiple; simple or ornamented with spines, etc.; colourless or coloured, and very frequently brown; in substance gelatinoid, chitinoid, of cellulose, or a cellulose-like material.

The Protozoa are aquatic, and inhabit both fresh and salt water; some are parasitic either ecto- or endo-parasitic; some are capable of a sub-aerial life in moist places. Some are social, others colonial, i. e. connected by processes which are

<sup>1</sup> Gruber's paper, referred to by Plate, is translated in *A. N. H.* (5) xvii. 1886.

integral parts of the body. Many of the freshwater forms are subject to the attacks of fungal parasites (*Chytrideae*) or *Bacteria*, which have been the cause of erroneous views as to their reproduction. Some of the marine forms, e.g. *Radiolaria*, are inhabited by symbiotic yellow algae, and in one or two instances by symbiotic diatoms. A few *Amoebae* appear to harbour symbiotic (?) fungi.

The classes of Protozoa are for the most part sharply delimited. The position of a few genera is indeterminate, and one group, *Proteomyxa*, contains organisms which at present cannot find a place elsewhere. Doubts attach to the animal nature of some, e.g. the Flagellate *Volvocina*. The question, however, as to what constitutes an animal is treated in the General Introduction.

A subject which presents some difficulty is the mode in which the classes are to be grouped. Bütschli has not yet published a general introduction to his 'Protozoa'; and the only writer who has dealt with this division of the Animal Kingdom in its entirety, from a modern point of view, is Ray Lankester in his article 'Protozoa' cited p. 824. By him the classes are grouped in two main divisions, *Gymnomyxa* and *Corticata*. The essential features of the first-named are (1) that the protoplasm of the vegetative phase of life is naked, i. e. partially or wholly exposed to the surrounding medium; (2) that solid food may be ingested at any spot or at any spot of a large limited area; (3) that the distinction between exo- and endoplasm sometimes recognised is not a permanent one, exoplasm becoming endoplasm and *vice versâ* at different times. The *Corticata* on the contrary have the protoplasm of the body permanently differentiated into two layers, an outer denser cortical substance and an inner more central fluid substance. In this division are included the *Acinetaria*, *Infusoria*, *Mastigophora*, and *Sporozoa*.

Certain objections present themselves to this mode of grouping which may be briefly summarised. Whilst it is perfectly certain that in some *Gymnomyxa*, e.g. *Foraminifera*, some very fluid *Amoebae*, the structure of the body is entirely similar throughout, it is by no means so certain that a constant intermixture of the peripheral and central protoplasm is always taking place in some of the more differentiated *Amoebae* and more especially most *Heliozoa*. Nor on the other hand is a differentiation into a permanently distinct cortex and medulla to be found in many *Corticata*: e.g. the majority of *Flagellata*, some *Infusoria*, and *Acinetaria*. It is possible indeed that the degree of distinctness may vary with the state of nutrition. Some *Flagellata* lose their permanent outline and become amoeboid; some *Gymnomyxa*, like the *Heliozoa*, always have a permanent outline, and when they pass into a *flagellula*, e.g. the fission products of *Clathrulina* or the spore of *Mycetozoa*, the outline of the body is invariably definite. Indeed certain adult forms, denominated by Bütschli *Rhizomastigina* (p. 841), may pass at will from one condition to another. If the pseudopodia of *Gymnomyxa* are extensions of the protoplasm, so are also cilia, flagella, membranellae, and they may even be retracted under certain conditions. There is also no absolute distinction as mentioned above (p. 819) between the two kinds of processes, and sometimes, e.g. in the *Heliozoa* and some *Radiolaria*, the pseudopodia are remarkably stable structures. Furthermore what is to be said as to the skeletal structures of both divisions? Gradations appear to exist in *Infusoria*, for example from a naked condition to one in which there is a somewhat modified superficial stratum of protoplasm, and from this in turn to a close-fitting or detached cuticular structure. Similar gradations may be traced in *Amoebina*; and it may be pointed out that nothing can exceed

the definiteness of outline conferred by the skeletal structures of many Gymnomyxans.

In the following pages the Protozoa are thrown into three divisions, depending on their modes of locomotion and of obtaining solid food, as well as on the dominant or adult phase of the life-history. For the *Gymnomyxa* the old term *Rhizopoda* is retained. The *Sporozoa*, which must be regarded as Rhizopods adapted to an endoparasitic life, are kept apart as *Endoparasita*. For the *Acinetaria*, *Infusoria* and *Mastigophora*, the designation *Plegepoda* is proposed, referring to their mode of progression by means of a rapidly repeated stroke (πληγή) of vibratile processes.

For *Erythroopsis agilis*, a Protozoon (?) of very peculiar structure, with an eye composed of a lens and pigment, known only from a single specimen, see R. Hertwig, M. J. x. 1885; C. Vogt., R. Hertwig, Z. A. viii. 1885. Metschnikoff (Z. A. viii) states that he once found a very similar organism which he believes to have been an Acinetarian.

For *Dumontia Opheliarum*, an endoparasite in the coelome of the Chaetopod *Ophelia*, which has a peculiar internal axis, a bilobed body with stable pseudopodia, and vacuolate exoplasm, and a peculiar mode of gemmation, see Kunstler, Bull. Soc. Zool. France, x. 1885. Kunstler is of an opinion that it is the type of a new group of Rhizopoda.

'Protozoa,' Bütschli, Bronn's Klass. und Ordn. des Tierreichs, Leipzig, 1880-5; does not yet include the *Acinetaria* and *Infusoria*. 'Protozoa,' Ray Lankester, Encyclopaedia Britannica (ed. ix), xix. 1885.

## PLEGEPODA.

PROTOZOA in which the organism is provided with cilia, flagella, or vibratile membranes as organs of locomotion and ingestion of food, or for one or the other purpose. Contour of the body stable, sometimes amoeboid, and then for the most part only in the last stage of the life-history. The cilia, flagella, and vibratile membranes are stable structures but retractile under certain conditions.

There are three classes, the *Acinetaria*, *Infusoria* s. *Ciliata*, and the *Mastigophora*.

## CLASS ACINETARIA S. TENTACULIFERA.

*Plegepod Protozoa with cilia confined to the bud or fission-product, and to a temporarily assumed motile phase. Fixed as a rule, and provided with prehensile tentacles of one or of two kinds. Rarely naked; a soft cuticle generally present or a resistant lorica. The nucleus is single, occasionally ramified. There are one or more contractile vacuoles, sometimes provided*

with an efferent duct. Reproduction takes place rarely by binary fission or external gemmation, usually by internal. Carnivorous, feeding on other Protozoa. Freshwater and marine.

The genus *Sphaerophrya* is free, and typically parasitic in various Infusoria. It may assume a complete or partial coat of cilia when wandering from one host to another. It has been observed that *Podophrya libera*, *P. fixa*, *Acineta mystacina*, and *Dendrocometes*, may retract their tentacles, or arms in the case of the last-named, become ciliate and wander away; and the first-named has been seen to attach itself again. Possibly the phenomenon is not uncommon. The majority of the class are fixed, not infrequently to some animal, and are either sessile or stalked. *Trichophrya* spreads itself along the surface to which it is attached; and *Dendrosoma* forms branching colonies, either erect on a narrow base, or springing from a creeping and anastomosing stolon.

The surface of the body is very rarely naked (*Sphaerophrya*, *Podophrya fixa*, *Podophrya sp.?*). It is provided with a soft, pliable, and distinct cuticle, or with a firm resistant lorica, e.g. in *Acineta*, but it is extremely probable that all loricate genera have the parts of the body not protected by the lorica covered with a soft cuticle, the part protected being naked. The soft cuticle perishes soon after the death of the Acinetarian; when fission takes place it divides with the rest of the body; in external gemmation it is continuous over the buds, and when they separate from the parent organism it separates with them. The lorica varies much in shape; it may be a shallow plate as in *Dendrocometes*, a stellate capsule (*Acineta stellata*), or it is a more or less complete cup inclosing the body of the organism to a greater or less extent. Its aperture may take the form of a slit, simple or toothed, of a circular or elliptical figure; or it may be double. It does not seem certain whether or no the cuticle covering the exposed surface is continuous with its edge. In substance it is firm; in *Acineta gelatinosa*, however, soft and gelatinous; similarly *Podophrya limbata* has generally a gelatinous investment. If a loricate Acinetarian dwindles in size from any cause, e.g. repeated gemmation, it secretes a septum or additional floor to the lorica on which its body rests. Of such septa there may be more than one. The stalk or peduncle when present is seldom a simple continuation of the cuticle (Fraipont), but has generally a firm tubular wall, sometimes striated both transversely and lengthwise, with clear contents. It is in this case a secreted structure, and when a lorica is also present it is continuous with it.

The body of an Acinetarian is often changeable in shape, especially in *Ophryodendron variabile*. The protoplasm has generally an external clear thin layer (ectosarc): the rest is more or less granular, and pigmented, when well fed. The pigment may be green, yellow, reddish, brown, and it appears to be a useless product of nutrition. When *Dendrocometes* assumes

a motile phase, it leaves a vesicle containing all its pigment attached to its lorical plate. There is no mouth. The sole organs for catching the living prey upon which an Acinetarian feeds are the tentacles. Of these there are two kinds. One is long, and either pointed or terminated in some cases by a knob; it may be absent, present with the other kind, or, as in the *Actinaria*, the sole kind present. It is sometimes motile, and its function is to retain the prey, which it does by bending round it, and then by contraction to bring it within the reach of the suctorial tentacles. It may be denominated therefore 'retinaculum' (Fangfaden). In *Ephelota Troid*, one of the Acinetaria which possess only retinacula, it has been observed to shorten, and finally to draw the prey completely within the body. The second kind of tentacle is shorter than the first, and terminates either in a trumpet-shaped sucker or in a knob, the latter being probably an extrusion of the axial substance (Maupas). It is said to consist in some cases of a cortical more contractile substance, and a more fluid axis; in others there is an axial tube. It sucks out the protoplasm of the prey by alternate movements of contraction and elongation, and the granular stream may be traced continuing the line of the tentacle into the body of the Acinetarian for some distance before it is diverted from its course and mingles with the protoplasmic currents of the body<sup>1</sup>. Both kinds of tentacles are eminently contractile, and *Podophrya libera*, which has only suctorial, has been observed using them for the purpose of creeping about. As they shorten a spiral fold or line twining round them becomes more and more conspicuous; it has been supposed to be muscular. They may be either almost completely or completely retracted, and then there is either no trace visible of them or they are visible as clear lines converging towards the centre of the body<sup>2</sup>. They are said to perforate the cuticle, but it is possible that the latter may be excessively attenuated and extend over them. As to number, *Rhynchaeta Cyclopus* has one suctorial tentacle of great mobility; *Urnula Epistylidis* one which may be branched; but there are usually a number, either scattered over the body, confined to the anterior surface, or grouped in two or more bundles. The following are peculiar. *Dendrocometes* has 4-6 arms radiating from the body, each arm branched terminally, and each branch ending in a number of short points with retractile tips. A tube is said to commence at

<sup>1</sup> See Maupas' account of the act in *Sphaerophrya magna*, A. Z. Expt. ix. 1881, p. 302-3.

<sup>2</sup> This persistence of the retracted tentacles is difficult to explain: it is well established in some instances, e. g. *Hemiphrya gemmipara*; but in others, e. g. *Sphaerophrya magna*, *Acineta fetida*, it does not occur, and the tentacles are processes of the peripheral zone of protoplasm (Maupas). It is possible that just as the protoplasm of the prey passes into the body in a stream continuing the axis of the tentacle, so the substance of the tentacles themselves may, owing to differentiation, follow the same path. See on the subject, Fraipont, Bull. Acad. Roy. Belge, xiv. 1878, p. 490; and for views for and against the resemblance of the tentacles to pseudopodia, see Id. *ibid.* p. 489; Maupas, A. Z. Expt. ix. 1881, p. 353-9.



the apex of each point, to traverse the arm and enter the body. The arms are slowly retracted when the animal assumes a temporary motile state. No trace of the retracted arms is discernible, and when they reappear, they do so as a process ending in one or more tubular points. The *Ophryodendridae* are characterised by having one or more contractile proboscides, simple in *Acinetopsis*, with the free end in *Ophryodendron* beset with numerous flexible and pointed cirri<sup>1</sup>.

The nucleus is single: in *Hemiophrya* it is at first horseshoe-shaped, but is subsequently much branched, and resolved into thicker portions connected by slender filaments; and in *Dendrocometes* it branches and extends unbroken through the colony and creeping stolon. It has a nuclear membrane with dense contents: the chromatin is disposed in fibrils when the nucleus divides. Paranuclei have been observed in a few, e.g. *Podophrya limbata*, *Acineta fetida*. There is always one contractile vacuole and sometimes more. A special vacuolar duct is found in *Podophrya Steinii*, *P. Wrzesniowskii* and *Dendrocometes*. The contraction of the vacuoles appears to be slow in some instances. Want of oxygen causes them to become much distended. The presence of a large bubble of gas (Carbon dioxide?) and its gradual absorption has been recorded in a *Sphaerophrya* (Engelmann). Trichocysts are said to occur in two species of the genus *Ophryodendron*.

Reproduction takes place by fission or gemmation, external or internal. Fission is universal in the genus *Sphaerophrya*; it has been observed in *Urnula*, in *Podophrya libera*, *P. fixa*, *P. mollis* and *Acineta mystacina*<sup>2</sup>. One of the parts is set free and retracts its tentacles completely except in *Sphaerophrya*, and becomes ciliate. The fission-product in *Urnula* and *Acineta mystacina* is decidedly smaller than its parent. External gemmation is characteristic of the genera *Hemiophrya* and *Ophryodendron*. In the former the buds are produced on the anterior face of the body, and so far as is known are ciliated on one aspect only. They have been observed with tentacles developed before detachment. As to the latter, the bud is non-ciliate, elongate, with a very mobile tubular process or neck; it is often termed 'lageniform zooid.' Internal gemmation is very general, and it occurs in *Ophryodendron* side by side with external. The process begins in *Podophrya quadripartita* by the forma-

<sup>1</sup> Maupas, op. cit. p. 328, compares the arms of *Dendrocometes* to a bundle of united tentacles. On p. 356 he states that Koch has found that 'the proboscis of *Ophryodendron* has an identical structure.' Koch's work, 'Zwei Acineten auf *Plumularia setacea* (Ellis),' Jena, 1876, has not been accessible to me.

<sup>2</sup> Saville Kent describes the process in *P. mollis* as taking place thus: the animal fixes itself by means of two tentacles in addition to its own peduncle; the two tentacles fuse and become the peduncle of the new animal which is formed by the division of the doubly attached body. He remarks that unless witnessed from the beginning the process would be interpreted as one of conjugation. See 'Manual of Infusoria,' p. 821. Gruber states (Z. W. Z. xxxvi. p. 118) that he has seen gemmation, fission, and the detachment of small fission-products in *Acineta mystacina*.

tion of a depression which widens at its inner end, but remains permanently open. It is open also in *Trichophrya*, but in *Dendrocometes* its aperture closes. The closed brood cavities of other Acinetaria may be formed in a similar manner, but the fact has not been observed. The bud is produced as a process of the floor of the depression or cavity. When it is single, as is commonly the case, it is of large size relative to its parent; when there are several buds, e.g. four in *Acineta fetida*, they are smaller, and a difference of size has been noted in various instances, dependent probably on the number formed<sup>1</sup>. The nucleus of the bud, whether external or internal, has been seen to originate by fission of the parental nucleus. It is beyond doubt always so formed. The bud or embryo, as it is sometimes called, is ciliated, in some instances uniformly, sometimes on one aspect only, e.g. *Hemiophrya*, sometimes in a zone, e.g. *Podophrya quadripartita*, *Dendrocometes*, *Dendrosoma*, and then the cilia appear to be disposed not infrequently in a spiral. The passage of the embryo into the parent form has been traced in several instances. That of *Dendrosoma*, which is sessile, develops suctorial tentacles over the whole free surface before a vertical stem begins to grow out<sup>2</sup>.

Conjugation has been observed in some instances; it may be temporary, as in *Dendrocometes*, or permanent<sup>3</sup>. In *Podophrya pyrum* a formation of internal buds has been recorded as taking place immediately after it. Encystation under unfavourable circumstances is frequent, the Acinetarian retracting its tentacles; binary fission of the contents of the cyst has been seen.

The Acinetaria are microscopic in size. The colony of *Dendrosoma*

<sup>1</sup> See Claparède and Lachmann, *Études sur les Infusoires*, etc. ii. 1860-1, in *Podophrya pyrum*, p. 123; *P. quadripartita*, p. 120-1; in *Acineta fetida*, Maupas, A. Z. Expt. ix. p. 320-1. Embryoes contained within pocket-like diverticula of the cuticle at the aperture of the lorica have been observed in *Acineta tuberosa* by Hertwig, M. J. i. p. 68, note 1, and in *A. mystacina*, cf. Saville Kent, *Manual of the Infusoria*, ii. p. 834. Hertwig suggests (loc. cit.) that they are due to a precocious fission of an endogenously-formed embryo, and states that the nucleus of the bud in *Hemiophrya gemmipara* may commence to branch, the first indication of budding, before the bud itself is detached. According to Saville Kent (op. cit. p. 844) external diverticula containing each an embryo are found singly or in groups near the apices of the stems in *Dendrosoma*. He never saw these buds become ciliate, but observed them with suctorial tentacles. Fraipont has given an account of the formation of external capsules, 'diverticules générateurs,' in *Acineta divisa*. They are pyriform, curved, with a terminal orifice: the protoplasm within them appears to be a process of the periphery of the body. It gives origin to an ovoid bud with a zone(?) of cilia. The process of protoplasm may give origin to a second, or to a series of such buds. See *Bull. Acad. Roy. Belg.* 44. 1877, p. 805.

<sup>2</sup> Whether spores are ever formed or not is an open question. Fraipont observed an encysted *Podophrya* (= *Hemiophrya*) *truncata* resolved into minute spheres (op. cit. ante, 45, 1878, p. 296), and Claparède and Lachmann state that *Urnuia Epistylidis* gives rise to them (op. cit. ante, p. 210), but they suggest also that the spores belong to a *Chytridium* (op. cit. p. 255, note).

<sup>3</sup> In *Dendrocometes* a bridge of protoplasm is formed: currents pass from one individual to the other, and the nuclei are subsequently broken up and regenerated (Plate). Conjugation might be mistaken for fission: see note 2, p. 827 ante.

may attain a height of  $\frac{1}{10}$  in. ; and the zooids of *Ophryodendron abietinum* a length of  $\frac{1}{30}$  in.

The affinities of the *Acinetaria* are very obscure. The fact that the bud is ciliated does not necessarily attach them to Infusoria, and Stein's view that they are embryonic forms of different Infusorians has been laid to rest long ago. It is probable, however, that they are descended from ciliated ancestors, and a remarkable Infusorian, *Actinobolus radians*, is known which is provided with retractile tentacles. The latter appear to be used for the softening of the cellulose membrane of the cells of *Cladophora* ; see Géza Entz, Z. W. Z. xxxviii. pp. 169, 171-2. He points out that the ends of the tentacles in *Acinetaria* kill and assist in breaking up the prey. See his remarks on affinities, pp. 173-5.

The *Acinetaria* are classified as follows by Saville Kent :—

I. *Suctoria*. Suctorial tentacles, with or without adhesive tentacles (= retinacula).

(a) Non-colonial. *Rhynchaetidae*, one or two tentacles only: *Rhynchaeta*, motile and naked; *Urnula*, sessile and loricate. *Acinetidae*, tentacles simple and numerous; (1) naked, with tentacles all suctorial, the free-swimming *Sphaerophrya*, the sessile and irregularly shaped *Trichophrya*, the pedicellate *Podophrya*, or with tentacles suctorial and adhesive, *Hemioophrya*; (2) loricate with suctorial tentacles, the sessile *Solenophrya*, the pedicellate *Acineta*, with tentacles suctorial and adhesive, *Podocyathus*. *Dendrocometidae*, sessile, with 4-6 branched arms, *Dendrocometes paradoxus*.

(b) Colonial. *Dendrosomidae*, sessile, with branched stems and stolon, *Dendrosoma radians*.

II. *Actinaria* (s. *Non-Suctoria*, E. Ray Lankester). Only retinacula.

*Ephelotidae*, tentacles simple, ray-like; animals pedicellate; the naked *Ephelota*, and loricate *Actinocyathus*. *Ophryodendridae*, tentacles represented by one or more retractile proboscisidiform organs; the organ simple, *Acinetopsis*, or with terminal cirri, *Ophryodendron*; but see note 1, p. 827, ante.

Plate proposes (Z. W. Z. xliii. p. 198) to divide the class into (1) *Radiformiae*, with isolated tentacles, and (2) *Fascicularia*, with tentacles borne upon arms or proboscides. The second subdivision includes *Dendrocometes* and *Ophryodendron*.

Saville Kent, *Tentaculifera*, Manual of the Infusoria, ii. 1880-1, pp. 801-56; Maupas, 'Contributions,' etc. A. Z. Expt. ix. 1881; Fraipont, 'Recherches,' etc. Bull. Acad. Roy. Belg. xlv. 1877; xlv. 1878; R. Hertwig, 'Beiträge,' etc. M. J. i. 1876, pp. 50-80.

*Rhynchaeta*, Zenker, A. M. A. ii. 1866, p. 345. *Acineta gelatinosa*, Buck, Ber. Senck. Ges. 1884; *Acinetæ and Ophryodendron variabile*, Gruber, Nova Acta, xlv. 1884, pp. 526-33; *Dendrocometes*, Plate, Z. W. Z. xiii. 1886, pp. 175-200. Many *Acinetaria* are described in papers relating to Infusoria: such papers are denoted by an asterisk on p. 839, infra.

*Changeability of form: in Acineta Livadina*, Mereschkowski, A. N. H. (5), vii. 1881, p. 214; in *Ophryodendron variabile*, Gruber, op. cit. supra.

*Assumption of a motile phase. Podophrya libera* = *P. fixa* var. *Algirensis*, Maupas, A. Z. Expt. v. 1876; *P. fixa*, R. Hertwig, op. cit. p. 78, note; *Acineta mystacina*, Bütschli, M. J. x. 1877, p. 307; *Dendrocometes*, Plate, op. cit. supra.

*Paranuclei*, Maupas, A. Z. Expt. ix. 1881, p. 360. *Gas bubble in a Sphaerophrya*, Engelmann, Z. A. i. 1878, p. 152.

*Fission*: *Urnula*, Claparède and Lachmann, Études sur les Infusoires, etc. ii. 1860-1, p. 208; *Podophrya libera=fixa*, Maupas, A. Z. Expt. v. 1876, p. 409; *P. fixa*, Cienkowski, Bull. Imp. Acad. St. Petersburg, xiii. 1855, columns 299-300; Carter, A. N. H. (3), xv. 1865, p. 287; *P. mollis*, note 2, p. 827, *ante*; *Acineta mystacina*, Bütschli, J. Z. x. 1877, p. 307; cf. Gruber, Z. W. Z. xxxvi. 1882, p. 118.

*Gemmation*. (1) *External*; *Hemiofrya=Podophrya gemmipara*, R. Hertwig, M. J. i. 1876; *H.=P. Benedeni*, Fraipont, op. cit. *supra*, xlv. p. 278; *Ophryodendron Belgicum*, Id. op. cit. xlv. p. 784. (2) *Internal*; *Podophrya quadripartita*, Bütschli, J. Z. x. 1877; *Trichophrya*, Id. *ibid.* p. 308; *Dendrocometes*, Plate, op. cit. *supra*. Cf. note 1, p. 828, *ante*. Embryoes are described in the general works, *supra*.

*Conjugation*: Claparède and Lachmann, op. cit. *supra*, ii. pp. 122, 123, 136, 228-9; Fraipont, op. cit. xlv. p. 502; cf. note 2, p. 827, *ante*; in *Dendrocometes*, Plate, op. cit. *supra*; A. Schneider, Tablettes Zoologiques, Poitiers, i. 1886, p. 82.

## CLASS INFUSORIA S. CILIATA.

*Plegepod Protozoa with a stable outline and a complete or partial investment of cilia. Compound cilia, pectinellae, and vibratile membranes are not uncommon. There is usually a special adoral band of cilia. The protoplasm may or may not be differentiated into an exo- and endo-plasm, and it may or may not be protected by cuticular structures. There is as a rule an oral tube or cytostome, and an anal spot or cytophyge constant in position, rarely an anal tube. The nucleus is single or multiple, and is accompanied by one or more paranuclei, except in a few multinucleate forms. A contractile vacuole is seldom absent, usually single, occasionally multiple, always constant in position. Conjugation is temporary or permanent: the conjugating individuals similar or dissimilar. Fission is in most instances binary, sometimes repeated rapidly, causing a diminution in the size of the organism. Gemmation is not common.*

The majority of Infusoria are free-swimming: a few lead a sedentary but free life within a gelatinous tube, which may be simple (*Stichotricha*), or dichotomously branched (*Maryna*, *Schizosiphon*). Some species of *Stentor* are able to attach themselves at will by pseudopodial processes; others inhabit a gelatinous tube, to which they cling by means of retractile setae: so too *Tintinnidium fluviatile* and *Stylocola*. Some genera, such as *Spirochona* and its allies, are permanently attached by a sucker-like disc or by a cement. Of the attached forms, some are simple, and then naked, stalked, e.g. *Vorticella*, or tubicolous, the tube or lorica being sessile or stalked; others are colonial, either naked and stalked, e.g. *Epistylis*, or protected by a gelatinous investment as in *Ophrydium*.

The Infusoria present great varieties of external shape: their body is sometimes eminently contractile, therefore changeable in outline. The *Hypotricha*, however, have a flattened locomotor or ventral surface, and a convex dorsal; and the fixed *Peritricha* are more or less bell-shaped. The surface of the body is rarely completely naked, but is invested with a cuticular layer of varying thickness and consistence<sup>1</sup>. It is elastic, generally hyaline, seldom granular, or marked by vertical lines (? rods or spaces); and is often scarcely distinguishable from the underlying protoplasm. There is sometimes, however, a very distinct cuticle, either a dorsal thickened cuirass (*Euplotidae* among *Hypotricha*), a bivalved cuirass (some *Dysteridae* in the same order), or rings of plates, as in the Holotrichan *Coleps hirtus*. The coat of needles in *Tiarina* (= *Coleps fusus*), or the similar structures covering the pedicles of some *Vorticellae*, are probably cuticular: so too the simple or denticulate ring which supports the sucker of all the Peritrichan *Urceolarina* save *Licnophora* and the corneous band or teeth of the Opalinid *Hoplitophrya*. A number of Infusoria secrete a distinct tube or lorica, usually fixed, sometimes free as in *Tintinnodea*, which may be, as in some species of *Stentor*, only a temporary structure. It may be gelatinous, or though at first soft and colourless, becomes hardened, dark in hue, and resistant to reagents. In the Tintinnodean *Codonella*, particles of silica are imbedded in its substance, and in its congener *Dictyocysta*, it is perforate and Radiolarian in appearance. Its chemical composition is unknown, save in the case of the hyaline investment of the colonial *Ophrydium versatile*, where it is composed of a cellulose akin to Tunicin (p. 107), and though apparently of a uniform structure, is really divisible into a number of coherent sheaths, one to each individual.

The cilia, which are so characteristic of the class, are extensions of the outer layer of protoplasm, and are retractile under certain conditions. They are sometimes used as organs of adhesion, and vary in character. The cilia proper are slender, of the same size from base to apex, vibratile throughout: the cirri, the elongated triangular membranellae s. pectinellae, the membranes, are composed of agglutinated cilia, and may be wholly or partially vibratile; the setae are slender, rarely compound, non-vibratile<sup>2</sup>. The modes in which the cilia are disposed afford a basis for classification. In the *Holotricha* they are arranged in parallel lines and are of uniform

<sup>1</sup> See Maupas, A. Z. Expt. (2), i. p. 574. *Opalina* is said by Zeller to be naked, but the superficial bands, supposed by him to be muscular, are probably cuticular. The chemical nature of the plastic cuticle is unknown: it is more resistant than protoplasm, but decomposes sooner or later in water.

<sup>2</sup> For cilia as organs of adhesion, see Maupas, A. Z. Expt. (2), i. pp. 629-30. Note that membranellae are said to appear in *Stentor* as a continuous membrane subsequently broken up. A temporary fusion of cilia into vibratile bundles has been sometimes observed. See Géza Entz, Mitth. Zool. Stat. Naples, v. p. 332.

size, but there may be a band of larger adoral cilia. The *Heterotricha* have an investment of fine cilia covering the body, but a band, straight or curved, of membranellae borders a naked peristome. Its posterior end, or left-hand end, enters the mouth with a spiral twist if the band is curved. In shape, extent, and position the peristome varies a good deal. It is much depressed in the *Tintinnodea*, and in some of them a row of fine paroral cilia lie to the inner side of the membranellae. Some species of *Stentor* possess fine setae, apparently pro- and re-tractile, mingled with the cilia of the body. The *Hypotricha* have the dorsal aspect either naked or beset with fine setae, of which one or more are posterior in position, long, and occasionally compound. Cilia are confined to the flattened ventral aspect: in the two families *Oxytrichidae* and *Euplotidae* they take the form of cirri, either claw-like at their apex (*uncini*) or straight (*styli*), which are grouped in a definite manner<sup>1</sup>. The same two families and the genus *Peritromus* possess a peristome in the shape of an arcuate groove on the left-hand anterior edge of the body. The cilia in connection with it are disposed in special lines or bands; one band is always present, an *adoral* fringe of membranellae; a second, known as *praeoral*, is very generally found near the dorsal edge. Two others, the *endoral* and *paroral*, are not so common. A vibratile membrane may take the place of the praeoral band. In the *Peritricha* the body is non-ciliate except in the Urceolarine genus *Trichodinopsis*; the cilia are confined to one or more encircling bands, or to a spiral band as in *Vorticellina*, *Vaginicolina*, and *Ophrydina*, which consists of membranellae (Bütschli). The right hand end of the spiral enters the mouth, and it is situate on a terminal retractile disc, which is protected in the retracted condition by the closing over of a raised wall or peristome, also by a thickened operculum attached below the peristome on one side (*Pyxicola*, *Pachytrocha*), or a moveable operculum within the lorica (*Thuricola*)<sup>2</sup>. Noteworthy peculiarities are the following:—the perioral contractile collar of the Peritrichan, *Torquatella typica*; the girdle of springing setae in *Halteria*; the tentacles, long, scattered, retractile, of *Actinobolus radians*, four, short, knobbed, perioral, of *Mesodinium pulex*, which, though Acinetarian in aspect, are not suctorial<sup>3</sup>.

<sup>1</sup> The groups in question are: (1) *frontal*, anterior and on the animal's right; (2) *ventral*, sometimes replaced by rows of cilia; (3) *anal s. transverse*; (4) *marginal*, a fringing row of short cilia, either continuous, or interrupted posteriorly. The *caudal* is really a group of dorsal setae according to Maupas; see A. Z. Expt. (2), i. p. 535 et seqq, and Saville Kent's Infusoria, fig. 1, p. 760.

<sup>2</sup> For the limitations of the term *Peritricha*, see Géza Entz, Mitth. Zool. Stat. Naples, v. p. 407; Id. Z. W. Z. xxxviii. p. 183 et seqq.; Bütschli, M. J. xi. p. 553. The terms 'right' and 'left hand' applied to the adoral band of cilia mean the animal's right or left, the mouth being considered as ventral in position. For the paroral cilia of *Tintinnodea*, see Entz, op. cit. *supra*, Naples, pp. 395-6; for the peristome of the Hypotrichans, Saville Kent's Infusoria, fig. 2, pp. 760-1, and Biol. Centralblatt, iii. p. 236.

<sup>3</sup> *Actinobolus*, Entz, Z. W. Z. xxxviii. p. 167; *Mesodinium*, Id. op. cit. *supra*, Naples, p. 308.

The protoplasm is either similar throughout, or it is divisible into an exoplasm (cortex) and endoplasm (medulla). In the former case it is variably granular, its movements slow as in *Oxytrichidae* and *Euplotidae*, and it is sometimes filled with non-contractile vacuoles<sup>1</sup>. When there is an exoplasm the transition from it to the more fluid endoplasm is gradual or abrupt. The granular character of the endoplasm depends much on the state of nutrition: the granules are albuminous, fatty, composed of glycogen, sometimes doubly refractile, occasionally distinctly crystalline and apparently formed of a urate. A mouth or cytostome with an oral tube, and an anal spot or cytoppyge, are absent only in the endoparasitic *Opalinidae*. The former may be terminal and anterior, even mounted on a protrusible eminence, e.g. *Actinobolus*, usually on one surface, hence the ventral, and frequently in connection with a peristome (*supra*). The cuticle lines the oral tube, which may have some extent. In the fixed *Peritricha*, e.g. *Vorticella*, there is a vestibule common to the oral tube, the anal spot and the duct of the contractile vacuole. The oral tube may be armed with cuticular stylets, protrusible (*Prorodon*, *Chilodon*), or even discharged upon the prey (the Peritrichan *Didinium*): or with more complex apparatus (*Dysteria armata*). In the fixed *Peritricha* a long vibratory seta, the optical expression according to some authorities of an undulatory membrane, projects from the vestibule. Food is conveyed into the oral tube by suction in carnivorous species, by the adoral band of cilia, which is prolonged into it in other instances, and it is then lodged in a food-vacuole. The anal spot is as a rule only visible at the moment of discharge, but in the parasitic Holotrichan *Nyctotherus*, and perhaps some others, there is an anal tube with cuticular lining. The spot is terminal or subterminal, lateral in *Stentor* and *Folliculina*, in the vestibule of *Vorticella* and its congeners<sup>2</sup>.

The protoplasm is generally colourless. It may be tinted by the food, e.g. Oscillatorians in *Nassula*, by a diffused pigment, such as the blue Stentorin of *Stentor coeruleus*, which yields a special absorption spectrum, the sea-green of *St. multiformis*, the blackish of *St. niger*, and dark-green of *Folliculina*, the yellow or brown of many species; or by pigment particles, such as the crimson globules of *Holosticha flavo-rubra*, the crimson granules of *St. igneus*, mixed with chlorophyl bodies which occur in that Heterotrichan, in *St. polymorphus*, *Ophrydium versatile*, and some others. Certain of the green-coloured forms, e.g. the last named, occur also colourless, and it has been supposed that the chlorophyl bodies are really symbiotic algae<sup>3</sup>. The exoplasm when differentiated is always

<sup>1</sup> *Trachelius ovum* (*Holotricha*); *Bursaria truncatella*, *Stentor coeruleus* (*Heterotricha*); *Loxodes rostrum*, *Condylostoma patens* (*Hypotricha*).

<sup>2</sup> On the supposed intestinal tube of *Didinium*, see Maupas, A. Z. Expt. (2) i. p. 597.

<sup>3</sup> See pp. 242-5. Add to the authorities there quoted, Engelmann, Pflüger's Archiv für

eminently contractile. Distinct muscular fibrils are sometimes met with, and have been best worked out in *Stentor* and *Vorticellina*. In the former they are visible as fine longitudinal lines beneath the clear bands which bear the cilia of the body: the peristome has a few circular and radial lines beneath the adoral membranellae. In the *Vorticellina* the fibrils spread from the apex of the body and are inserted into a thickened cuticular ring, the spot where the posterior ciliary wreath develops when the animal becomes free. Thence they extend to the edge of the peristome, which has its own fibril-system. They are continued in the opposite direction down the pedicle in *Vorticella*, *Zoothamnium*, and *Carchesium* as a spiral band. In the last-named the band is interrupted at each bifurcation of the pedicle. Trichocysts are lodged in the exoplasm of a few genera, for the most part Holotrichan. They are minute, fusiform bodies: when discharged they bear a fine thread attached to one end, or they are converted into straight filaments, pointed at each end, one end however furnished with a minute appendage<sup>1</sup>.

There is a nucleus (endoplast) accompanied by one or more paranuclei (nucleoli s. endoplastules). It lies superficially as a rule, but is said to rotate in some instances with the endoplasm. It may be round or ovate, band-like, and then sometimes moniliform, i. e. beaded, the segments being connected by a delicate thread. There is a nuclear membrane, and contents variously disposed in different Infusoria. The paranuclei appear to be diminutive nuclei, and either lie near the nucleus or are apposed to it. Their number varies, indeed is inconstant in the same species. There is always one, but there may be more, e. g. 3-4 in *Spirochona gemmipara*, 28 in *Stentor Roeselii*. When the nucleus is beaded, a paranucleus may correspond to each segment, or the number of paranuclei may exceed or fall short of that of the segments<sup>2</sup>. In shape a paranucleus is globular; it has a membrane. There are some interesting variations from the typical structure. *Loxodes rostrum* and *Holosticha Lacazei* (*Hypotricha*) have a number of nuclei with paranuclei, apposed one to each nucleus in the former, scattered in the latter. A few *Holotricha* e. g. some species of *Opalina*, and *Hypotricha* e. g. some species of *Holosticha*, have

Physiologie, xxxii. 1883; Ryder, Proc. U. S. National Museum, vii. 1884. Stokes states (Journal New York Micr. Soc. i. 1885) that *Leucophrys emarginata*, though coloured by chlorophyll bodies is exceedingly voracious. On the other hand, Gruber's *Strombidium oculatum* has no mouth (Nova Acta, 46, p. 514). Stokes' *Vorticella smaragdina* is green throughout, but is perhaps not tinted with chlorophyll (Amer. Naturalist, xix. p. 19). The marine Vorticellid *Spatostyla* (*Rhabdostyla*) *Sertulariarum* harbours symbiotic *Zooxanthellae* (Entz, Mitth. Zool. Stat. Naples, v. p. 416).

<sup>1</sup> See Maupas, A. Z. Expt. (2), i. p. 611, and Entz, op. cit. *supra*, p. 383. It is generally asserted that the filament is coiled within a sac and everted, as in the nematocysts of e. g. Hydroids. Greeff maintains that the freshwater Peritrichan, *Epistylis flavicans*, has Hydroid-like nematocysts, but other observers have failed to find them.

<sup>2</sup> See Maupas, A. Z. Expt. (2) i. pp. 527, 660-1.



a number of similar globular nuclei, which multiply with mitosis in *Opalina*. Irregularly shaped nuclear fragments are found as well in some species of *Holosticha*; and in the Holotrichans *Choenia teres* and *Trachelocerca Phoenicopterus* the nucleus is reduced to chromatin granules scattered irregularly, but the condition may not be a permanent one. The Opalinids *Benedenia* and *Opalinopsis*, which are endoparasitic in Cephalopoda, vary at different times. The nucleus of the former is a long convoluted band, which branches and segments into globular or irregular fragments; that of the latter is reticulate, but may break up into fragments. The Heterotrichan *Plagiotoma Lumbrici* is said to resemble *Benedenia*. During fission or gemmation the round or ovate nucleus and the paranuclei divide with mitosis: the band-like nucleus is said not to do so. In many multinucleate forms fission does not affect the nuclei<sup>1</sup>, but in *Holosticha scutellum* and *Opalinopsis* their previous fusion has been observed. The small encysted fragments of *Opalina Ranarum*, *O. obtrigona*, and *O. dimidiata* become uni-nucleate just before or just after their exclusion from the cyst. During conjugation, the nucleus is resolved into fragments, the paranuclei divide with mitosis. Interchange of a paranucleus, or of a portion of one, and fusion of the interchanged structure, whichever it may be, with a corresponding one *in situ* has been observed (Gruber, Maupas). A new nucleus and paranucleus are then formed from the old paranuclei. It is not certain, however, how far the fragments of the old nucleus are excluded from any share in the process; whether they are extruded or absorbed<sup>2</sup>.

The contractile vacuole is rarely absent, as in the Opalinid genera *Opalina*, *Opalinopsis*, and *Benedenia*, and in a few *Hypotricha*<sup>3</sup>. It is nearly always superficial in position, and is usually single, but there may be more, e. g. 2 in *Paramecium*, and Vorticellids with a well developed cuticle, several in *Chilodon*, 50 in *Trachelius ovum*, or even 100 in *Prorodon margaritifera*. Or small secondary vacuoles, irregular in position and appearance, may be present, e. g. in *Prorodon teres*. When distended it is usually globular, rarely linear as in some Opalinids. It is discharged by a pore,

<sup>1</sup> Maupas, op. cit. p. 654.

<sup>2</sup> Joseph has observed a natural fragmentation of the nucleus in *Stylonychia*, one induced by confinement in the dark in *Paramecium caudatum*. An exchange of portions of the nucleus has been seen by Schneider in *Anoplophrya circulans*, of portions of the paranucleus by Joseph, Gruber, and Maupas. The first-named of the three has recorded movements of the chlorophyll bodies in *Ophrydium versatile* indicating an interchange of protoplasm. Plate observed the resolution and re-constitution of the nucleus in *Lagenophrys ampulla* when about to quit its tube, or after fission (*Z. W. Z.* xliii. pp. 213-14), or during gemmation (*Ibid.* pp. 214-15). But in the permanent conjugation of two young *Spirochona gemmipara*, he saw both nuclei and paranuclei fuse without previous change (*loc. cit.* pp. 206-9). See the authorities quoted p. 840, *post*.

<sup>3</sup> See Maupas, A. Z. Expt. (2), i. p. 633. Maupas thinks (*op. et p. cit.*) that *Strombidium urceolare* and *S. sulcatum* have also no vacuole. Saville Kent assigns one to them. So does Géza Entz to *Actinotricha*, which has not got one according to Maupas, with the remark that there is a long pause between the discharge and formation *de novo* of the vacuole.

which is sometimes permanent if the cuticle is thick, e. g. in *Paramecium Aurelia*, or in the *Vorticellina* by a canal leading into the oral vestibule. The new vacuole may arise as a simple expanding drop, by the coalescence of a number of droplets disposed irregularly or in a rosette, sometimes, however, taking the shape of converging linear or branched canals.

Reproduction is by fission, gemmation, and spore-formation. Fission is usually binary and transverse; oblique in *Stentor*, *Lagenophrys*, and *Vaginicola*; longitudinal in *Vorticella* and most of its allies. The ciliary disc and peristome of *Vorticella* are retracted or obliterated during the process to be reproduced at its close<sup>1</sup>. One of the two individuals retracts its disc, develops a posterior girdle of cilia on the ciliary ring (p. 834, *ante*), breaks away and swims off to affix itself elsewhere. So too in *Spirochona tintinnabulum* the funnel and peristome may be retracted, a median ciliary wreath be evolved, and transverse fission then takes place. The anterior part swims away, the posterior develops a new funnel and peristome. In the Vorticellids *Epistylis*, *Zoothamnium*, and *Carchesium* (?) repeated fission gives rise to 4-8-10 microzooids disposed in a rosette<sup>2</sup>. They are detached. Each individual has a rudimentary ciliary disc, and a well developed posterior ciliary circlet: it is probably always destined to conjugate with an ordinary individual or macrozooid (p. 837, *infra*). In the *Opalinidae* variations occur. *Haptophrya gigantea* is resolved by repeated binary fission into a chain of eight individuals. Two small posterior segments are produced simultaneously in *Anoplophrya nodulata*: a posterior region is marked off in *A. prolifera* and *Benedenia*, and is then divided into a chain of segments. *Opalina* itself breaks up into a number of portions by repeated transverse or oblique divisions: and the fragments thus formed encyst and are devoured by the tadpole of the Frog with its food<sup>3</sup>. The peristome of the new individual in *Stentor* and some other *Heterotricha*, and probably in most *Hypotricha* begins to develop before separation is completed. The products of fission may grow in size before the process is repeated; if they do not do so, the result is a rapid diminution in size of the individual remedied eventually by conjugation. The products of fission may remain living in societies (p. 830): or if they are organically connected by a stalk or pedicle they constitute colonies, as in the *Vorticellina*. New colonies are founded by individuals which retract or lose the peristome, develop a posterior ciliary wreath, are detached and swim away to settle in a new spot. In some species of *Zoothamnium*, e. g. *Z. arbuscula*, this duty falls upon special large spheroidal

<sup>1</sup> Bütschli says the cilia persist, M. J. xi. p. 561.

<sup>2</sup> Binary fission of one of two individuals just produced by fission has been seen in *Vorticella microstoma*, and an instance of the formation of microzooids recorded; see D'Udekem, Mém. Acad. Roy. Belg. xxxiv. p. 8, Pl. I. fig. 5a. In the genus *Vorticella* microzooids are perhaps formed as a rule by gemmation.

<sup>3</sup> See on this subject, Gruber, Biol. Centralblatt, pp. iv. 712-13, 715-16.

individuals. The function of the slender elongate zooids of *Z. alternans* and *Epistylis ophioidea* is not known.

Gemmation is rare. It is the sole mode of reproduction observed in *Spirochona gemmipara*, and may be exhaustive of the parent. It occurs also in *Stylochona nebalina*, *Lagenophrys ampulla*, and in some species of *Vorticella*, e.g. *V. microstoma*. The free-swimming bud is unlike its parent; in *Lagenophrys* it is Hypotrichan in its ciliation (Stein), or provided with a terminal ciliary wreath (Plate); in *Vorticella* it resembles a rosette microzooid (*supra*), and has a similar destiny.

The term spore-formation is applied to the production by fission of small individuals within a cyst. The number produced varies from two in *Prorodon teres* and *Amphileptus* to 16 in *Chilodon cucullulus*, or even 1000 and upwards in *Ichthyophthirius multifiliis*, an ectoparasite on some freshwater fish. Encysted Vorticellids with many nuclei have been observed. In *Vorticella nebulifera* Everts saw emerge from the cyst 6–10 minute globular bodies each with a ciliary girdle and in its centre a mouth. They multiplied by fission, but eventually affixed themselves by the oral end, developed a peduncle and ciliary disc. The young *Ichthyophthirius* is unlike its progenitor. Small Infusoria differing from the adult form have been observed, but whether produced from cysts or not is not known<sup>1</sup>.

Conjugation is universal and for the most part temporary. The conjugating individuals are as a rule small in size, produced by rapidly repeated fission. They unite by their oral aspects, e.g. in *Paramecium*, *Stentor*, or by their lateral as in *Hypotricha*. The union brings about changes; the nucleus is broken up; the paranuclei divide with mitosis; protoplasm may be interchanged as well as paranuclei (p. 835 and note 2, *ante*), the cilia may be withdrawn, the peristome obliterated. Separation brings about a reconstitution of all these organs, followed by growth or rejuvenescence. Permanent conjugation (=copulation of Engelmann) is met with in *Stylonychia* and some other *Hypotricha*, and in some *Vorticellina*. In *Vorticella* and *Epistylis* it takes place between a microzooid, whether a fission-product or a bud, and an ordinary individual<sup>2</sup>. It is followed by a

<sup>1</sup> Everts looked on the reproduction of *V. nebulifera* as an instance of Alternations of Generations. Dimorphism may affect the ordinary fission-product, e.g. *Folliculina (Freja) ampulla*, according to Möbius, undergoes unequal longitudinal fission, and the part set free is uniformly ciliated, but when settled develops its bilobed peristome and Heterotrichan ciliation (Biol. Centrablatt. vi. p. 540). The so-called internal germs are probably always due to parasites, or to diseased nuclear products, caused by Bacteria. See on the whole subjects, Engelmann, M. J. i. pp. 584–602; Bütschli, Abhandl. Senck. Ges. x. pp. 343–55; van Rees, Z. W. Z. xxxi. 1878.

<sup>2</sup> See Engelmann, M. J. i. pp. 582, 622, 624, and summary, p. 628 et seqq. In *Epistylis flavicans* he states that a zooid A. gives rise by fission to two zooids B.B. Of these, one is resolved into microzooids. The detached microzooid always conjugates with an individual B, never with A. Hence he concludes there is a sexual distinction; the microzooid is male, the zooid B. female. Engelmann's statement that the paranucleus is absent in *Vorticellina* appears to be wrong: nor has it the sexual value which he and other authorities of the time supposed.

fragmentation of the nuclei and the formation of a new nucleus. Lateral union between two or three ordinary individuals has been witnessed in *Vorticella microstoma*, *Epistylis brevipes* and *Carchesium polypinum*. The united zooids develop posterior ciliary wreaths, and are detached from their peduncles. Similar union may take place between zooids of *V. campanula*, already free. The united animals may either settle down again or encyst, the latter being perhaps the normal result<sup>1</sup>.

All Infusoria appear to encyst; and the Hypotrichan *Gastrostyla vorax* has been preserved alive in this condition for two years. Cilia, peristome, all organs save the nucleus and contractile vacuole are lost. The cyst is spheroidal, as a rule smooth, occasionally ridged or papillate; flask-shaped in *Stentor coerulesus*, and closed by an operculum. Its membrane may be single or double. The formation of a gelatinous envelope has been observed in *Zoothamnium mucedo* inclosing 1-9 individuals *in situ* on their stalks<sup>2</sup>.

The Infusoria are for the most part microscopic in size; some however are visible to the naked eye, e.g. *Stentor polymorphus*, which attains a length of  $\frac{1}{20}$  in.; so too the colonies of some *Vorticellina*, especially the arborescent colonies of *Zoothamnium arbuscula*; and *Ophrydium versatile* gives rise to gelatinous hollow masses 5 in. across when full grown. Infusorians inhabit fresh, salt and brackish waters; some species, indeed, e.g. *Chilodon cucullulus*, *Zoothamnium arbuscula* are common to both fresh and salt. The faunae of different seas are not more dissimilar than are the faunae of different freshwaters, and many littoral or brackish-water forms are met with in salt lakes (Géza Entz). A few Infusorians are parasitic; some ectoparasitic, e.g. *Ichthyophthirius* on freshwater fish, others endoparasitic in Vertebrata and Non-vertebrates alike, e.g. the *Opalinidae*. A Heterotrichan *Balantidium coli* is found in the large intestine of the human subject and in the rectum of swine. Dimorphism is restricted to certain colonial forms (p. 837) or products of fission or gemmation (p. 837 and note 1).

The Infusoria are classified as follows:—

1. *Holotricha*: free-swimming, more or less completely ciliate; cilia similar or slightly dissimilar, especially the adoral cilia; an extensile or undulatory membrane sometimes present; trichocysts not uncommon: *Paramecium*, *Prorodon*, *Nassula*, *Coleps*, *Trachelius*, *Ichthyophthirius*, &c.; *Opalinidae*, e.g. *Opalina*, *Anoplophrya*, *Benedenia*.

2. *Heterotricha*: free or attached either at will, or rarely permanently; naked or tubicolous; cilia of small size covering the body, sometimes supplemented by non-

<sup>1</sup> Claparède and Lachmann, Études sur les Infusoires, etc. ii. p. 229 et seqq.; Stein, Organismus, etc. (*infra*), ii. pp. 10, 113.

<sup>2</sup> Gruber, Nova Acta, xlv. pp. 520-1; cf. Géza Entz, Mitth. Zool. Stat. Naples, v. p. 418; Nachtrag, p. 439. Species of *Amphileptus* prey upon the colonial *Vorticellidae*, and encyst on the ends of the branches after a meal. Cf. Entz, op. cit. p. 420.

vibratile setae; a set of adoral membranellae, disposed in a straight or curved line, in the latter case surrounding a peristomial area: *Bursaria*, *Balantidium*, *Stentor*; *Tintinnodea*, &c.<sup>1</sup>

3. *Peritricha*: free or fixed; solitary or colonial; naked or tubicolous; with an adoral spiral of membranellae, or one or more ciliary girdles; otherwise destitute of cilia: see note 2 p. 832: *Torquatella*; *Halteria*; *Didinium*; *Trichodina*, &c.; *Vorticellina*, e.g. *Vorticella*, *Epistylis*, *Carchesium*, *Spirochona*; *Vaginicolina*, e.g. *Vaginicola*, *Cothurnia*; *Ophrydina*, e.g. *Ophrydium*.

4. *Hypotricha*: free, rarely tubicolous; with one surface, the ventral, flat, the other, the dorsal, more or less convex; ventral surface either entirely ciliate or with compound cilia disposed in special groups or lines; dorsal surface sometimes provided with immobile setae; adoral membranellae usually present; a complex peristome in two families (*Oxytrichidae*, *Euplotidae*): *Chilodon*, *Loxodes*, *Dysteria*, &c.; *Stichotricha*, *Schizosiphon*, *Oxytricha*, *Stylonychia*, &c.; *Euplotes*, &c.

Manual of the Infusoria, Saville Kent, ii. 1881-82 (with lit.); Organismus der Infusions-thiere, Stein, Leipzig, i. *Hypotricha*, 1859; ii. *Heterotricha*, 1867; Études sur les Infusoires, &c., Claparède and Lachmann, 2 vols., Geneva, 1858-61 (Mém. Inst. Nat. Genevois, v. vi. vii).

\*Protozoen des Hafens von Genua, Gruber, Nova Acta, 46, 1884, p. 509 et seqq.; \*Infusorien des Golfes von Neapel, Géza Entz, Mitth. Zool. Stat. Naples, v. 1884; \*Ein kleines Beitrag. &c., von Daday, ibid. vi. 1886; Contributions à l'étude morphol. et anat. des Infusoriens ciliés, Maupas, A. Z. Expt. (2), i. 1883; \*Protozoaires des Vieux-Port de Marseille, Gourret, A. Z. Expt. (2), iv. 1886; Neue Infusorien, *Schizosiphon* (= *Stichotricha*) *socialis*, *Maryna*, &c., Gruber, Z. W. Z. xxxiii. 1878<sup>2</sup>.

*Holotricha*. *Coleps hirtus*, Maupas, A. Z. Expt. (2), iii. 1885; *C. fusus* = *Tiarina*, Bergh, see Naples Zool. Jahresbericht, 1880, Protozoa, p. 170; *Opalina*, (various species), Zeller, Z. W. Z. xxix. 1877; *Anoplophrya circulans*, Schneider, Tablettes Zoologiques, Poitiers, i. 1886; Balbiani, Recueil Zool. Suisse, ii. 1885; *Benedenia*, *Opalinopsis*, Foettinger, Archives de Biologie, ii. 1881; *Infusorian parasites of Termites*, Leidy, Journal Acad. Nat. Sc. Philadelphia, (2), viii. 1881; *Ichthyophthirius*, Fouquet, A. Z. Expt. v. 1876.

*Heterotricha*. *Bursaria truncatella*, Brauer, J. Z. xix. 1885, Schuberg, M. J. xii. 1886; *Folliculina* (= *Freja*) *ampulla*, Moebius, A. N. H. (5), xvi. 1885; *Tintinnidium fluviatile*, *Codonella lacustris*, Géza Entz, Mitth. Zool. Stat. Naples, vi. 1886 (with lit. on family, p. 214).

*Peritricha*. *Actinobolus radians*, *Mesodinium acarus*, and on limits of order, 'Beiträge,' &c., Géza Entz, Z. W. Z. xxxviii. 1883; *Didinium*, Balbiani, A. Z. Expt. ii. 1873; *Trichodina*, Rosseter, Journal Roy. Micr. Soc. (2), vi. 1886; *Epistylis*, *Ophrydium*, &c., 'Beiträge,' Wrzészniowski, Z. W. Z. xxix. 1877; *Vorticella nebulifera*, Everts, Z. W. Z. xxiii. 1873; *Vorticellidae*, Greeff, A. N. 36, (1), 1871;

<sup>1</sup> By Saville Kent the *Tintinnodea* are divided between the *Heterotricha* and *Peritricha*; they appear to be entirely Heterotrichan. The Urceolarine *Trichodinopsis* he classifies similarly with the *Heterotricha* on account of its general ciliation; it is better to consider it as an aberrant Peritrichan. See references quoted, note 2, p. 832, ante.

<sup>2</sup> The asterisks mean that Acinetarians are included in the papers.

*Dimorphic zooids of Zoothamnium ophioidea*, Kellicott, Journal R. Micr. Soc. (2), v. 1885, p. 78; *Connection of Vorticellidae to other Infusoria*, Bütschli, M. J. xi. 1885; *Gerda*, Phillips, J. L. S. xvii. 1883; *Spirochona, Lagenophrys*, Plate, Z. W. Z. xliii. 1886, pp. 200-15; *Torquatella*, E. Ray Lankester, Q. J. M. xiv. 1874.

*Hypotricha*, 'Beiträge,' &c., *Oxytrichidae*, Sterki, Z. W. Z. xxxi. 1878; cf. Wrzèsniowski on Kowalewski in Biol. Centralblatt. iii. 1883-4, p. 235.

*General Anatomy*, Maupas, A. Z. Expt. (2), i. 1883, pp. 570-661.

*Envelope of Ophrydium*, Halliburton, Q. J. M. xxv. 1885; Harker, Brit. Association Reports, 1885, p. 1074.

*Adoral cilia = pectinellae*, in *Heterotricha and Hypotricha*, compound nature of ventral cilia of latter, Moebius, Biol. Centralblatt. vi. 1886-7, p. 539; cf. van Rees, 'Zur Kenntniss der Bewimperung der Hypotrichen,' Amsterdam, 1881; *action and insertion of cilia*, Engelmann, Pflüger's Archiv für Physiol. xxiii. 1880, pp. 507, 521, 530; *Bristle of Vorticellidans = a membrane*, Gruber, Z. W. Z. xxxiii. 1880, p. 460-1; Bütschli, Z. W. Z. xxviii. 1877, p. 67 on Fig. 21, Taf. vi; Géza Entz, Mitth. Zool. Stat. Naples, v. 1884, p. 417. *Organs of attachment in Stentor*, Gruber, Z. A. i. 1878.

*Muscle fibrils*, Brauer, J. Z. xix. 1886, pp. 500-11; Wrzèsniowski, Z. W. Z. xxix. 1877, pp. 287-95.

*Glycogen*, Maupas, C. R. ci. 1885, p. 1504; Barfurth, A. M. A. xxv. 1885, pp. 314-18. *Birefringent corpuscles*, Maupas, A. Z. Expt. (2), i. 1883, p. 616; *ibid.* iii. p. 352 and note. *Stentorin*, E. Ray Lankester, Q. J. M. xiii. 1873; *chlorophyl*, see p. 245, and note 3 p. 833, *ante*.

*Nucleus and paranucleus*, Jickeli, Z. A. vii. 1884; *multinucleate forms*, Gruber, Biol. Centralblatt. iv. 1884-5; *Id.* Z. W. Z. xl. 1884, pp. 140-48; Maupas, A. Z. Expt. (2), i. 1883, pp. 652-61; *division of nuclei in Opalina*, 'Zur Kenntniss,' &c., Pfitzner, M. J. xi. 1885.

*Contractile vacuole*, Wrzèsniowski, Z. W. Z. xxix. 1887, pp. 309-13; Fischer, Archives Slaves de Biologie, 1886; *two in some Vorticellae*, Stokes, Amer. Monthly Micr. Journal, vi. 1885; cf. Lembach, in Journal R. Micr. Soc. (2), 1882, p. 355.

*Conjugation. Exchange and union of paranuclei—or their parts*, Maupas, C. R. cii. 1886, p. 1569; ciii. 1886, p. 482; Gruber, A. N. H. (5), xviii. 1886, p. 164; *exchange of parts of nuclei*, Schneider, Tablettes Zoologiques, i. 1886, pp. 79-80; cf. Bütschli, Abhandl. Senck. Ges. x. 1876, pp. 262 et seqq; Engelmann, M. J. i. 1876; *significance of process*, Plate, Z. W. Z. xliii. 1886, pp. 215-28; p. 239.

*Distribution of marine Infusoria*, Géza Entz, Mitth. Zool. Stat. Naples, v. 1884, pp. 432-9; *Marine Tintinnus in Swiss lakes*, Imhof, Z. A. viii. 1885, p. 293.

*Influence of light on growth*, Fatigati, C. R. lxxxix. 1879, p. 959. *Rate of multiplication*, Maupas, C. R. civ. 1887, p. 1006; cf. *Id. Leucophrys patula*, *ibid.* ciii. 1886, p. 1270, and civ. 1887, p. 308.

## CLASS MASTIGOPHORA.

*Plegepod Protozoa in which the organism during the chief part of its life is provided with one or more vibratile flagella as organs of locomotion and alimentation. A mouth and oesophagus sometimes present; nutrition*

*holozoic, saprophytic, or, when chromatophores are present, holophytic. Reproduction by simple binary fission in the motile condition ; or in the encysted state, when it may be simple or continued, giving rise to a few or to numerous small individuals. Conjugation frequent, the conjugating individuals being either similar or dissimilar. Solitary or colonial. Freshwater, marine, in decaying infusions ; rarely parasitic.*

The number of forms included in the Mastigophora is great. The class may be subdivided into four sub-classes, the *Flagellata*, *Chonoflagellata*, *Dinoflagellata* and *Cystoflagellata*, the mutual relations of which are uncertain.

1. *Flagellata*. The members of this sub-class are characterised by the possession of one or more vibratile flagella. The body is usually more or less elongated and monaxial, sometimes asymmetrical, sometimes bilaterally symmetrical either in shape or arrangement of parts ; contractile in some instances, in others more or less amoeboid. A well-developed cuticle may be present, or a membranous or gelatinous envelope.

The amoeboid condition is most strongly developed in the *Monadina Rhizomastigina*. The pseudopodia are either simple or branched digitiform processes (*Mastigamoeba*), or radiant and Heliozoid in aspect (*Dimorpha*, *Ciliophrys*, ? *Actinomonas*), coexisting with one or two flagella, except in the two last-named. They may be partially retracted in *Mastigamoeba*, wholly in *Ciliophrys* and *Dimorpha*. An amoeboid condition, especially of the posterior region of the body, is apt to occur in some other *Flagellata*, e. g. *Cercomonas*. The flagella vary in length, thickness, relative size, number, and disposition. When only one or two they are restricted to the anterior pole of the body. And in *Heteromastigoda* one of them—the pulsellum (gubernaculum of James Clark)—is large and bent backwards beneath the body. An undulatory membrane is found in some parasites, e. g. *Trypanosoma*, in which it extends along one side of the body. A thick layer of exoplasm is present in *Mastigamoeba*, and the anterior extremity of the body is in some cases formed of clear protoplasm free from chromatophores, &c. As a rule, however, no distinction into layers is recognisable. A circulation of the protoplasm has been seldom observed ; its vacuolation is rare and perhaps pathological<sup>1</sup>.

A cuticle is absent in the simpler *Monadina*, *Iso-* and *Heteromastigoda*, hence the possibility of an amoeboid condition ; but when the outline of the body is fixed it is present. It is best developed in some *Euglenoidea* where it is hyaline, homogeneous, obliquely or longitudinally

<sup>1</sup> *Mastigamoeba aspera* has frequently delicate hair-like processes at its posterior end, such as occur in *Amoeba*, &c. Its surface is covered with very small rod-like bodies of uncertain nature, whether processes of the body or a coat of adherent *Bacteria*, very similar to what are seen in *Deinamoeba*.

striated, and when thick of considerable resistance. Special cuticular structures occur as peduncles or envelopes either gelatinous or membranous. A peduncle secreted by the hinder end of the body, solid, stiff and branched, is seen in *Dendromonas* and *Anthophysa* among *Monadina*, secreted by the anterior end by which the animal fixes itself in *Chlorangium*, and the Euglenid *Colacium* where it becomes branched<sup>1</sup>. A gelatinous envelope is formed in many instances under conditions unfavourable to the organism; it occurs normally in *Mastigamoeba verrucosa*, and as a common investment to the colonies of *Uroglena*, *Spongomonas*, *Syncrypta* and *Colacium*, or as a branched tubular structure, the individuals inhabiting the ends of the tubes, in *Cladomonas* and *Rhipidodendron*. The membranous envelope has two forms. In the first, it may invest the body loosely as in *Haematococcus* and *Volvox*, but more usually closely as in the Euglenid *Trachelomonas*, the *Chlamydomadina* and *Volvocina*. In the two latter it is pierced by holes for the passage of the two flagella, and in *Volvocina* the colony has a special gelatinoid (?) investment as well. The second form is more or less cup-like, homogeneous, transparent, colourless or brownish, with a large cavity and wide mouth; it is seen in some Monads, e.g. *Codonoeca*, *Bicosoeca*, *Dinobryon* some *Isomastigoda*, e.g. *Epipyxis*. *Dinobryon* is free, *Epipyxis* fixed by the end of the shell, the others by a peduncle. In *Bicosoeca*, *Dinobryon*, and *Epipyxis* a delicate contractile basal thread connects the animal to the cup. *Coccomonas* among Chlamydomonads has a shell which readily breaks into two parts, *Phacotus* a lens-like bivalved shell. The envelope is composed of cellulose in *Chlamydomonas* and *Haematococcus*; in others of an unknown substance which dissolves spontaneously in water to set free the products of fission.

The colourless *Flagellata* are for the most part holozoic. Food may be captured by means of pseudopodia, or by a process formed for the purpose containing a vacuole, as in many *Monadina* and probably some other small forms, or it enters by a distinct aperture near the base of the flagella. A mouth in the same position with an oesophageal tube is present in Euglenoids, some *Heteromastigoda*, in *Chilomonas*, and *Cryptomonas*. In many Euglenoids, however, it serves as an outlet for the contractile vacuole and is not used for purposes of nutrition<sup>2</sup>. Where chromatophores are present, the organism is holophytic: some colourless forms related to or derived from coloured are saprophytic<sup>3</sup>. Food

<sup>1</sup> The old stems of *Anthophysa* become brown; the granules visible in the substance of the young stem appear to be of an excretory nature. In an animal fed with indigo or carmine the particles of this pigment are soon excreted, and stored up in the newly formed portion of the stem.

<sup>2</sup> Kent states (Manual of the Infusoria, p. 380) that he observed not only accumulations of particles of carmine in the body of *Euglena viridis* when that animal was kept in water, containing in suspension finely pulverized carmine, but also the entrance of particles at the anterior extremity of the oesophagus.

<sup>3</sup> The ingestion of solid food by a coloured form *Chromulina* (*Chrysomonas*) *flavicans* is



vacuoles occur when the food is ingested by means of a vacuole, rarely in other instances. Indigestible remnants are expelled at the hinder end of the body as a rule, rarely anteriorly as in *Bicosoeca*, or in amoeboid forms at any spot. A contractile vacuole is seldom absent. It is usually single, rarely double, more rarely multiple. It is constant in position except in the amoeboid condition, and is frequently placed at the base of the flagellum or laterally; it is superficial except in some Euglenoids where it debouches into a reservoir opening in its turn into the oesophagus.

The nucleus has not been observed in some of the smallest forms. It is typically vesicular, and in Euglenoids often reticulate with or without a nucleolus. *Trepomonas* has two nuclei, other *Flagellata* only one. A diffuse colouration of the protoplasm never occurs. Chromatophores, always superficial in position, are common in certain groups, e. g. *Isomastigoda*. They are firm, soft, of definite shape, and consist of a colourless basis infiltrated with green chlorophyl or brown diatomin, or a mixture of both substances in variable proportion; hence a corresponding variation in their tint. They multiply by fission. They are numerous, small, round, or oval in Euglenoids, two in number, large and plate-like in *Dinobryon*, &c.; single and enveloping the whole surface in *Chlamydomonas*, *Gonium*, and probably in other *Chlamydomanadina* and *Volvocina*. Allied forms may be coloured or colourless, e. g. *Chlamydomonas* and *Polytoma*, *Cryptomonas* and *Chilomonas*; and colourless species may occur in coloured genera, e. g. *Euglena*<sup>1</sup>. Clear bodies, one or more, known as pyrenoids or amyllum-bodies, are found in connection with the chromatophores of some Euglenoids, of Chlamydomonads and *Volvocina*. They multiply by fission and consist of a core, the pyrenoid, a clear substance which stains readily, coated in nearly all instances with starch or amyllum, rarely with paramylum. Starch granules have been observed scattered in the protoplasm of *Cryptomonas* as well as in some colourless saprophytic forms when well nourished, e. g. *Chilomonas*. Paramylum, a substance of the same centesimal composition as starch, but not stained by iodine, occurs as laminated grains of varying size, oval, rod- or ring-like in shape, in the protoplasm of Euglenoids<sup>2</sup>. When the green-coloured organism passes into a rest-

beyond doubt, and it possibly occurs in other instances. Some colourless forms (septic monads) have been observed to take in solid particles in quantity when in an amoeboid state. *Bodo caudatus* is able to pierce the cuticle of *Chlamydomonas*, and even of Infusoria, and to suck out the contents by means of its mouth.

<sup>1</sup> *Polytoma* and *Chilomonas* live in putrifying solutions, and are saprophytic, as are also colourless *Euglenae*. *Chlorogonium* and *Carteria* (Chlamydomonads) are said to become colourless under conditions in which they may be saprophytic.

<sup>2</sup> For the characters of paramylum, see Bütschli, Protozoa, Bronn's Thierreich, i. pp. 727-30. Amyloplasts, or starch-builders, are said to be present in *Chilomonas* (Fisch, Z. W. Z. xlii. 1885, p. 82). For these starch-builders, see Sachs' Lectures on Physiology of Plants, transl. by Ward, 1887, p. 316, and Schimper, Q. J. M. xxi. 1881.

ing phase, and rarely while it remains motile, its colour changes to red owing to the formation of haematochrome dissolved in droplets of fat. The formation begins centrally, and spreads to the periphery, disappearing in the reverse direction. It masks the chromatophores when they do not, as is sometimes the case, entirely vanish. Special red-specks, the eye specks or stigmata, of a rounded or rod-like shape, simple, or when large composite, are present to the number of one or more in most coloured and in some colourless forms. They may be placed near the base of the flagellum, the middle of the body (*Volvocina*, some Chlamydomonads), or even at its hinder end (other Chlamydomonads). A lens-like structure is said to co-exist with the stigma in the Euglenoid *Phacus*, and a colourless strongly refractile body in the position of a stigma in some colourless forms, e.g. *Monas*. The function of the stigmata is doubtful, but they are said to disappear in darkness. Forms devoid of them are said to react to light in the same way as those which possess them. Trichocysts similar to those of Infusoria, are lodged at the anterior end of the freshwater Euglenoid *Gonyostomum* s. *Merotricha semen*; their presence elsewhere is doubtful.

Reproduction takes place by fission in the free or encysted state, the latter being frequently preceded by conjugation. Fission in the free state may be binary, and it may be continued without an interval for the growth of the progeny. It is sometimes transverse, but as a rule longitudinal. It occurs while the organism is in the flagellate motile condition, rarely when the flagella have been cast off, the organism remaining motile or becoming motionless as in some *Euglenina*, or still more rarely when it is amoeboid as in *Ciliophrys*, the two products in this case being flagellate. Details vary, but fission of the organism itself occurs only after the principal organs have been already doubled by division, or by new formation as is the case with the contractile vacuole, and sometimes with the flagella even in longitudinal fission. Repeated fission takes place in some Chlamydomads under the protection of the cuticle while the parent organism is motile, and sometimes results in the formation of numerous small individuals or microgonidia. The products are set free by rupture of the cuticle which may be gelatinised previously. Encystation previous to fission occurs in some species of *Euglena*, &c. The cyst varies in thickness and consistence; fission within it is binary, sometimes continued to 4-8 or even more, and the products of fission may grow, encyst, divide, without assuming a free state; consequently clusters of encysted forms are frequently met with resembling the algal *Pleurococcus*. Microgonidia are sometimes thus produced.

The products of fission sometimes remain associated, or even organically connected, to form colonies. In *Dinobryon* and *Poteriodendron* the young individual attaches itself to the edge of the parental cup.

The Dendromonads are grouped singly or in numbers at the ends of a branching solid stem; the Spongomonads *Cladomonas* and *Rhipidodendron* at the ends of branching tubes, whilst the individuals of *Uroglena*, *Synura*, and *Spongomonas* are enveloped in a jelly-like mass, and in the first two may or may not be connected at its centre. In *Syncrypta* the envelopes of the zooids are united at a common centre; in the *Volvocina* they are contained by a common investment. The number of individuals in a colony varies from a few, e.g. 4-16 in *Gonium*, 16 in *Pandorina*, 32 in *Eudorina*, to as many as 12,000 in *Volvox globator*. Each individual may undergo repeated binary fission within its own envelope to form a new colony which is set free; or, as in *Volvox*, this power is restricted to certain large non-flagellate individuals, the parthenogonidia, always few in number, e.g. eight in *V. globator*. Every individual in *Volvox* is connected to each of the six individuals immediately surrounding it by a protoplasmic thread. The colonies of *Eudorina* and *Volvox* are hollow.

Permanent conjugation has been observed in some Monads, in *Bodo*, in Chlamydomads (except *Haematococcus* and *Coccomonas*), and in *Volvocina*. In small species of Monads and *Bodo* several individuals may become amoeboid, then non-flagellate, and fuse into a plasmodium, which encysts and undergoes repeated fission. In other instances a partially amoeboid stage may supervene, the individuals fusing in pairs, at first only by their hinder extremities; or if not amoeboid, they may differ in size, points of structure, and life-history. The contents of the cyst may give rise to minute flagellate individuals (zoospores), or to a more or less granular fluid, the granules of which are said to grow into flagellate individuals, e.g. in *Dallingeria*. The Chlamydomonads have as a rule small individuals or microgonidia, which either fuse one with another in pairs or a microgonidium with an ordinary individual (macrogonidium). The two unite by their anterior ends, their envelopes dissolving at this point. The flagella and stigmata are eventually lost and the zygote or zygospore becomes rounded and encysts, a formation of haematochrome taking place in green-coloured species. Further development generally takes place only after the zygote has been dried for a time, or, in *Polytoma*, has been transferred to a fresh infusion. Two or four individuals are then formed by fission. In *Carteria*, however, a Pleurococcoïd condition has been observed (*ante*, p. 844). As to *Volvocina* there appears to be a conjugation of microgonidia in both *Gonium* and *Stephanosphaera*. In *Pandorina* each individual gives origin to a colony of eight. The parent colony, now motionless, sinks; its coat and the coats of the original individuals slowly soften and gelatinise. The cells in each colony of eight acquire a transitory common coat and cilia. They are eventually set free, and conjugate in pairs. A difference of size in the conjugating individuals is said to be noticeable. This difference is much more marked in *Eudorina*

and *Volvox*. One individual, the macrogonidium (female), is large and ovoid, and in *Volvox* devoid of cilia; the other (male) is elongate, biflagellate, of a yellowish tint, grouped in colonies which are produced by fission from a single large cell, and contain 16, 32, 64 individuals in *Eudorina*, or even 128 in some species of *Volvox*. The two sorts of individuals are contained in different colonies in *Eudorina*, *Volvox Carteri*, and sometimes in *V. minor*, or in *V. globator* in the same colony. *V. minor* is said to develop first one, then the other sort. Every individual in a given colony of *Eudorina* is modified; in *Volvox* only a certain number which resemble at first the parthenogonidia above mentioned (p. 845), but are as a rule much more numerous. The male colony is set free as a whole in *Eudorina* and *V. minor*. After conjugation a double cyst is formed by the zygote, which now develops haematochrome, and is set free by the death and resolution of the original colony. In *Volvox (V. minor)* it appears to rest during the winter; in spring its contents undergo fission and are set free as a young colony of about 500 cells.

Hypnocysts are formed by all *Flagellata* when the conditions of life become unfavourable. They have thick and often multiple walls. In the Chlamydomonads the cyst is formed within the envelope, which is then lost, and in *Volvocina* (? *Volvox* itself) every individual of a colony encysts at the same time. Resting green forms turn red. In a few instances encystation of the nucleus, plus a small quantity only of protoplasm, has been observed, the rest of the protoplasm perishing<sup>1</sup>. Fission of the contents of the hypnocyst occurs in *Stephanosphaera* and *Haematococcus*, in the latter sometimes giving rise to Pleurococcoïd crusts.

The great majority of known *Flagellata* inhabit fresh water; a few are marine, and a few parasitic in Vertebrata, Arthropoda, especially Insecta and Myriopoda, in some Mollusca and Nematodes, inhabiting the digestion tract, blood-vascular system, or the epidermis like *Bodonecator*, so destructive to young trout. They sometimes swarm in great numbers imparting a colour to water, green, e.g. *Euglena viridis*, *Haematococcus*, red, e.g. *Euglena sanguinea*, or even to snow, like the red *Haematococcus*, or the yellowish-green *Chlamydomonas flavovirens*. The contents of the reproductive cysts of some saprophytic species are capable of withstanding a great heat without being killed, e.g. an *Oikomonas* 261°F. in a moist condition, 300°F. in a dry. An artificial adaptation of saprophytic species to life at higher and higher temperatures has been successfully carried out. The green *Flagellata* evolve oxygen under the influence of sun-light, and how far they can endure darkness and live appears a moot point. They are sensitive to light, being attracted or repelled by

<sup>1</sup> See Fisch, Z. W. Z. xlii. 1885, p. 72 (*Chromulina*), p. 110 (*Arhabdomonas*), p. 114 (*Monas guttula*).

differing intensities and perhaps also at different stages of their life. Small as they are, *Flagellata* are not exempt from the attacks of parasites, e.g. the colonies of *Volvax* afford shelter and food to two species of the Rotiferan *Notommata* and to the Proteomyxan *Pseudospora*; and many of them are infested by species of the fungus *Chytridium*, which live and multiply within them; hence erroneous views as to their reproduction.

(ii.) *Choanoflagellata* (*Craspedomonadina*, s. *Cyclomastiges*). This sub-class, found in both fresh and salt water attached to various objects, especially the stalks of Vorticellids, is distinguished by two special features: (1) the possession of a single fine flagellum, implanted at one extremity of the body, within an area surrounded by (2) a clear funnel-shaped collar of protoplasm.

The body is ovate, contractile, and sometimes very liable to assume an amoeboid condition (*Proterospongia*); it is minute, and never exceeds  $\frac{1}{1000}$  in. in size, of a bluish tint, and consists of a colourless protoplasm charged with more or fewer granules. The collar is expansile and retractile, either short, narrow, and smaller at its aperture than at its base (*Phalansterina*), or as is more general, the reverse (*Craspedomonadina*). It is extremely sensitive to movements in the water. It appears functionally to be connected with nutrition (? in *Phalansterina*). The motion of the flagellum brings floating particles from behind forwards, and when they impinge against the collar they adhere to its outer surface. They are then either carried by a flow of protoplasm upward to its edge, over it, and downwards to the central area where they are engulfed (Kent); or the direction of the flow is the reverse, and the particles when they reach the base of the collar are either taken up by a vacuole formed temporarily (Bütschli) or carried into the body by a separation of a portion of the protoplasm of the collar (Entz). The food may be lodged within food vacuoles, and consists principally of *Bacteria*. Faecal residues are expelled within the area surrounded by the collar. The nucleus is small, round, vesicular, placed near the base of the flagellum. Contractile vacuoles are always present at the base of the body, usually two in number, but as many as five have been seen.

The animal may be sessile or stalked, and in the latter case the stalk may be simple and support a single individual, or carry a number of individuals attached to its apex by short contractile threads (*Codosiga*) or it may be branched (*Codonocladium*). The simple forms are generally social. *Hirmidium* (= *Desmarella*) occurs in floating colonies in which the individuals are united side by side in band-like rows, or irregularly; *Astro-siga* is similarly free, but the members of the colony are united by their posterior extremities into stellate clusters. Some are furnished with a gelatinous investment, either clear (*Proterospongia*) or somewhat granular,

with the outlines of the constituent tubes visible, and either incrusting or erect and branching (*Phalansterium*). In the *Salpingocina* each individual is lodged in a sessile or stalked theca; it may be free, or attached to the bottom of the theca by a delicate filament of protoplasm. The theca itself is rarely thick and soft, usually thin, firm and colourless, ovate, vasiform, horn-like, or, if it incloses the collar as well as the body, expanded terminally. In *Polyoecca* the peduncle of one theca is attached to the margin of another. The theca may be detached, and then the animal swims about with it, the flagellum, as is always the case in a free Choanoflagellate, pointing backwards in the line of motion.

Reproduction is by binary fission, transverse in *Phalansterium*, and most commonly in *Salpingoecca*, longitudinal in others, so far as is known. In the former case the collar and flagellum are retracted, and the detached portion may be amoebiform, but eventually becomes a free-swimming monad with a single flagellum until it settles down and forms a collar, &c. In the latter case, as observed in *Codosiga botrytis*, the flagellum is withdrawn, the body divides as does the collar, after however the protrusion of two flagella, one for each new individual. Fissiparous individuals of large size have been noticed in *Codosiga cymosa*. The occurrence of conjugation is uncertain. Retraction of the flagellum and collar, assumption of a spherical shape and formation of a cyst membrane has been observed, in many instances accompanied by division of the contents of the cyst into two, or as a rule into a number of spherical bodies which are set free as uniflagellate monads. After swimming about the latter become fixed and develop a collar, &c.

(iii.) *Dinoflagellata* (*Cilioflagellata*, *Peridinea*, *Arthrodele Flagellata* in part). This sub-class is characterised by a more or less pronounced bilateral aspect of body, coupled with a certain degree of asymmetry; by the presence, save in a few cases, of an envelope or cuticle of a substance akin to cellulose, though not identical with it<sup>1</sup>; by having two flagella implanted close to one another, one directed parallel to the long axis of the body, the other usually transverse to it. The majority of genera are marine and widely distributed; a few are marine and freshwater, whilst one genus, the Peridinidan *Hemidinium*, is exclusively freshwater. Marine forms are said to occur in Alpine lakes, but some doubt attaches to the identification of the species. The sub-class is divisible into the *Adinida* and *Dinifera*.

In the *Adinida* the body is elongated, compressed laterally, and covered by a porous bivalved cuticle; the two flagella are implanted at

<sup>1</sup> According to Klebs the membrane in *Hemidinium* and *Glenodinium pulvisculus* is formed of a substance not akin to cellulose.

one of its extremities, hence the anterior. One of them is extended forwards, whilst the other is wound transversely round its base. The *Dinifera* vary much in shape. The body is as a rule marked by two furrows, a transverse or equatorial furrow, sometimes spiral to a greater or less degree, and a ventral longitudinal furrow which unites the ventral ends of the transverse furrow and extends backwards behind them, and often to a variable degree in front of them. The two flagella are situated at the spot where the furrows meet. The longitudinal flagellum extends backwards along the corresponding furrow; the transverse is lodged in the transverse furrow, and encircles the body from left to right round the dorsal aspect. It appears to be the principal agent in locomotion, and the short wave-like undulations which pass along it from base to apex were formerly interpreted as indicating a ciliation of the furrow; hence the name *Cilioflagellata*. The longitudinal flagellum is in some instances very contractile; the animal probably glides upon it as do some *Flagellata*. There are three families of *Dinifera*.

The *Peridiniidae* are rarely naked (*Gymnodinium*, all species (?), *Hemidinium*). The cuticle is seldom structureless (*Glenodinium*), but is usually broken up into a number of plates arranged as a rule in a definite manner on each side of the transverse furrow<sup>1</sup>. They vary however in number size, &c., in different genera. An apical set crowns the anterior pole of the body, i. e. that end which is usually directed forwards in locomotion. They are generally prolonged into a conical tube open at its extremity. An ant-apical set crowns similarly the opposite pole; whilst two circles of plates, a prae- and post-equatorial lie respectively in front of and behind the equatorial furrow, which is usually placed near the centre of the body, rarely anteriorly. When the furrow is absent the arrangement of the plates marks the equatorial line. The furrows are lined by a delicate cuticle, and in *Ceratium* the longitudinal usually expands into a sub-triangular area. In the same genus the posterior pole is produced into a horn, sometimes recurved; and one or more horns may proceed from the right and left post-equatorial plates. They contain prolongations of the body. The aperture for the longitudinal flagellum is a slit. The second family, the *Dinophysidae*, differs from the foregoing in several respects. The body is elongate, and sometimes remarkably so (*Amphisolenia*). The transverse furrow which is circular, is generally approximated to the anterior pole, or almost terminal, and the longitudinal is very short<sup>2</sup>. The aperture for the longitudinal flagellum is round and somewhat tubular. The cuticle is wanting in *Amphidinium* alone; it constitutes a bivalved shell, and its valves are right and left. The margins of the furrows tend

<sup>1</sup> The structureless cuticle of *Glenodinium* is said to resolve itself into a number of plates under certain conditions.

<sup>2</sup> In the Peridinida *Oxytoxum* and *Ceratocorys* a similar approximation is found, unless Stein's view is right, and the furrow is posterior in these two genera.

to become produced into lamellae. The lamellae of the transverse furrow are directed forwards so as to form two cones one within the other; the anterior is the cephalic, the posterior the nuchal. The right margin of the longitudinal furrow is but slightly produced; its left greatly, and in some instances into broad lamellae, which may be supported by three, rarely more, rib-like thickenings. Cuticular lamellae may also be produced along the junction of the valves of the shell posteriorly. The *Polydinidae*, or third family of *Dinifera*, has but one genus, *Polykrikos*. It is barrel-like in shape, compressed dorso-ventrally, and devoid of cuticle. The body is encircled by eight somewhat spiral transverse furrows, each lodging a transverse flagellum, and all connected by a longitudinal furrow. The longitudinal flagellum is typically single, and situated a little in front of the posterior end of the body. A second terminal and posterior flagellum is sometimes present (Bütschli).

The cuticle is brittle, colourless and hyaline, and at first structureless. It generally develops delicate ridges, inclosing in *Dinophysidae* areolae, with thicker ridges in the *Peridinidae* along the line of union of the plates. Growth of the plates in the last-named family, and of the valves of *Dinophysidae*, is supposed to take place at the edges which are often transversely striated<sup>1</sup>. In *Dinophysidae* each areola is perforated by a pore, and pores are probably present also in *Peridinidae*. The protoplasm has a clear layer of exoplasm in some naked forms, but probably not in other instances. It may be reddish in hue when chromatophores are absent. These last-named structures are as a rule numerous, small and placed peripherally. A single and reticulate chromatophore liable to break up occurs in *Ceratium*; a single central one with out-runners in *Pyrophacus*, &c., and two thin plate-like bodies in *Exuviaella*. Their colour varies from brown to various tints of green, according as diatom or chlorophyll predominate in them. Unmixed chlorophyll occurs in the marine *Protoperidinium viride*. Colourless genera occur, e.g. *Polykrikos*, colourless species in other genera, as well as colourless examples of normally coloured species. Starch-granules, said to be lamellate in *Ceratium*, are present even in colourless individuals. Oil drops, yellow or reddish, are found especially in individuals about to pass into a resting condition, or actually in that state. A drop of large size and tinted red with haematochrome, the so-called eye-spot or stigma, is not infrequently present in freshwater species beneath the longitudinal furrow. A black mass of pigment, with an apposed transparent refractile body, supposed to be an eye, has been observed in a marine species of *Gymnodinium* by Pouchet. The nucleus is globular, ovate or band-like; it has a reticulate structure, and is single

<sup>1</sup> The old plates, according to Joseph's account of *Peridinium stygium*, may remain overlying a new cuticle (Z. A. ii. p. 116). A lamination of the old cuticle has been noted in an old *Ceratium tripos*.



except in *Polykrikos*, which has four, one behind the other. Each of these four nuclei is said to have 3-6 small paranuclei apposed to it, as in some Infusoria. The protoplasm is sometimes vacuolate; and one or two large vacuoles are common, whether contractile or not is uncertain<sup>1</sup>. *Polykrikos* has nematocysts similar in structure to those of Coelenterata, but supposed by some authorities to be taken in with food. Some and probably all coloured Dinoflagellates are holophytic. Solid foreign bodies have been observed in naked forms, and in two instances even their actual ingestion<sup>2</sup>.

Reproduction takes place by binary fission, longitudinal in *Exuviaella* and *Dinophysidae*, oblique in most *Peridiniidae*, but transverse in *Hemidinium* and *Polykrikos*. The process rarely occurs except in *Ceratium* and *Polykrikos*, while the animal is in a motile condition. It usually loses its flagella, the protoplasm contracts from the cuticle and very generally forms a cyst of a cellulose-like substance (?) within the cuticle, which is detached by the swelling of the cyst before or after fission has been accomplished. The cyst is in some instances gelatinous. In *Peridinium* membranous semilunar cysts may be produced in which four, or in a marine species eight, individuals are produced fissiparously. These cysts appear to be attached temporarily by one horn<sup>3</sup>. The chromatophores collect together and generally undergo resolution, the organism acquiring a prevailing red tint. Fission is sometimes incomplete, resulting in double individuals. It is uncertain whether conjugation ever takes place. No such significance can be assigned to the chains of two or more individuals observed in *Ceratium* and in one or two other instances; they are probably formed, at least in the genus named, by fission (Bergh).

Some *Dinoflagellata* have been observed encysted in a resting condition. Examples naked or protected by a fine cuticle are occasionally met with, probably derived from such cysts. Growth, however, appears to be accompanied by moults which may also be produced by unfavourable conditions. Some marine species, e.g. *Ceratium tripos*, *C. fusus*, *Prorocentrum micans*, are phosphorescent. Fossil species of *Peridinium* have been recognised in rocks belonging to the cretaceous series in Germany.

<sup>1</sup> The two vacuoles usually flow together, and at the same time a fine canal is stated to be visible leading to the surface, towards the bases of the flagella. The view that the vacuoles serve to take in fluid nourishment, or are analogous to the sap-vacuoles of vegetable cells, is improbable.

<sup>2</sup> Bergh, e.g. observed solid masses of apparently ingested food in *Gymnodinium gracile*, *G. spirale*, and *Polykrikos auricularia*. An oesophageal tube is said to exist in *Prorocentrum*, and by Entz in *Gymnodinium pulvisculus* (Z. W. Z. xxxviii. p. 188). Kent observed his *G. marinum* chasing monads, and swallowing them by a mouth near the base of the flagellum (Manual of Infusoria, i. p. 444), and Maupas observed an undetermined marine *Peridinium* devouring large Infusoria by means of a sucking tentacle (A. Z. Expt. ix. p. 365).

<sup>3</sup> Pyriform fixed cysts have been observed in *Exuviaella lima*; so too in *Gymnodinium pulvisculus* attached to the tail of an *Appendicularia*; Pouchet, J. de l'Anat. et Physiol. (Robin), xxi. p. 61 et seqq.

(iv.) *Cystoflagellata* s. *Rhynchoflagellata*. Two genera, both marine, are contained in this sub-class:—*Noctiluca* with probably only one species, *N. miliaris*, which is widely distributed, and *Leptodiscus medusoides*, found by R. Hertwig at Messina. In both genera the protoplasm is broken up into a central mass with branching cords extending from it.

*Noctiluca* is from one point of view globular, from another at right angles to the first, somewhat kidney-shaped. It is divisible into two halves, a right and left. In the median plane is an elongated depression, the peristome, at the base of which is a slit-like mouth. At one end, the anterior, of the peristome is a flat tentacle, and close behind it on the right side two small ridges one behind the other, one ending in three or four points, the tooth, the other somewhat semicircular in outline, the lip. A flagellum is inserted at the anterior end of the lip. Each margin of the posterior end of the peristome is bordered by a slight fold; the two folds approach one another and are continued onwards behind the peristome as the 'staff-organ,' until they meet at a point corresponding to one end of a diameter, which joins at its other end the anterior border of the peristome. In size the animal may attain .5–1 mm. ( $\frac{1}{2}$  in.) or even more (Giglioli).

The surface of the body is covered by a delicate clear layer, the cuticle of some authors, which is probably a superficial stratum of the protoplasm differing somewhat from the rest in physical and chemical characters. A mass of protoplasm containing the nucleus lies beneath the peristome, the mouth opening directly into it. From this mass radiate branching and anastomosing cords, their fine ends ending in a thin superficial layer. The cords are separated by large vacuoles; they contain, as does also the superficial layer, small non-contractile vacuoles, and they show a slow movement of granules. Special cords of protoplasm pass to the tentacle, tooth, lip, and staff-organ. The food is always inclosed in a food vacuole. The nucleus is oval or round, and possesses a distinct nuclear membrane. The tentacle is slightly concave on one side, convex on the other. Its movements are slow; it can be extended, contracted, or rolled up towards its concave aspect, but does not seem to subservise locomotion. It usually attains a length of about half the diameter of the body. Structurally, it consists of a delicate membrane-like investment filled by an extension of the protoplasm. The concave side is transversely striate owing to a parallel arrangement of the bands of protoplasm<sup>1</sup>. The tooth, which is yellowish in colour, the lip, and flagellum are also extensions of the protoplasm. The movements of the flagellum

<sup>1</sup> The tentacle is said by Vignal to resemble physiologically a muscle. It contracts at the opening and closure of a constant current, and passes into tetanus lasting 3–4 minutes under an interrupted current. It ceases to contract spontaneously when poisoned by curari, but remains electrically excitable. See Vignal, Arch. de Physiol. norm. et patholog. (2), v. 1878.

are various ; it may be retracted and shot out, lashed about, traversed by short rapid, or long and slow undulations. It appears to have periods of quiescence.

*Noctiluca* passes into a resting condition but forms no cyst. The tentacle is absorbed, the mouth closed, the peristome, &c. obliterated, but the central mass of protoplasm persists. How the organs in question are regenerated is not known to a certainty<sup>1</sup>. Reproduction is by fission and gemmation. It is possible that the former may occur in an ordinary individual, but as a rule the tentacle is thrown off, and all the organs with the exception of the mouth obliterated. The animal becomes elongated transversely, the nucleus first divides with mitosis, then the central mass of protoplasm, and finally a median furrow cuts the two halves asunder. A new tentacle begins to bud out before separation is complete ; the peristome and other organs are also reconstituted. Gemmation is often, perhaps always, preceded by conjugation, which takes place by the fusion of two ordinary or resting individuals. The two always come into contact by the peristome or the spot where the peristome lay. The tentacles of the ordinary individuals are said to be thrown off. In gemmation the central mass of protoplasm forms a superficial projection, the nucleus divides, and then the projection ; and by continuous binary fission, carried out in the same way, a number of spores, amounting to 256 or more generally 512 (*circa*), take origin. The branching cords of protoplasm are retracted during the process, and the nuclei enter the dividing projections as soon as they number 64. The ripe spore is attached to the parent by a slender pedicle and it develops a flagellum before detachment. It is .076— .020mm. in length, and viewed laterally has the shape of a coffee bean with one end, the anterior, broad, and the other, or posterior, pointed, with one aspect, the dorsal, convex, and the other, or ventral, slightly concave. The concavity is bordered on each side by a ridge, the two ridges meeting posteriorly (=staff-organ?). Its anterior end is crossed by a furrow from which springs the flagellum, and, according to Cienkowski, a thick rod-like process (=tentacle?). The flagellum is 6-7 times the length of the body, and is an organ of locomotion. There is a bean-shaped nucleus, and a slowly contractile vacuole (Robin); the protoplasm is homogeneous. The further development of the free spore is not known. It probably passes into the adult by direct growth<sup>2</sup>.

*Noctiluca* is a voracious animal and floats on the surface of the sea. It is phosphorescent when the water is disturbed, and it appears to emit

<sup>1</sup> The *Pyrocystis pseudonoclituca* of Wyville Thomson and Murray, is probably a resting *Noctiluca*; and *P. fusiformis* a similar condition of an unknown Cystoflagellate. See Bütschli, Protozoa, pp. 1061-2, and Wyville Thomson and Murray, P. R. S. xxiv. 1876, p. 533, Pl. 21.

<sup>2</sup> Cienkowski describes some abnormal forms of attached spores which favour this supposition; see A. M. A. ix. p. 56.

sometimes a constant feeble light. The seat of the phosphorescence is said to be the superficial layer of protoplasm.

*Leptodiscus medusoides* has the form of a shallow concavo-convex disc .6–1.5 mm. in diameter. It swims vigorously by contraction of the disc into a bell-like form, the contraction including the whole disc; a portion only or two opposite portions of its circumference, however, may be thus affected.

The disc thins away towards its periphery, and a circular line of granules divides it on its concave aspect into a central and peripheral portion. There are two tubular depressions on the convex aspect, one wide, the other narrow, both inclined obliquely towards the centre of the concave side where lies a central mass of protoplasm inclosing the nucleus. A bundle of parallel protoplasmic fibres extends to the base of the wide depression. The narrow depression, however, reaches the central mass and gives exit to a fine flagellum. There is said to be a distinct cuticular membrane, thicker on the convex side where it is interrupted by the apertures of the two depressions above-mentioned. Branching and anastomosing cords of protoplasm radiate from the central mass to the periphery on the concave aspect of the disc, and the gaps between the larger branches are filled by a finer network. Branching cords extend from the central mass and its central radial outrunners to the convex aspect of the disc; the corresponding extensions arising towards the periphery are unbranched. The ends of these cords are attached each to a small rod-like body placed vertically to the surface, possibly an internal projection of the cuticular membrane. The intervals between the cords are filled by a clear jelly. Fine radial fibres, supposed to be contractile, stretch from the circular line of granules (*supra*) to the centre. Supposed fission-forms have been described by Hertwig, but nothing is known as to the reproduction of the organism<sup>1</sup>.

The Mastigophora are classified by Bütschli as follows:—

I. *Flagellata* : animal provided with one or more vibratile flagella; subdivisible into four orders.

1. *Monadina* : small or very small in size, and simple in structure; naked and very frequently more or less amoeboid; sometimes furnished, however, with a theca; for the most part colourless; chromatophores rare; a single large anterior flagellum and sometimes 1–2 small accessory flagella; special oral aperture absent or situate at the base of the flagellum, but never prolonged into a well-developed oesophagus; includes five families, *Rhizomastigina* (*ante*, p. 841); *Cercomonadina*, e.g. *Oikomonas*; *Codonoecina*; *Bicoecina*, e.g. *Bicosoea*, *Poteriodendron*; *Heteromonadina*, e.g. *Monas*, *Dendromonas*, *Anthophysa*, *Dinobryon*, *Uroglena*.

2. *Euglenoidina* : in general large and well-developed; with one, rarely two,

<sup>1</sup> Bütschli thinks (*Protozoa*, pp. 1078–9) that the *Gymnodinium pseudonoctiluca*, described by Pouchet, *Journal de l'Anat. et Physiol.* xxi, pp. 71–5, is possibly a spore-form of *Leptodiscus*.

flagella; monaxial or a little asymmetrical; sometimes extremely contractile; a cuticle; colourless or green; an oral aperture at or surrounding the base of the flagellum; an oesophagus with a contractile vacuole close to it, often provided with a reservoir; includes seven families—*Coelomonadina*, e.g. *Chromulina*; *Euglenina*; *Chloropeltina*, e.g. *Phacus*; *Menoidina*; *Paranemina*; *Petalomonadina*; *Astasiina*.

3. *Heteromastigoda*: of variable size and colourless; two flagella at least, one smaller and directed forwards, the other large and trailing backwards; an oral spot and in large species a distinct mouth and pharynx; holozoic; includes two families—*Bodonina*, e.g. *Bodo*, *Dallingeria*; *Anisonemina*.

4. *Isomastigoda*: of small or medium size; monaxial, rarely bilateral or asymmetrical; anterior end with two, four, rarely five similar flagella, arising as a rule near one another; includes ten families—*Amphimonadina*; *Spongomonadina*, —*Spongomonas*, *Cladomonas*, *Rhipidodendron*; *Chrysomonadina*, e.g. *Synura*, *Syn-crypta*; *Chlamydomonadina*, e.g. *Polytoma*, *Chlamydomonas*, *Haematococcus*; *Volvocina*—*Gonium*, *Stephanosphaera*, *Pandorina*, *Eudorina*, *Volvox*<sup>1</sup>; *Tetramitina*; *Polymastigina*; *Trepomonadina*; *Cryptomonadina*, e.g. *Chilomonas*, *Cryptomonas*; *Lophomonadina*.

II. *Choanoflagellata*: a single flagellum surrounded by a protoplasmic collar: includes two orders.

1. *Phalansterina* s. *Gelatinigera*: collar short, narrow, constant in shape; a gelatinous envelope to each individual or to every two individuals; colonial; colony disc-like, or erect and dichotomously branched; *Phalansterium*.

2. *Craspedomanadina*: collar large, funnel-shaped, of changeable shape; solitary or colonial; divisible into *Codonosiginae*, e.g. *Monosiga*, *Codosiga*, *Proterospongia*, and *Salpingoecina* with a delicate test of variable shape, *Salpingoeca*, *Polyoeca*.

III. *Dinoflagellata*: two flagella at least, one parallel to the long axis of the body, the other transverse to it: includes two orders.

1. *Adinida*: two flagella at anterior pole; a bivalved envelope pierced by pores; *Exuviaella*, *Prorocentrum*.

2. *Dinifera*: one flagellum as a rule turned backwards; one or more transverse flagella lodged in one or more transverse furrows; (i) *Peridinidae*, with a single transverse furrow at or near the middle of the body; sometimes naked; e.g. *Peridinium*, *Ceratium*, &c.; (ii) *Dinophysidae*, transverse furrow single, more or less anterior; a bivalved envelope; e.g. *Dinophysis*, *Amphidinium*; (iii) *Polydinidae*, several transverse furrows; naked; *Polykrikos*.

IV. *Cystoflagellata*: protoplasm reticulate, a single flagellum; marine; *Noctiluca*, *Leptodiscus*.

(i) *Flagellata*. Bütschli, Protozoa, Bronn's Klass. u. Ordn. des Thierreichs, i. pp. 620–876; Kent, Manual of Infusoria, i. 1880–81, pp. 216–322, 366–96, 401–38;

<sup>1</sup> The *Chrysomonadina*, *Chlamydomonadina*, and *Volvocina* are holophytic, and provided with chromatophores. Botanists usually consider them as Algae, and Bütschli unites them under the common designation of *Phytomastigoda*.

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<sup>1</sup> Saville Kent (*op. cit.* ii. p. 858) has replaced the generic name *Protospongia* by *Proterospongia*.

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## ENDOPARASITA.

Protozoa, in which the organism is either devoid of all special organs of locomotion or is provided with slowly changeable pseudopodia; nutrition takes place solely by absorption; endoparasitic in all stages of life.

There is one class—the *Sporozoa*.

## CLASS SPOROZOA.

*Endoparasitic Protozoa, rarely motile, reproducing by spores which are usually provided with an envelope (chlamydo-spores), and are seldom naked. The spores give origin in turn to a variable number of germs, sporozoites or falciform bodies. Conjugation may take place, but as a rule is a mere juxtaposition of two or more individuals.*

There are four sub-classes, the *Gregarinida*, including the *Coccidiidae*, the *Amoebosporidia*, *Sarcosporidia*, and *Myxosporidia*.

(i) *Gregarinida*. The Sporozoa contained in this sub-class are, with few exceptions, in their early stages intracellular parasites. The *Coccidiidae* are sometimes found in the connective tissues, but as a rule remain within the cell-host until encystation takes place. The other *Gregarinida* quit it at a certain period of growth and enter either the coelome or the cavity of the digestive tract.

The *Coccidiidae* are round or oval in shape, and in the adult condition motionless; they are mostly minute in size, but range from .025 up to 1 mm. in the *Klossia* of the Cephalopoda. The other *Gregarinida* are usually elongate, very rarely globular (*Adelea*), and are often flattened. An anterior extremity is distinguishable, and may be furnished with organs of adhesion. The majority are small, .001-.02 mm. in length; some

attain a fair size, e. g. *Monocystis magna* of the Earthworm  $\frac{1}{8}$  in. (5 mm.) ; but the giant of the group is *Porospora gigantea* of the Lobster, which may attain  $\frac{3}{4}$  in. The adult is sometimes quite inert, sometimes active, gliding evenly along, but the mode in which locomotion is effected has not been discovered. Changes of shapes have been observed, especially in the young form ; they are apparently due to movements or local accumulations of protoplasm, which may or may not cause movements. The subclass is divisible into two orders, the *Monocystidea*, in which the body is simple, and the *Polycystidea*, in which it is divided by two septa into three segments, with the doubtful exception of *Porospora* and the certain one of *Gamocystis*, which has two segments, one large, the other very minute in size, corresponding probably to the two first segments of other forms. The first segment is the epimerite ; it is the part from which the other two segments bud out, and is in later stages an organ of fixation in the cell-host. It is either immersed in the protoplasm of the cell-host, or if cup-shaped, as in *Lophorhynchus insignis*, grasps the ends of a number of intestinal epithelial cells. The second segment is the protomerite, the third and by far the largest, the deutomerite, in which the nucleus is lodged. A Polycystid possessing all three segments is known as a Cephalin or Cephalont. Sooner or later it loses the epimerite, more or less completely, and is then known as a Sporadin or Sporont<sup>1</sup>.

*Klossia* alone among *Coccidiidae* has a distinct cell-membrane. The remaining *Gregarinida* have a delicate cuticula, which is often finely striated in a longitudinal direction. The striae in *Lophorhynchus insignis* are due to the cuticle consisting of delicate vertical lamellae set on edge side by side. Delicate hair-like processes are present in *Callyntrochlamys*, lobular processes in *Conorhynchus*<sup>2</sup>. The reticular processes of the epimerite, when present, are probably formed by the ectoplasm. The protoplasm of the body, except in *Coccidiidae*, is usually divisible into a clear exoplasm and a granular fluid endoplasm or entocyte. The former is best developed at the two extremities of the body and constitutes the chief bulk of the epimerite ; an outer firmer layer, the sarcocyte, is very commonly differentiated from it. In the *Polycystidea* it is frequently traversed by fine fibrils, usually transverse, rarely reticular, homogeneous, or in *Porospora*, composed of granules apposed in linear series. To these fibrils a muscular function was at one time assigned, and they were supposed to constitute a special contractile layer or myocyte. But the

<sup>1</sup> Schneider entertains the idea apparently that the epimerite is the equivalent of a monocystid Coccidiidan, the proto- and deutero-merite, the equivalent of its spores. See his *Tablettes Zoologiques*, p. 113 et seqq.

<sup>2</sup> The species of *Monocystis* which inhabit the vesiculae seminales of the Earthworm live within the spermatospores. When the latter give origin to spermatozoa the Gregarine appears to be coated with cilia ; and the moult that was supposed to take place merely signifies the escape of the parasite from the sperm-blastophore.



Gregarines in which they best developed are the most inert. The septa of the *Polycystidea* are constituted by exoplasm or sarcocyte. Movements in the endoplasm are never propagated through them. The granules of the endoplasm sometimes display molecular movements; they are variable in size and shape; and in some instances either contain or consist of an amyloid substance. Colouration is rare, and appears to be due to the intestinal secretions of the host. Contractile vacuoles are absent; non-contractile are seen in *Conorhynchus Echiuri*. The nucleus is single; it is large when full grown, vesicular, with chromatin globules or ribbons. It lies in the endoplasm, with the movements of which it shifts, and in the *Polycystidea* always in the deuteromerite, into which it migrates from the epimerite before the septa are complete.

The *Coccidiidae* encyst as soon as they have attained their definitive size. The cyst has rarely a single, but usually a double wall, is very resistant, and has in *Eimeria* and *Coccidium* a micropyle. The contained protoplasm gives origin to a single spore (*Monosporea*), to two or four (*Oligosporea*), or to a large number (*Polysporea*). The spore is naked in *Orthospora*, *Eimeria* and *Gymnospora*, in other instances with a spore-membrane which may be double. The spore-protoplasm gives origin to a single elongate falciform body in *Coccidium oviforme* of the Rabbit, to 2 in some species of *Klossia*, to 2-4 in *Cyclospora*, to 4 in *Orthospora*, to many in *Eimeria*, &c. In the last-named genus they are formed on one aspect only of the spore. A small quantity of protoplasm, the 'nucléus de reliquat,' may remain after the formation of the falciform bodies. The division of the nucleus in the formation of spores and falciform bodies has been observed in some instances. The falciform body may move while still within the spore case, more energetically after its escape. It does so either by bending into a semicircle, by gliding, rotating round a point, or by feeble amoeboid motions (*Eimeria falciformis*). It probably enters a cell whilst in the falciform condition. The cycle of development is usually completed in a single host; in some instances in its faeces, as in *Coccidium oviforme*, the intestinal *Coccidia* of the Rabbit and birds and in *Cyclospora* from *Glomeris*<sup>1</sup>.

As to other *Gregarinida*. The Monocystids of the Earthworm quit the sperm-blastophores in which they live; the Polycystids lose the epimerite wholly or in part, e.g. in *Clepsidrina*, or its retinacular processes are alone absorbed (*Echinocephalus*). A conjugation so-called may take place; the two anterior extremities come into contact (apposition), as

<sup>1</sup> A parasite, *Drepanidium Ranarum*, inhabits the red blood-corpuscles of the Frog, and has a close structural resemblance to a falciform body, and is perhaps derived from a *Coccidium* infesting the intestinal and renal epithelia. It has been observed to quit one corpuscle and enter another. Other Gregariniform parasites have been found in the blood of *Emys lutaria*, *Lacerta viridis*, and several birds. See Ray Lankester, Q. J. M. xxii. 1882; Danilewski, A. M. A. xxiv. 1885; Id. Biol. Centrblatt. v. 1885-6, and Archives Slaves de Biologie, i. 1886.

in *Monocystis*, &c.; or the anterior extremity of one individual with the posterior of another (opposition), as in Polycystids, leading occasionally to the formation of strings of individuals. The union is more or less firm<sup>1</sup>. Solitary individuals may encyst, or conjugated individuals may become inclosed in a common cyst. They may, as is probably generally the case, be separated by a septum, or they may rotate over one another and perhaps in some instances fuse. Encystation is always accompanied by the assumption of a globular shape. The cyst is said in *Monocystis* to be formed by the cuticle and sarcocyte; in the majority it is certainly a new structure. It may be single or double, and the outer layer sometimes thick and concentrically striate. A delicate inner membrane is present when there are special sporoducts (*Gamocystis*, *Clepsidrina*). The outer membrane is ornamented with tubercles, &c., in *Stylorhynchus* and its allies. The size of the cyst varies; it is resistant to the action of water. It undergoes fission in *Porospora gigantea*; the two first formed halves divide a second time, and the old cyst-wall degenerates into a transparent mass imbedding the cysts secreted by the new parts.

The contents of the cyst proceed to develop either while it is *in situ*, or after it is expelled in the faeces, if the Gregarine inhabits the digestive tract. The nucleus becomes invisible; many superficial nuclei, doubtless derived, as in *Coccidiidae*, by fission of the primitive nucleus, have been observed in *Clepsidrina Blattarum*. The protoplasm either segments entirely into a number of nucleated sporoblasts, or only the superficial zone does so. In the Monocystids of the Earthworm, the sporoblasts are said to be formed centrally, to be extruded successively, and arranged in concentric zones, until the whole protoplasm is used up. They are formed as buds projecting from the surface in *Clepsidrina* and *Stylorhynchus*, in the last-named motile. The protoplasm not used up is usually resolved into a fluid; in *Stylorhynchus* it collects into a central spherical mass, the pseudocyst. The sporoblast assumes by degrees its definitive shape, elliptical and pointed at the ends, which in *Syncystis* have four bristles, cylindrical with conical truncate ends, as in *Clepsidrina*, or purse-shaped, as in *Stylorhynchus* and its allies. In *Urospora* it has a tail<sup>2</sup>. It acquires an envelope, single or double, as in *Clepsidrina*, bivalved in *Adelea*, porous in *Porospora*, where it is readily resolved into minute rods; brown or black in *Stylorhynchus* and its congeners. Spores belonging to the same species may be large in one cyst, small in another (macro-, micro-spores). Except in *Porospora gigantea* the contents are resolved into falciform

<sup>1</sup> The genus *Didymophydes* of Stein was founded on two conjugated Sporonts. Frenzel has established a genus *Aggregata* for a Polycystid inhabiting the intestine of *Cancer Maenas*, which conjugates in strings of individuals.

<sup>2</sup> The elliptical spore pointed at both ends is sometimes termed 'pseudo-navicella.' The term 'psorosperm' has been applied to the *Coccidiidae*, Gregarine spores, Myxosporidian spores, and to the *Sarcosporidia*.

bodies or sporozoites, a small quantity of protoplasm remaining as the 'nucléus de reliquat.' The number of falciform bodies in each spore-case is probably a constant one; eight, as in *Clepsidrina*, appears to be very general. The falciform body is homogeneous, pointed at one end, rounded at the other, or terminated by a fine process, as in *Stylorhynchus*, and it has been found to be nucleated whenever properly examined<sup>1</sup>.

The spores are discharged from the cyst by special tubular sporoducts in *Clepsidrina* and *Gamocystis*; in other instances by its disruption caused by an accumulation of liquid (?), or in *Stylorhynchus* by the swelling of the pseudocyst. They are set free either perfectly loose or else cohering end to end in chaplets. The escape of the falciform bodies from the spore-case by its dehiscence along one edge has been observed in *Stylorhynchus longicollis* infesting *Blaps* when the case was exposed to the action of the digestive fluids of the host. The bodies in question executed movements by bending from side to side. The presence of a small nucleated oval or rounded cell, formed beyond doubt from a falciform body, in the intestinal epithelium of the proper host, the growth from it of a process which gradually projects into the cavity of the digestive tract, the appearance of constrictions dividing the growth into segments (*supra*), and the descent of the nucleus into the deutomerite before the completion of the septa, have been recorded in several Polycystids. The spore of *Porospora gigantea* gives origin, according to E. Van Beneden, to a non-nucleated amoeboid 'moner'; this in its turn to two processes, one of which grows faster or starts earlier than the other. The longer process is vibratile and breaks away; the other becomes vibratile as soon as it has absorbed the remaining protoplasm. Each process is termed by Van Beneden a 'pseudofilaria'; it turns motionless after a time, develops a nucleus, lengthens, becomes septate and adult. *Urocystis* (= *Monocystis*) *Sipunculi* is said by Lankester to have a 'pseudofilaria' stage, followed by a 'pseudocercaria' stage, i. e. one with a slender tail and large body like a *Cercaria*. The body is nucleated, the tail drops away, and its fate is unknown. It must be borne in mind that the life-history of only a few *Gregarinida* has been traced.

Longitudinal fission occurs in the young *Urocystis Sipunculi*; transverse fission into two or three parts in the adult *Monocystis porrecta* and *M. cuneiformis* of the Earthworm, the parts thus formed undergoing encystation at the same time.

The *Coccidiidae* are found in various Vertebrata, Mollusca and Insecta; the *Monocystidae* chiefly in Urochorda, some Chaetopoda, Gephyrea,

<sup>1</sup> Ruschhaupt maintains that in the *Monocystis* of the Earthworm the falciform body is a mass of reserve material; that the rest of the protoplasm grows at its expense. The ripe spore set free by the rupture of the cyst is taken up by an amoeboid spermatospore of the vesicula seminalis. The spore-case slowly thins away, and by growth the spore passes into the adult. Cf. Schneider's critique in his *Tablettes Zoologiques*, i. 1886.

Nemertea and Turbellaria, rarely in Arthropoda; the *Polycystidae*, the division to which the greater number of genera belong, are almost confined to Insecta, but have been found also in *Phalangidae* and some *Acarina* among Arachnida, and two are known from Urochorda.

(ii) *Amoebosporidia*. This sub-class has been established by Schneider for the genus *Ophryocystis*, represented by two species, *O. Bütschlii*, from the Malpighian vessels of *Blaps*, and *O. Francisci* from *Akis*. The hosts are beetles belonging to the family *Tenebrionidae*. The organism is amoebiform, with granular protoplasm, and more or less hyaline pseudopodia-like processes, sometimes simple, sometimes branched, and probably endowed with extremely slow contractility. It is nucleated; small individuals are uni-nucleate, larger multi-nucleate. The nucleus appears to be vesicular with one or two nucleolar spots. The multi-nucleate masses become spherical and divide into a number of uni-nucleate individuals, connected to one another at a central spot by clear or somewhat granular prolongations. They throw out pseudopodia-like processes from their broader ends, and are detached by degrees from one another; the connecting prolongations are slowly absorbed. Two uni-nucleate individuals have been observed to conjugate and encyst. The cyst has a simple wall in *O. Francisci*, but its contents give origin to a number of coats, one within the other in *O. Bütschlii*. It is marked by an equatorial line, along which it separates into two portions. The outer coats in *O. Bütschlii* do so whilst their successors are forming. The two nuclei give origin to six, and then the central region, with two of the nuclei which probably conjugate, is converted into a spore; the remaining nuclei and protoplasm degenerate into residual masses, which disappear. The ripe spore is elliptical with pointed poles; it has a double spore-membrane; its contents divide into eight (?) uni-nucleate falciform bodies and a 'nucleus de reliquat.' It is rare for a cyst to contain two spores.

(iii) *Sarcosporidia*. There are three Sporozoans included in this sub-class—two, *Miescheria* and *Sarcocystis*, which are found within the striated muscle fibres of certain mammals, and one, *Balbiania*, recently discovered in the sub-mucous coat of the large intestine of a *Macropus penicillatus*. The two first are most commonly found in the diaphragm, walls of the abdomen, eye-muscles, tongue, and the muscles of the thorax. The heart, pharynx and larynx are also favourite localities. They occur in various Mammals, especially the Pig, and have been detected in the Fowl and some other birds. In size they usually range from 3 mm. downwards, but specimens  $\frac{1}{2}$  in. long have been seen in the Rat, 2 in. in the Roe-deer. They are usually elongate and pointed at the ends, but if the muscle fibres in

which they are lodged are detached they become ovate. *Balbiana* is sub-spherical.

There is a membrane, either delicate (*Miescheria*, *Balbiana*), or composed of close-set rods (*Sarcocystis*). The contents are gelatinous, protoplasmic, with a number of minute, refractile, fatty (?) granules and protoplasmic corpuscles or germs (?). Rotation round the longer axis and contractions have been observed in a *Miescheria* of the Pig by Waldeyer. In large specimens the contents, except at the two extremities, are broken up into a number of spores (?), polygonal from mutual pressure, but globular when set free. The polygonal bodies contain large numbers of reniform or semi-lunar germs, which in *Balbiana* at any rate are developed in the peripheral bodies at an earlier period than in the central, and are set free by the breaking down of the inclosing membranes. This is probably the case also in the two other genera. The germs are homogeneous or granular, and often contain a bright spot or vacuole at either extremity. The vacuoles have been said not to exist in fresh germs. No nucleus has been detected either in the germs, the bodies within which they are formed, nor in the parent organisms.

The *Sarcosporidia* are sometimes spoken of as 'Miescher's vesicles,' or 'Rainey's corpuscles,' the names of their first discoverers in Germany and England respectively.

(iv) *Myxosporidia*. The Sporozoans known by this name are parasitic in various freshwater Fish and certain *Elasmobranchii*. The skin of the head and opercular cavities, the branchiæ and viscera are the commonest localities; the muscles of the body are seldom infected, and the central nervous system is completely exempt. They are sometimes found in delicate cysts with nucleated walls, probably derived from the tissues of the host, ranging in size from about  $\frac{1}{8}$  in. downwards, but the *Myxosporidium* of the Pike's urinary bladder lives free on the surface of the mucous membrane. The organism is *Amoeba*-like, more or less rounded or elongate; it shows a distinct division of exoplasm and endoplasm. The surface of the exoplasm may be covered completely or partially with fine, simple, or branched retractile processes. The endoplasm is granular, sometimes coloured with yellow or brown fatty granules, and crystals of haematoidin: it is multinucleate. Movement may be slowly effected by lobose pseudopodia. Spore-formation commences at an early period, and is perhaps a continuous phenomenon. The number of spores present is variable. Their development has been traced in the *Myxosporidium* inhabiting the Pike's bladder. Clear globules of protoplasm make their appearance in the endoplasm, containing six nuclei apiece. A delicate membrane appears round each of them, and then each divides into two tri-nucleate halves, the spores, which become fusiform. Two of the nuclei

disappear leaving one in the centre. The spore has no membrane and at either end of it a clear 'polar body' becomes visible. This body contains a long internal and spirally coiled thread, which is shot out on the application of alkalis, &c. It is therefore a trichocyst, and it is supposed that the discharged thread serves to anchor the spore to any soft body into which it may happen to penetrate. The spores of other *Myxosporidia* may be flattened and lens-like with one pole somewhat pointed, more rarely ovate, or fusiform, and pointed at each end. The spore-case is generally bivalved and drawn out into a simple or forked process. The pointed pole is always open, and trichocysts to the number of one, two, three, rarely four or eight, are lodged at the aperture. The escape of an *amoebula* from the spore-case has been observed.

There are two Sporozoans of doubtful position, *Lithocystis Schneideri*, and *Amoebidium parasiticum*. As to the former, it is found in the coelome of the Spatangid Echinoid, *Echinocardium cordatum*, on the inner aspect of the test and the outer of the intestine, in the shape of large irregular black masses, perhaps plasmodial in nature. They may attain a size of about  $\frac{3}{8}$  inch long, and  $\frac{1}{5}$  broad. Adherent to these black masses are a variable number of hyaline spheres  $\frac{1}{25}$ — $\frac{2}{25}$  inch in size. Each sphere has a structureless membrane, one, rarely more, masses of crystals which are dispersed in later stages, and a number of spores. The latter are at first disposed round a yellowish spot or mass to which they adhere each by two filaments. During the course of development they become rearranged if the cyst is large enough and adhere by their other extremities, the filaments then looking like rigid flagella. The spore contains a granular protoplasm which is resolved into 3–6 falciform bodies, and a residual mass which becomes reduced to 2–3 granules or disappears completely. Giard, who discovered this organism, believes that the falciform bodies give origin to some of the amoebae, so common in the coelomic fluid. See C. R. 82, 1876, or A. N. H. (4), xviii. 1876, p. 192.

*Amoebidium parasiticum* was discovered by Cienkowski. It is a tubular organism, about .5 mm. long and occurs attached by one end to the feet and branchiae of larval Phryganids and Libellulids, and certain freshwater Crustacea, *Gammarus*, *Asellus*, &c. The tube has a delicate wall, finely granular protoplasm, often vacuolate, and containing a series of nuclei placed at regular intervals along the axis. The protoplasm segments, a portion to each nucleus, forming small fusiform bodies which escape and either grow into new *Amoebidia*, or their nuclei divide once or twice and their protoplasm segments, giving rise to *amoebulae*. The parent organism may produce similar *amoebulae*. The latter move about by means of lobose pseudopodia. They either form thick-walled resting cysts, the contents of which eventually break up into a number of fusiform bodies, either within the cyst or after escaping from it inclosed in a delicate membrane, or they form an oval thin-walled cyst the contents of which break up at once in the same manner. By Cienkowski, *Amoebidium* was considered to be a fungal; Balbiani groups it with the *Sarcosporidia*. See Cienkowski, Botan. Zeitung, xix. 1861; Balbiani, op. cit. *infra*, p. 116; Bütschli, op. cit. *infra*, p. 611.

The *Gregarinida* are classified by Bütschli, op. cit. *infra*, as follows :—

I. *Monocystidea*. Body not septate.

(i) *Coccidiidae*: a provisional group distinguished from (ii) *infra*, by the fact that the various genera appear to be intra-cellular parasites throughout their whole lives, the cyst being extruded when it is fully formed: subdivided by Schneider into three sub-groups.

(1) *Monosporea*: the contents of the cyst constitute a single spore. *Orthospora*, from the intestinal epithelium of the Newt (*Triton*); the spore gives origin to four falciform bodies. *Eimeria* with three species, one from the intestine of the mouse, the kidneys of the horse, &c., a second from the intestine of *Lithobius*, a third from the Malpighian vessels of *Glomeris*; the cyst has one to two micropyles, and the falciform bodies are produced by a process of one-sided gemmation.

(2) *Oligosporea*: the cyst gives origin to a few spores, constant in number. *Cyclospora*, two species, one from the intestine of *Glomeris*, the other from that of the cat; two spores with 2-4 falciform bodies apiece. *Isospora*, from *Limax*; two spores with many falciform bodies. *Coccidium*, sp. ? from various Vertebrata; cyst ovate with a micropyle, four spores, each with but one falciform body.

(3) *Polysporea*: the cyst gives origin to a number of spores with 2-4-6 falciform bodies apiece. *Klossia* with several species from the nephridia of *Helix hortensis*, *Succinea amphibia*, *Neritina fluviatilis*, and *Chiton*, and nearly every organ of *Sepia* and *Octopus*: from *Blaps*, *Gyrinus*, and *Scolopendra morsitans*.

(ii) *Monocystidae*: free in the unencysted condition. Several genera, e.g. *Adelea*, from intestine of *Lithobius*; *Monocystis* from the vesiculæ seminales of *Lumbricus*; *Urospora* from the Ascidian *Ciona intestinalis*, *Tubifex*, *Sipunculus*, various Nemerteans, &c.

II. *Polycystidea*. Body septate; rarely consisting of two segments only from the first (*Gamocystis*, *Porospora* (?)), usually of three, an epimerite, which is eventually cast off more or less completely, a protomerite, and deutomerite. A large number of genera is known, e.g. *Clepsidrina*, *Stylorhynchus*: but their arrangement into families is uncertain at present. Schneider is treating of them in his *Tablettes Zoologiques* and promises a complete monograph.

The remaining sub-classes contain but few genera and do not need subdivision.

Bütschli, Bronn's Klass. und Ordn. des Thierreichs, i. Protozoa, pp. 479-616. Balbiani, Leçons sur les Sporozoaires, Cours d'Embryologie comparée du Collège de France, Paris, 1884.

(i) *Gregarinida*. *Coccidiidae*: Schneider, A. Z. Expt. ix. 1881; Id. *Klossia*, op. cit. (2), i. 1883; Id. *Tablettes Zoologiques*, i. Poitiers, 1886, pp. 4, 88, cf. p. 104. *Globidium* (= *Eimeria* ?), Fleisch, Recueil Zool. Suisse, i. 1884. *Gymnospora*, Moniez, Bull. Soc. Zool. France, xi. 1886. *New Sporozoa*, Pachinger, Z. A. ix. 1886, p. 471. Cf. Leuckart, 'Parasites of Man,' transl. by Hoyle, i. Edinburgh, 1886, p. 202. *Monocystidae* and *Polycystidea*, Schneider, A. Z. Expt. ii. 1873; iv. 1875; x. 1882; Id. *Tablettes Zoologiques* (*supra*), pp. 25, 90. *Gregarines of Earthworm*, Ruschhaupt, J. Z. xviii. 1885. *Marine Gregarines*, Frenzel, A. M. A. xxiv. 1885. *Monocystid of Blatta Americana*, Kunstler, C. R. 98, 1884. *Neozygetis Aphidis*, Witlaczil, A. M. A. xxiv. 1885. *Gregarines of Phalangidae*, Rössler,

Z. W. Z. xxxvi. 1882, p. 700. *Urospora of Ciona intestinalis*, Parona, Journal de Micrographie, x. 1886: *U. (Monocystis) Sipunculi*, Ray Lankester, Q. J. M. xii. 1872. *Conorhynchus Echiuri*, Greeff, 'Die Echiuren,' p. 128, Nova Acta, 41, 1879. *Haematozoal forms*, note 1, p. 859 ante.

*Amyloid granules*, Maupas, C. R. 102, 1886; Bütschli, Zeitschrift für Biologie, xxi. 1885.

*Development of Polycystids. Clepsidrina Blattarum*, Bütschli, Z. W. Z. xxxv. 1881. *Stylorhynchus longicollis*, Schneider, A. Z. Expt. x. 1882, p. 423; (2), ii. 1884; of various forms, Id. Tablettes Zoologiques (*supra*), pp. 10, 81; cf. p. 104.

(ii) *Amoebosporidia*: *Ophryocystis*, Schneider, A. Z. Expt. (2), ii. 1884, cf. A. N. H. (5), xiv. 1884; Id. Tablettes Zoologiques (*supra*), p. 1.

(iii) *Sarcosporidia*: Blanchard, Bull. Soc. Zool. France, x. 1885; Leuckart, op. cit. *supra*, p. 199.

(iv) *Myxosporidia*: Bütschli, 'Fischpsorospermien,' Z. W. Z. xxxv. 1881; Mégnin, 'Role pathologique,' &c., Bull. Soc. Zool. France, x. 1885.

## RHIZOPODA.

PROTOZOA in which the organism is provided with pseudopodia as organs of locomotion and ingestion of food, or for the latter purpose alone. Contour of the body, whether provided with an envelope or test or not, either stable or amoeboid. The pseudopodia are sometimes very stable, usually changeable, always retractile. The first stage of the life-history, or the fission-product is sometimes flagellate.

There are six classes, the *Heliozoa*, *Radiolaria*, *Foraminifera*, *Amoebina*, *Mycetozoa*, and *Labyrinthulidea*, and a group, *Proteomyxa*, including an assemblage of forms which cannot at present be located elsewhere.

## CLASS HELIOZOA.

*Rhizopod Protozoa with radiant and stable pseudopodia, seldom branched or anastomosing, and a globular body of unchanging outline; rarely fixed. The protoplasm is very generally divided into an ectosarc and an endosarc, not delimited by a membrane; the organism is uni- or multi-nucleate; vacuoles both contractile and non-contractile are commonly present. A skeleton is sometimes absent; when present it is gelatinous, or siliceous, and then either composed of loose spicules, plates, &c., or of a continuous lattice-shell. An adventitious skeleton is rare. Biflagellate spores have been observed in some instances. Widely distributed; freshwater and marine.*

A skeleton is absent in one section of the class, the *Aphrothoraca*. When present it is either gelatinous(?) or siliceous, rarely adventitious. As to the first-named, it occurs in the *Chlamydothorax*, and takes the form of a soft more or less mobile envelope, homogeneous, granular or striated;



said to be separated from the body by a space (? a homogeneous jelly). There is some doubt as to its constitution. Three facts appear to point to its organic nature: (1) the presence in *Heterophrys* of minute points or processes of its free surface which contract under the action of carmine staining fluid; (2) its constant elevation round the bases of the pseudopodia; (3) its occurrence in a loose and crumpled condition round an encysted *Sphaerastrum*. On the contrary it has been said to consist in *Heterophrys* of a coat of finely interlaced needles which resist the action of strong sulphuric acid, and are consequently supposed to be siliceous. An undoubtedly siliceous skeleton exists in the two remaining sections of the class, the *Chalarothoraca* and *Desmothoraca*. In the former, it is composed of loose parts: spherules in one to three layers (*Pompholyxophrys pumicea* = *Hyalolampe*); round plates in a single layer (*Pinacocystis rubicunda*); leaf-like plates pointed at each end and pierced by pores (?) (*Pinaciophora fluviatilis*); spicules placed tangentially to the surface, straight or curved, and pointed at both ends (*Raphidiophrys*); spines radially placed, with basal plates, and either simple or forked at their outer extremities, together with tangential spicules (*Acanthocystis*). These loose structures are held together either by protoplasm derived from the pseudopodia, or by a soft secreted material; the fact that the parts retain their position when the animal is contracted and encysted favours the latter view. In *Raphidiophrys* the skeleton is so loose that it is raised into eminences where the pseudopodia protrude. A clear interval may separate the skeleton from the body of the animal, whether a space or homogeneous jelly is doubtful. In the *Desmothoraca* the skeleton is a lattice-sphere through the apertures of which pass the pseudopodia. It turns brown with age and is attached by a siliceous peduncle in *Clathrulina*; it is free in *Orbulinella*; and in both instances it is larger than the body of the animal. An adventitious skeleton of sand-grains occurs in the marine *Lithocola* and *Raphidiophrys arenosa*, of sand-grains mixed with diatom-shells in the freshwater *Elaeorhanis*.

The animal is attached by a chitinous peduncle in the skeleton-less *Actinolphus*, otherwise it is free though inclosed in a fixed shell in *Clathrulina*. The protoplasm, which varies in consistence, and is rarely coloured of a yellow tint, is clearly divisible into an ectosarc, and an endosarc in *Actinophrys*, *Actinosphaerium* and *Actinolphus*, and probably in all skeletogenous forms except the *Desmothoraca*. The ectosarc is more or less granular, and the seat of digestion, the endosarc, homogeneous; in *Actinosphaerium*, however, the characters of the two parts are reversed. In *Actinolphus* and *Acanthocystis* the endosarc is excentric and touches the surface at one spot, in others it is central. There is no separating membrane between the two parts, yet the transition from one to the other is usually somewhat sudden. Some species are coloured: *Actinolphus*

often contains numerous orange particles in its ectosarc; *Chondropus* peculiar green spherules; *Acanthocystis flava* reddish-yellow granules; *Pinacocystis*, &c. reddish-brown; *Pompholyxophrys exigua* a single central ruby-red globule. Chlorophyl bodies occur occasionally in *Actinophrys* and sometimes in the endosarc of *Actinosphaerium*, constantly in the ectosarc of *Acanthocystis* and *Heterophrys myriapoda*, in *Sphaeratrurn Fockii*, *Raphidiophrys viridis*, and *R. elegans*. But colourless forms of these species occur, and in this case colourless bodies, resembling the chlorophyl bodies may be present<sup>1</sup>. Contractile vacuoles have not been observed in *Actinolophus*, nor in all the species of some skeletogenous genera, e.g. of *Raphidiophrys*. As to their number, *Actinophrys* has one, *Actinosphaerium* one to five; but larger numbers are sometimes found, e.g. twenty in *Raphidiophrys pallida*. They are either deeply placed in the ectosarc, are not large, and do not bulge the surface, or they are quite superficial, swell to a very great size, e.g. in *Actinophrys* the vacuole may almost equal the body in diameter and project freely above the surface. The new vacuole appears in the same place as the old, and may originate from a remnant of it. Non-contractile vacuoles are sometimes absent, sometimes sparingly present, in *Actinolophus* and most skeletogenous genera. There are many in *Actinophrys* and *Actinosphaerium*, confined to the ectosarc in the former, in the latter small and irregular in the endosarc, large, radially arranged, and close set in the ectosarc. In both forms the largest are peripheral. A young *Actinosphaerium*, however, has but a single radial layer. The ectosarc vacuoles disappear under mechanical and electrical stimuli. A nucleus has not been observed in some of the little known forms. It is single in most instances, but specimens occur with two or sometimes with several nuclei, e.g. of *Raphidiophrys pallida*. *Acanthocystis Italica* has been only seen with several nuclei; *Actinosphaerium*, except in the youngest stage, is always multinucleate; a large example of it may contain 1-200 nuclei, and one, 0.85 mm. in size, is said by Carter to have had between 3-400. They multiply by binary fission and with mitosis. The nucleus always lies in the endosarc, centrally or excentrically as in *Actinolophus*, *Acanthocystis*,

<sup>1</sup> Are these bodies a part of the Heliozoon, or are they symbiotic Algae? They multiply by fission, but so do chlorophyl bodies (Greeff, A. M. A. xi. p. 12); they are very generally accompanied by colourless bodies resembling them; and when they are absent, similar colourless bodies are as a rule, if not always, present. The occasional expulsion of some of them in *Acanthocystis viridis* has been witnessed by Greeff (A. M. A. v. p. 484); so, too, of certain yellow bodies in *A. spinifera* (Id. op. cit. p. 494). Entz states that *A. turfacea (viridis)* never ingests food (Biol. Centralblatt. ii. p. 463); that he has seen the chlorophyl bodies expelled from *A. aculeata* before encystation, their subsequent multiplication, and rupture of the spinose skeleton (op. cit. p. 459). On the other hand, Greeff has seen them in an encysted *A. viridis* (A. M. A. v. p. 489). Hertwig and Lesser observed a colourless *Acanthocystis* turn green with chlorophyl bodies derived from digested algal spores (A. M. A. x. suppl. p. 203). Leidy has figured a specimen containing bright red bodies, with a few green (Freshwater Rhizopoda of N. America, Pl. xliii. fig. 9). At present the question cannot be regarded as decided.

and *Raphidiophrys*. It is vesicular and has in the resting phase a distinct nuclear membrane, a nucleolus and clear nuclear fluid.

The pseudopodia are fine, straight, radiant, and developed from the whole surface except in *Actinolophus* near the peduncle. They rarely branch or anastomose. Their length varies from about one half the diameter of the body, e.g. in *Actinosphaerium* to two or three times its diameter, e.g. in *Acanthocystis* and *Clathrulina*. They can be displaced from their radial position by currents of water, or bent at a sharp angle by the sudden impact of a foreign body. They are supported by axial filaments, which extend close to or up to the nucleus in *Actinophrys*; to just within the limits of the endosarc in *Actinosphaerium*, or to a central corpuscle which unites them all, in *Actinolophus*, *Acanthocystis*, *Raphidiophrys*, and perhaps *Clathrulina*<sup>1</sup>. In most cases they show a more or less lively granule-stream. The movements of the Heliozoa, whether on a solid surface or whilst floating suspended in water, are as a rule extremely slow and as yet by no means explained. Some Heliozoa appear to feed preferentially on animals, others on plants (algae, &c.), others indifferently upon either. The pseudopodia draw the prey towards the body, and in *Actinosphaerium* into a pit which closes over it. In *Actinophrys* a special broad pseudopodium-like process incloses the food, and the same method is said to obtain sometimes in *Actinosphaerium*, *Acanthocystis* and *Raphidiophrys*. There is generally a food vacuole. Faecal residues are expelled anywhere, and have been seen extruded along a pseudopodium in *Acanthocystis aculeata* (Hertwig and Lesser).

The species of *Raphidiophrys* and *Sphaerastrum* frequently occur in a colonial condition. The skeletal envelopes of the individuals in a given colony are fused. Each individual is united to its neighbours by slender protoplasmic cords, and the pseudopodia radiating from the colony come only from the outer surfaces of the individuals. Two or more individuals of *Actinophrys* may become united by broad protoplasmic bridges in which both vacuoles and food may be seen. These colonies may change their shape, divide into sub-colonies, or their constituent individuals separate. Partial or complete fusion between individuals of *Actinosphaerium* has been observed, as well as between *Actinosphaeria* produced by the fission of individuals artificially brought together.

<sup>1</sup> The axial filaments have been carefully investigated in *Actinosphaerium* by Brandt. They are organic, not mineral, in composition. A new pseudopodium commences as a conical process; a needle-like structure within it is the first trace of its filament. A newly formed filament is readily dissolved again by the protoplasm, an old one is more resistant: the former consists of vitellin (?), the latter contains an admixture of other bodies. New filaments may fuse *inter se*, they may shorten by contraction, and then either thicken, or display thickened nodes. The filaments, whether old or young, are completely absorbed when the pseudopodia are retracted in encystation. It is possible that they may also be partially dissolved during an accidental contraction of the pseudopodia.

Separation of the fused individuals usually ensues in a few hours. It is doubtful whether the phenomena detailed have any connection with reproduction. Encystation with its consequences (*infra*) may ensue, however, in *Actinosphaeria* made to fuse artificially<sup>1</sup>.

Binary fission has been observed in comparatively few Heliozoa, *Actinophrys*, *Actinosphaerium*, *Acanthocystis*, *Clathrulina*, and *Hedriocystis*. If *Actinosphaerium* is disturbed during the process, the incompletely separated individuals reunite. In *Hedriocystis* transverse fission has been seen in a young and still shell-less individual. The two (or four) parts into which the individual divides in *Clathrulina*, retract their pseudopodia if they are not retracted before fission occurs, and one or all then quit the shell, become *Actinophrys*-like, and finally develop a new peduncle and shell. The young *Clathrulina* frequently attaches itself to the old shell. Fission in the same animal may also give rise to three or four parts; if to three the larger part remains in the shell, the two smaller quit it, as do all the parts when four in number. But the escaped portions become biflagellate (uniflagellate, Foulke) spores, with a single nucleus and some posteriorly placed contractile vacuoles; they eventually attach themselves and develop pseudopodia, a peduncle, and shell. *Actinosphaerium* may be multiplied by artificial fission. Gemmation appears to occur in *Acanthocystis* and *Clathrulina*. *A. viridis* has been seen with a small uni-nucleate sphere, possessed of a contractile vacuole and one or two chlorophyll bodies lying beneath an elevation of the shell. It escaped, became uni- or bi-flagellate, and then *Actinophrys*-like (Korotneff). In *A. aculeata* round or oval nucleated bodies were observed by Hertwig lying in a depression of the parent's body. They escaped through the shell, and in some instances developed two flagella. A rounded and nearly detached segment of the shell containing a non-nucleated (?) sphere of protoplasm was seen in one specimen. The sphere was resolved into six portions, which were set free one by one and became *Actinophrys*-like. The parent produced a second similar structure. *Clathrulina* is said to become vacuolate, and to develop small knobs on the surface which are detached, become *Actinophrys*-like, form a peduncle and shell<sup>2</sup>.

<sup>1</sup> Leidy has described a *Raphidiophrys socialis*, the individuals of which are simply entangled by their pseudopodia. Gruber has found in *Actinophrys sol* that fusion may occur (1) between two small non-nucleated specimens, (2) between a non-nucleated individual and a nucleated, a specimen of the latter absorbing three of the former, but repelling a fourth, and (3) between two nucleated individuals, repulsion however often occurring. He concludes that the process indicates an augmentation of substance, and not a reproductive phenomenon. The non-nucleated individuals referred to are of unknown origin. They have pseudopodia, an ecto- and endo-sarc, non-contractile vacuoles, and sometimes a contractile vacuole; they move and feed. See lit. p. 873, *infra*.

<sup>2</sup> Biflagellate zoospores have been seen given off from a green *Actinophrys sol*; they sometimes contained a chlorophyll granule (Archer, Q. J. M. x. pp. 306-7; xvi. p. 300). Biflagellate spores have been also observed in the same Heliozoon by R. Hertwig (J. Z. xi. p. 340). Greeff saw a multitude of minute *Amoebae* creep out of a dead *Actinosphaerium* and change into flagellate

Encystation occurs, in some instances preceding reproduction, in others of unascertained significance. *Actinophrys* secretes a gelatinous capsule and retracts the pseudopodia, whilst the vacuoles disappear. The inner part only (?) of the protoplasm divides, and each part forms a double cyst; the outer cyst ruptures, the inner with its contents escapes; the contained mass shows a separation of ecto- and endo-sarc, develops a contractile vacuole and pseudopodia, by which the inner cyst is pierced and dissolved (Cienkowski). Or there is a double cyst, within which the animal may or may not divide; a contractile vacuole persists; both cysts are ruptured to give exit to the contents (Lieberkuhn). In *Actinosphaerium* the radiant pseudopodia are withdrawn, but branched pseudopodia of varying length are thrown out and the animal creeps about for twenty-four hours. A thick gelatinous coat is then formed, the vacuoles disappear, and the nuclei are said to diminish in number (Schulze, Brandt). The protoplasm next divides into 2-35 portions successively (Schulze, Greeff), or simultaneously (Brandt). Each portion is uni-nucleate, or else becomes so (Schneider), and surrounds itself with a siliceous cyst (Schulze). Or they fuse in pairs so as to reduce the number present by one half, with or without an odd member (Greeff); or again, each part forms a thin membranous cyst, divides into two within it, the two parts subsequently fusing and the cyst disappearing (Brandt). Ultimately a siliceous cyst is formed, continuous or of small pieces (Schneider, Brandt), single, or double (Greeff). The young *Actinosphaerium* escapes in spring, and is uni-nucleate (Schulze) or multi-nucleate (Schneider, Brandt). When *Clathrulina* encysts it contracts and develops a spinose siliceous envelope; or it divides previously into two or more portions, each of which then forms a separate and similar envelope. *Actinolophus* surrounds itself with a gelatinous coat, on the outer surface of which appears a layer of loosely arranged hexagonal siliceous plates. The pseudopodia are retracted, their axial filaments and central granule disappear, whilst the nucleus divides into two. Further changes have not been witnessed. The contraction of the body into a small sphere, the formation of a thin or thick envelope round it, or of a siliceous cyst (*Pompholyxophrys*, *Acanthocystis turfacea* s. *viridis*), has been recorded in several genera.

The Heliozoa are a class widely distributed over the world. The greater number of genera are freshwater and are found especially in peat

spores (SB. Niederrhein. Ges. in Bonn, 1871). Foulke states that a *Clathrulina* became filled with green particles actively motile, which were expelled, a number together, in a thin sac; by the bursting of the latter they were set free, but were not traced further (A. N. H. (5), xiv. p. 269). It is probable that these and similar observations refer to parasitic organisms. Brandt indeed has confirmed Greeff (*supra*), but has seen the organisms in large numbers within the food vacuoles, and their multiplication when expelled from the body. He refers them to a parasite akin to the fungus *Pythium* (Monatsb. k. Acad. Berlin, 1881, p. 399). Foulke has described the ejection of globules from two fused *Actinosphaeria* which eventually developed into the parent form (A. N. H. (5), xii. p. 206).

districts. A few are exclusively marine, e.g. *Actinolphus*. Some are common to both media, e.g. *Actinophrys*, *Heterophrys*, *Acanthocystis*. The genus *Orbulinella* inhabits salt-pools near Klausenberg in Transylvania.

*Ciliophrys infusionum* and *Dimorpha mutans* are sometimes regarded as Heliozoans. Bütschli classes them among the Flagellate *Rhizomastigina* (p. 841). The same authority includes among Heliozoa, *Vampyrella*, *Nuclearia*, *Monobia*, and *Myxastrum*, which are here retained among *Proteomyxa* (p. 915 et seqq.) where they are placed by Ray Lankester.

Two organisms, *Microcometes paludosa* and *Wagnerella borealis*, are regarded by some authorities as Heliozoans. The former was found under freshwater gelatinous algae in North and South Russia by Cienkowski. It has a globular membranous capsule pierced in a few places by round holes. The body is smaller than its capsule; it has an excentric nucleus, 2-3 peripheral contractile vacuoles; and it emits through the openings of its capsule one or more long slightly branched pseudopodia. It feeds on Algae which are either drawn into the capsule or have their cell-contents sucked out by the pseudopodia. Binary fission was seen, both parts quitting the capsule; also encystation within a tough cyst, the capsule at the same time becoming spinulose. (Cienkowski, A. M. A. xii. 1876, pp. 46-7, cf. Allman, J. L. S. xiii. p. 302). *Wagnerella borealis* from the White Sea was described by its discoverer, Merejkowski, as a sponge. It occurs also in the Mediterranean and was found by Mayer to be a Protozoon and probably a Heliozoon, a view to which Merejkowski has given his adhesion. It is attached by a conical base prolonged upwards into a cylindrical peduncle supporting a globular body. The peduncle may attain 1.1 mm. in length; the head .18 mm. in diameter. A thin membrane covers both head and base and contains curved siliceous spicules. There are also long slender siliceous spicules radiating from the head. The nucleus is in the base, but at times wanders thence into the head and divides into eight nuclei, which are destined one for each of the reproductive buds. There are pseudopodia. (Merejkowski, Mem. Imp. Acad. St. Petersburg, (7), xxvi. 1879, No. 7, p. 15; A. N. H. (5), i. 1878; viii. 1881; Mayer, Z. A. ii. 1879; iv. 1881).

The *Zooteira religata* of Strehill Wright is probably a Heliozoon. It has an ecto- and endo-sarc, very numerous pseudopodia, a contractile peduncle, and a basal gelatinous tube into which the animal can be withdrawn. Q. J. M. ii. 1862, p. 217.

Bütschli thinks that R. Hertwig's *Sticholonche zanclea* may possibly belong to the Heliozoa *Chalarothoraca*. By Fol it is made the type of a new order (? class) *Taxopoda*. It is marine, and was found by Hertwig at Messina. In outline it is bean-shaped and about .15 mm. in length. It contains a bean-shaped capsule or nucleus triangular in cross section. The capsular membrane is tough, covered by minute rods according to Fol, or to Hertwig by perforated elevations which are prolonged into tubes; its contents are homogeneous with one large or several small vacuoles. The body is clothed by a membranous investment composed of separate pieces. Its outline is not even but elevated into prominences. Each of the latter carries a circlet of about twenty hollow chitinous spines grouped round a larger spine. Pseudopodia, in the proper sense of the word, are absent; in place of them there are four rows of scarcely contractile 'arms' which contain, at least at their

bases, a special axial substance (Fol). In locomotion the 'arms' were observed by Hertwig to be simultaneously applied to a surface, and to move the body onwards with a jerk. The protoplasm is granular or homogeneous with, in most instances, clear globules of refrangibility identical with its own (Fol). There are no contractile vacuoles. Fol observed near the concave side of the nucleus globules, a few in small individuals, many in large. The globules divided into two groups which came to lie one on each side of the animal. In some instances one or both these heaps was replaced by a large body with a figure of 8 cavity. Later on, it contained a spirally constricted body which was set free as a multinucleate holotrichous organism, considered by Fol not to be a parasitic Infusorian but a spermatophore, the small globules of other specimens being ova (!). He thinks that the peculiar bodies seen by Hertwig in Acanthometrids are of analogous nature and to be considered as embryos. R. Hertwig, J. Z. xi. 1877, pp. 325-331; Id. Organismus der Radiolarien, Dk. Jen. Ges. ii. 1880, p. 176; Fol, Mem. Inst. Nat. Genève, xv. 1883.

The Heliozoa are classified as follows:—

1. *Aphrothoraca*: no skeleton present; *Actinophrys Sol*, *Actinosphaerium Eichhornii*, *Actinolphus*, *Haeckelina*; *Lithocolla*, *Elaeorhanis*, *Chondropus*.
2. *Chlamydothoraca*, with a continuous soft (? gelatinous) skeleton: *Heterophrys*, *Sphaerastrum*, *Astrodisculus*, *Astrococcus*.
3. *Chalarothoraca*: a loose siliceous skeleton: *Pompholyxophrys* (= *Hyalolampe*), *Raphidiophrys*, *Pinacocystis*, *Pinaciophora*, *Acanthocystis*.
4. *Desmothoraca*: skeleton, a siliceous shell, more or less globular, pierced by apertures; free *Orbulinella*, *Elaster*; fixed and pedunculate, *Clathrulina*, *Hedriocystis*.

Bütschli, Bronn's Klass. und Ordn. des Thierreichs, i. Protozoa, pp. 261-331; Archer, Résumé, Q. J. M. xvi. 1876; xvii. 1877, and Allman, J. L. S. xiii. 1878, pp. 284-305; Leidy, 'Freshwater Rhizopoda of N. America,' U. S. Geological Survey of the Territories, xii. 1879, pp. 233-76 (except pp. 253-8).

*Actinosphaerium*, Brandt, Inaug. diss., Halle, 1877. *Haeckelina*, Merejkowski, A. M. A. xvi. 1879, p. 211. *Elaeorhanis*, Greeff, A. M. A. xi. 1875, p. 23. *Acanthocystis*, R. Hertwig, J. Z. xi. 1877, p. 331. *Acanthocystis Italica*, *Raphidiophrys arenosa*, Gruber, Nova Acta, xlvi. 1884, pp. 507-8. *R. socialis*, Leidy, A. N. H. (5), xii. 1883, p. 209. *Orbulinella*, Entz, Naturhistor. Hefte des Nat. Mus. in Buda-Pesth, pt. 1, 1877. *Elaster*, Grimm, A. M. A. viii. 1872, p. 531.

*Axial filaments and movements of Actinosphaerium*, Brandt, SB. Ges. Natf. Freunde zu Berlin, 1878, p. 171; *structure of protoplasm of same*, Bütschli, M. J. xi. 1886, pp. 91-2; *digestion in same, and Amoeba*, Greenwood, Journal of Physiology, vii. 1886; *mode of catching prey*, Maupas, A. Z. Expt. ix. 1881, pp. 357-8. *Chlorophyl bodies*, see note 1, p. 868 ante. *Nucleus*, Gruber, Z. W. Z. xl. 1884, pp. 131-4; cf. Id. and Brandt, Biol. Centralblatt. iii. 1883-4; *fission of nucleus in Actinosphaerium*, R. Hertwig, J. Z. xvii. 1884.

*Fusion of Actinophrys Sol*, Gruber, Z. W. Z. xxxviii. 1883, p. 62-8; cf. Cox, Amer. Monthly Micr. Journal, ii. 1882; *encystation of do.*, Cienkowski, A. M. A. i. 1865, p. 227; *and fusion*, Lieberkuhn, Arch. f. Anat. und Physiol., 1856, pp. 505-7. *Reproduction of Actinosphaerium*, Brandt, SB. Ges. Natf. Freunde zu Berlin, 1877,

p. 73; cf. note 2, p. 870 *ante*; of *Clathrulina*, Foulke, A. N. H. (5), xiv. 1884. Budding in *Acanthocystis*, R. Hertwig, J. Z. xi. 1877, pp. 337-40; Korotneff, A. Z. Expt. viii. 1879-80, p. 481. Spores and amoebiform young, see note 2, p. 870 *ante*.

### CLASS RADIOLARIA.

*Rhizopod Protozoa, with the body divided into a central part or capsule lodging the nucleus, and an extra-capsular region, by a membranous capsule only exceptionally absent. Capsular membrane pierced by fine pores, or by one or several apertures. Extra-capsular region supported by a gelatinous skeleton or calymna. Pseudopodia for the most part radiant, sometimes branching and anastomosing. Skeleton seldom absent, either spicular or continuous, composed of acanthin or of silica. Reproduction by flagellate uninucleate spores produced in the central capsule. Solitary or colonial; exclusively marine.*

Skeletal elements are rarely absent, as in *Colloidea*, *Nassoidea*, and *Phaeodinida*. They consist in *Acantharia* of an organic substance, *acanthin*, destroyed by a red heat and by acids; it is supposed to be either identical with vitellin (Brandt) or akin to chitin (Haeckel). This Acantharian skeleton takes the form of solid radial spines, which meet in the centre of the central capsule and are connected at their bases in one of four ways—(1) by simple apposition, (2) combined also with leaf-like ad-central processes, (3) by fusion of all, or (4) of opposite pairs, the last a mode seldom found. In number the spines in question are usually twenty, disposed in a regular manner according to Müller's law<sup>1</sup>; indefinite in number and arrangement only in the Acanthometrid family *Actinelida*. They are often provided with lateral outgrowths (apophyses), which may be incomplete or united in the *Acanthophracta* to form a lattice-shell. But in the family *Sphaerocapsida* the shell is composed of small plates, each pierced by a pore and united by a cement; the spines undergo partial atrophy in two genera, complete atrophy in a third, twenty apertures, however, marking the places where they should protrude. In all other Radiolaria the skeleton consists of silica, which is probably deposited in an organic matrix<sup>2</sup>; that of *Phaeodaria* is blackened by heat, stained by carmine, and destroyed by

<sup>1</sup> This law may be thus expressed. Imagine a globe with an axis of rotation, and five circles inscribed on it, an equatorial, two tropical and two polar. The twenty spines lie four in each of these circles, the equatorial and polar spines in the same meridian lines, 90° apart, i. e. at 0°, 90°, 180°, 270°; the tropical in meridian lines exactly intermediate, i. e. at 45°, 135°, 225°, 315°. The twenty spines are rarely all equal. See Haeckel, 'Challenger Reports,' xviii. pp. 717-20, for a summary of the variations known.

<sup>2</sup> For the organic matrix, see Brandt, 'Kolonie-bild. Radiolarien,' Fauna und Flora des Golfes von Neapel, xiii. p. 63. Calcareous bodies, shaped like the rowel of a spur, occur in the calymna of some Radiolaria. They are supposed by Haeckel, who terms them 'calcastrellae,' not to be skeletal elements, but either unicellular algae, or of foreign origin. See Haeckel, op. cit. *supra*, p. lxx, note D.



boiling caustic alkalis; and in two families of the same sub-group (*Circo-porida*, *Tuscarorida*) it has a porcellanous aspect by reflected light, and consists of fine siliceous needles imbedded in a granular matrix. Its elements are solid, except in most *Phaeodaria*, where they are hollow siliceous tubes filled with a gelatinous substance. The shapes taken by the skeleton are numerous. It may be spicular (beloid), as in the *Beloidea* among *Spumellaria*, and the *Phaeocystina* among *Phaeodaria*, the spicules being of various shapes and disposed more or less tangentially, radially only in the Phaeodarian family *Aulocanthida*. In all other instances it forms a connected whole; a simple ring or several rings united in various planes, the Nassellarian *Stephoidea*; radial spines united at a centre which lies eccentrically near the oral pole, the Nassellarian *Plectoidea*; a lattice-shell, the bars of which lie either in one plane, or in different planes, and in this case spongy in texture, as is not uncommon among *Spumellaria*, in shape spherical, ellipsoidal (= prunoid), discoidal, lent-elliptical (= larcoïd) i. e. with three principal axes of unequal length, cyrtoid i. e. with two dissimilar poles, an apical and basal, or finally conchoid. The last-named consists of two valves, and is confined to a few *Phaeodaria*. The cyrtoid skeleton may be monothalamous, and then ovate or cap-shaped, as in some *Nassellaria*, where it is termed cephalis, a few *Phaeodaria*, e. g. *Challengerida*, and very rarely in *Spumellaria*; or it may be in some *Nassellaria* polythalamous, the cephalis being simple, bilobate, or multilobate, with, especially when simple, new joints added at the basal pole; incomplete internal septa correspond to the external constrictions. The shell is rarely multiple, except in the Spumellarian *Sphaeroidea*, where there may be two spheres, three, four, five, or even ten, rarely more, one within the other, all united by radial bars<sup>1</sup>.

The division of the body into a peripheral or extra-capsular, and a central or intra-capsular portion is constant. The central capsule is delimited by a resistant chitinous (?) membrane, a skeletal structure which is double in *Phaeodaria*, and is absent in the young stages of some forms, but appears just before sporulation. *Collozoum inerme* is said to develop it only when forming isospores, and in *Sphaerouzoum neapolitanum* it is permanently absent (Brandt). When it is thus absent the contour of the body is variable. The capsule is normally spherical, but it becomes adapted to the general shape of the skeleton as well as to its peculiarities. Its surface is lobed in many Spumellarian *Sphaeroidea*; and in the Nassellarian *Spyroidea* and *Cyrtoidea* it has 3-4 lobes projecting through the basal or cortical plate of the shell. When the shell is double or multiple the capsule generally incloses the inner or two or three of the inner shells during its growth. Its membrane is always perforated either by innumerable

<sup>1</sup> The innermost or two innermost shells, termed medullary, differ sometimes in the character of their lattice-work from the outer or cortical shells. See Haeckel, op. cit. *supra*, pp. lxxxv-vi.

fine pores, evenly distributed as in *Spumellaria*, or aggregated in groups or lines with imporous intervals, as in *Acantharia*; or, as in *Nassellaria*, by pores confined to a special membrane or porochora, situated at the basal pole of the capsule, primitively circular in shape, but lobed or even broken up into tracts according as the lobes of the capsule itself are more or less prominent (*supra*); or again there is a main oral aperture or astropyle, with or without the addition of secondary apertures or parapylae, as in *Phaeodaria*. The astropyle consists of a tubular proboscis, rising from the centre of a radially striated disc or operculum. The parapylae are perforations symmetrically placed near the main axis of the capsule, but at the opposite end to the astropyle. Two are commonly present, rarely one three, six, or more (*Circoporida*, *Tuscarorida*). A parapyla consists of a small ring or short tube, from which springs a conical or cylindrical tubule, the paraboscis.

The intra-capsular protoplasm is finely granular; a radial striation is observable in many *Spumellaria*, which becomes masked by the formation of vacuoles, &c.; the peripheral zone may be broken up into radial granular wedges, separated by clear intervals. In the *Nassellaria* a portion of it undergoes differentiation as the podocone, a conical mass with its base resting on the porochora and traversed by striae from base to apex. It is more resistant to reagents and stains more deeply, especially at its apex, than the rest of the protoplasm<sup>1</sup>. In the large *Phaeodaria* the peripheral zone of protoplasm is fibrillated, the fibrils, which are perhaps of a muscular nature, running meridionally from one pole of the capsule to the other and radiating towards the capsular apertures, beneath which only they are sometimes visible. The protoplasm contains vacuoles, oil-globules, pigment, crystalloids, concretions, and the nucleus. Vacuoles, or hyaline spheres, are, except in *Nassellaria*, commonly present, sometimes in great numbers and of so large a size as to become polyhedral through mutual pressure (some *Thalassicollida*). They are hyaline, their contents a saline fluid or gelatinous sphere, the jelly apparently of similar character to the extra-capsular (*infra*), or a coagulable albumen (some *Thalassicollida*)<sup>2</sup>. Fatty granules are universally present. Oil-globules are very general in *Spumellaria* and *Nassellaria*, rare in *Acantharia*, absent as a rule in *Phaeodaria*. There is one, central and large in most colonial species, but in other cases

<sup>1</sup> The porochora of the central capsule contains vertical rods which stain deeply. They are perforated according to Hertwig, solid according to Haeckel and Bütschli. The striae of the podocone correspond to these rods; they are tubular (Hertwig), or perhaps contractile, i. e. muscular, threads (Haeckel).

<sup>2</sup> Haeckel regards the vacuoles as belonging to two categories, (1) true vacuoles which are droplets in the protoplasm, and (2) alveoles with a special but thin enveloping membrane. It is perhaps doubtful if the latter exist. An extreme stage of vacuolation is seen in *Acanthometra elastica*, where the protoplasm is reduced to a thin superficial reticulation, connected by threads to a central portion surrounding the spines.

there are several globules for the most part numerous and peripheral. They are highly refractile, usually colourless, but may be yellow, brown, red, blue; and in the *Spumellaria*, especially the colonial, with a laminated organic substratum, not albuminous according to Brandt. Pigment, red, yellow, brown, rarely violet or blue, still more rarely green, is present as minute granules. Crystalloids, usually known as crystals, are of two kinds—(1) small, more or less like a whetstone, destined to be inclosed as reserve material one in each spore, not observed in *Nassellaria* or *Phaeodaria*; (2) large, apparently of an excretory nature, and indestructible by a red heat, present only in some colonial *Collosphaerida*, side by side with the small. Both kinds are formed only when sporulation is about to take place, as is the blue pigment of *Collosphaera Huxleyi* and *Myxosphaera coerulea*. Masses of crystals (? excretory) occur in the vacuoles of *Thalassicollida* and some *Phaeodaria*. Laminated circular or elliptical concretions of unknown nature are found in some *Spumellaria* and *Nassellaria*; violin-shaped and highly refractile bodies in the same two groups and some *Acantharia*. The nucleus is at first single, but in the colonial *Spumellaria* and very many *Acantharia*, it undergoes division into many nuclei at an early period. The single nucleus is central and often of large size, e.g. 1–2 mm. in some large *Thalassicollida*; in most *Phaeodaria* it attains  $\frac{2}{3}$ – $\frac{3}{4}$  of the diameter of the central capsule. Its shape is typically spherical, but varies concomitantly with that of the capsule; it is sometimes irregular and occasionally has radial claviform processes (*Thalassophysa*, *Thalassophila*). It may inclose by growth one or more of the inner shells when the shell is multiple. The small nuclei of the colonial *Spumellaria* are homogeneous, but in the *Acantharia* they may be nucleolate. The single nucleus has a distinct membrane, thick, double contoured, and in *Thalassicollida* probably porous. It is more or less homogeneous, and may possess nucleoli (some *Spumellaria*, the *Nassellaria* and *Phaeodaria*). A chromatin network with nucleolar enlargements has been demonstrated in *Thalassicolla coerulea*.

The extracapsular portion of the body consists of a gelatinous skeleton or calymna, and protoplasm with various inclosures. It has been shown experimentally on *Thalassicolla nucleata* that it can be regenerated from the central capsule if the latter be removed artificially. The calymna is separated from the central capsule by the sarcomatrix (*infra*). It is hyaline, rarely opalescent, of the same degree of refrangibility as sea-water, structureless but occasionally laminated, of a soft consistence in the young form, but varying in the adult, where it is sometimes as firm as cartilage. It grows during life, and is greatly developed in the Spumellarian *Collo-daria*. It resembles the skeleton in shape, and in *Nassellaria* and *Phaeodaria* usually incloses it completely. In the *Acantharia* a regularly polygonal network of fibres is disposed superficially between the calymnal

sheaths of the spines. The protoplasm forms a layer or sarcomatrix immediately surrounding the central capsule; it is massed over the single aperture of the *Nassellaria* and the astropyle of *Phaeodaria*<sup>1</sup>. From this layer a more or less irregular network of protoplasmic threads, the sarcoplegma, radiates to the surface of the jelly, where it forms a superficial network, the sarcodictyum, from which originate the pseudopodia. These structures vary in length and number; they are radiant, but may anastomose, especially in *Nassellaria* and *Phaeodaria*, two groups in which the sarcoplegma and pseudopodia are chiefly derived from the protoplasm issuing from the single aperture of the one or principal aperture of the other. In *Acantharia* the pseudopodia are disposed in an orderly way, and certain of them, the axopodia, either placed one between each pair of spines, or surrounding in a circle the bases of the spines, are supported by stiff axial filaments penetrating the central capsule. Some *Discoidea* possess also a single thick striated sarcode-flagellum, of eminently contractile nature, but otherwise motionless, formed by the fusion of pseudopodia and traceable as far as the nucleus. Peculiar protoplasmic processes or myophrics, 5-30 or more, extend from the edges of the calymnal sheaths to the apices of the spines in *Acantharia*. They are contractile and expand the calymna. At death they are set free from the spines and remain projecting from the sheaths as the so-called 'ciliary coronas' or 'gelatinous cilia.' The protoplasm of the sarcomatrix, &c., is more or less granular; some of the granules consist of fat; oil-globules occur in the large *Collodaria*, albumen globules in *Thalassolampe primordialis* and *Collozoum*. Vacuoles formed in the course of the sarcoplegmal threads and of small size are found in most Radiolaria. Large vacuoles are confined to the *Collodaria* and a few *Sphaeroidea* among *Spumellaria*, to *Nassella*, and some *Plectoidea* among *Nassellaria*, and to the *Phaeocystina*. They are frequently so numerous as to give the calymna a frothy appearance. When the animal is irritated they disappear progressively from the periphery towards the centre, but are formed anew when it is left at rest. In some colonial forms, e. g. *Collosphaera*, the central part of the colony is occupied by a soft sphere of jelly<sup>2</sup>. Black or blue pigment occurs in some large

<sup>1</sup> The sarcomatrix is said by Bütschli (Protozoa, p. 431) to be wanting at the apical or aboral pole of the Nassellarian *Cystidium* and *Plagiacantha*. Haeckel states (op. cit. *supra*, p. lxvii.) that it is often so thin at this spot in *Nassellaria* that it can be demonstrated only by reagents. Brandt points out that the sarcomatrix, as well as spindle-shaped masses in the sarcoplegma of *Collozoum inermis*, *C. fulvum*, *Sphaerozoum neapolitanum*, *Sph. acuferum* stains strongly with osmic acid, and violet with iodine, while the rest of the protoplasm of the body does not do so. To the portions which stain he gives the name of 'Assimilation-plasma.' In *Siphonosphaera tenera* it is aggregated in masses, each of which has 2-5 central capsules round it. See his monograph cited, pp. 14-15, 18, 92-4. The same authority describes (p. 21) globular or plate-like masses of protoplasm in the sarcoplegma of young Collozoa, especially *C. pelagicum*, and in *Acrosphaera spinosa*, which contain brownish granules, and are perhaps connected with vacuole-formation.

<sup>2</sup> The distinction between true vacuoles and alveoles, mentioned note 2, p. 876, is applied by

*Collodaria*, brown in many Spumellarian *Sphaeroidea* and *Discoidea*, red in some *Acantharia*. The *Phaeodaria* are characterised by a dark mass, the phaeodium, of a greenish-brown or black hue surrounding the astropyle. It consists of rounded bodies, the phaeodellae, sometimes nucleated, ranging from .001 to .05 mm. in size, mixed with minute black particles. It is not certain whether or no they belong to the organism or are symbiotic algae.

The colonial Radiolarians, i. e. some Spumellarian *Collodaria* and *Sphaeroidea*, differ from the non-colonial in possessing numbers of central capsules, each with its own sarcomatrix, but with a common calymna and sarcoplegma: The individuals in these colonies, when adult are usually placed peripherally, whilst one or more vacuoles occupy the centre; they retreat on irritation from the surface. The colony may be spherical, elongated, rarely ring-shaped. Colonies of the same species, even if in different stages of growth, fuse when brought into contact, either naturally or artificially; and colonies of different species may adhere without fusion, especially if the water is somewhat foul.

Reproduction takes place by fission or spore-formation, rarely by gemmation. Binary fission of the young central capsule appears to occur in the colonial genera and in some tripylean *Phaeodaria*, i. e. those with three apertures to the central capsule. It is possible that it may be general. Young colonies of some species of *Collozoum* and *Sphaerouzoum* contain in the sarcoplegma structures known as 'extra-capsular bodies,' produced by gemmation from the central capsules. They are strongly refractile, non-granular, provided with differentiated nuclei and groups of oil-drops. They give origin to anisospores in some instances, in others probably to central capsules. In the colonial *Collosphaera* and its allies the stage of growth in which a few individuals furnished with shells, and many without them, make up the colony, is perhaps comparable (Brandt). The colonies themselves are said also to multiply either by breaking at their nodes, e. g. the elongated beaded adult colony of *Collozoum*, or by simple constriction whilst young, e. g. spherical colony of *Collosphaera*. It may be noted that a young colony, at least in some instances, contains many more individuals than an adult.

Spores have been observed in the four main sub-divisions of the class, but the mode of their formation is most accurately known in the colonial *Collodaria*. It takes place in the central capsule, the extracapsular region having no share in it, unless a small portion of the sarcomatrix is retracted. There are two kinds of spores, iso- and aniso-spores, which differ from one another (1) in the mode of their formation, (2) in the character of their nuclei, and (3) in *Collozoum* and *Sphaerouzoum* by their

Haeckel to the vacuoles of the extracapsular region. Brandt denies the existence of a special membrane to the central jelly-spheres of *Collosphaera*, &c., said to be present by Hertwig and Haeckel: see pp. 59-60 of his monograph cited p. 874, note 2.

shape, a difference which probably does not obtain in *Collospira* and its allies. In the formation of isospores the nuclei, which are doubly refractile, and become more and more so, are scattered through the capsular protoplasm; they multiply by binary fission. Small crystalloids make their appearance, one for each spore, even before the required number of nuclei is attained. The oil of the oil-globule is dispersed as minute granules, some of which are destined for each spore. The protoplasm is resolved into as many portions as there are crystals. The ripe isospore is pointed anteriorly, rounded posteriorly. Two flagella spring from the point. The nucleus is large and anterior; the crystalloid with oil-granules posterior. The formation of anisospores in *Collozoum* and *Sphaerouzoum* contrasts with the above (1) in the grouping of 2-3 nuclei together, and the more refractile and homogeneous character of the protoplasm directly inclosing each group; (2) in the multiplication of the nuclei in each group and an increase of size in the corresponding mass of protoplasm; (3) in the differentiation of a nuclear chromatin network; and (4) the formation of a group of oil-drops in each mass, whilst the central oil-globule dwindles, the oil-drops increasing in number *pari passu* with the nuclei, but being ultimately dispersed in granules. The ripe anisospore is bean-shaped; it may or may not contain a minute crystalloid; whether it has a single or double flagellum is uncertain. It is of two sizes; a large, the macrospore, with a fine chromatin network in the nucleus, and a small, the microspore, one half less in all dimensions, with a coarse chromatin network. Both forms of spores occur in the same central capsule. It has been suggested that they are sexually differentiated, but copulation has not been observed. If the suggestion is true and if the isospores are regarded as asexual, then there is Alternation of Generations. In *Collospira* and its allies a corresponding state is evidenced by the transient grouping of nuclei, which however become scattered and then differentiated into macrosporal and microsporal nuclei (*supra*), the two kinds however in different central capsules. Crystalloids are also always present. The changes undergone during sporulation by the extracapsular region of the body are—the disappearance of the vacuoles, the dwindling and softening of the jelly, the aggregation of the capsules in the centre of the colony, the retraction of the pseudopodia and sarcoplegma, and the sinking of the colony in the water. The capsular membrane appears to be resolved and the spores escape. Then the remains of the protoplasm break up into smaller and smaller portions which shrink into brown globules and disperse. The spores of *Acantharia* are small and pyriform; with several, probably three, flagella, two at one spot, and one vis-à-vis to it; a crystalloid may or may not be present<sup>1</sup> (Brandt).

<sup>1</sup> The flagella of the spores are exceedingly difficult to see. It must remain doubtful for the present whether or no there is any instance of a single flagellum only. The life-history of the

The nuclei of the spores in *Thalassicolla nucleata* (and probably other species of the genus) are said to be derived from the nucleoli of the single nucleus (Hertwig).

The simple Radiolaria are mostly of small size, under  $\frac{1}{25}$  in. *Thalassolampe maxima* (*Colloidea*) reaches  $\frac{1}{2}$  in. *circa*, but the Phaeodarian family *Coelographida* contains the giants of the class, several species reaching  $\frac{3}{4}$  in. and *Coelothamnus maximus*  $1\frac{1}{4}$  in. The dimensions of the colonies vary much. The globular *Myxosphaera coerulea* may have a diameter of  $\frac{1}{5}$  in.; the elongated colony of *Collozoum inerme* is nearly 1 in. long, whilst *C. pelagicium* has not rarely a length of 4 in., and has been observed over 10 in., with a thickness of  $\frac{3}{25}$  in. Most Radiolaria are phosphorescent. The light centres round the intracapsular oil-globules, and is emitted readily in response to physical or chemical stimuli. With the exception of the *Phaeodaria*, most Radiolaria contain 'yellow cells' or symbiotic algae; see p. 243. They are either extracapsular, or in *Acantharia* intracapsular. They may be present or absent in a given species, and when present their numbers are inconstant. The extracapsular cells possess a distinct cell-membrane of cellulose, a nucleus, yellow pigment granules and granules of amyllum, i. e. starch, or of an amyllum-like substance. They multiply by fission within the cell-membrane, each cell giving origin to four which then escape. If removed from their host artificially, or naturally by its death, the cell-membranes swell up and gelatinise; the cells themselves become amoeboid and multiply by binary fission. They may escape from their gelatinous coats, and form them anew repeatedly; but if brought into a plentiful supply of water, they wander out and become biflagellate. They are destroyed however during the sporulation of some colonial forms with assimilation-plasma (note 1, p. 878), e. g. *Collozoum inerme*. The intracapsular yellow cells of the *Acantharia* occur most commonly in the *Acanthometra*, rarely in the *Acanthophracta*. They are sometimes found outside the capsule, and appear to be devoid of a cell-membrane. Both forms of cells are supposed to contribute oxygen and starch to their host. Radiolarians appear to be capable of nourishing themselves also in the ordinary way by their pseudopodia, digestion taking place either superficially or sometimes even within the calymna when there is no shell. Living diatoms have been observed within a *Collozoum* and its allies; *Myxosphaera coerulea* and young *Collozoa* are infested parasitically by a species of *Hyperia* (Amphipod). *Thalassicolla sanguinolenta* frequently takes up coccoliths and coccospheres, &c.,

colonial *Spumellaria* is divided by Brandt into (1) the spore-stage, (2) the young vegetative stage, (3) the young reproductive stage when extracapsular bodies or their analogues are formed, (4) the old vegetative stage, and (5) the old reproductive or fructificative stage when sporulation takes place. It may be noted that Brandt believes the peculiar nucleus of *Acanthometrida*, described by Hertwig (Dk. Jen. Ges. ii. pp. 148-53), to be an internal bud, which is probably extruded, and grows into an *Acanthometra*; see p. 209 of his monograph cited p. 883.

in such quantity that it becomes deformed, the soft jelly being drawn out into arms by the weight. It was in this state supposed to be a distinct genus, *Myxobrachia*.

The Radiolaria are found in all seas and in every latitude; their wide distribution is due to oceanic currents. The variety of species is greatest in tropical regions. The Pacific Ocean has an extremely rich fauna, both in species and numbers, and is probably closely approached by the Indian Ocean. They are found at all depths, pelagic, i. e. at or near the surface, zonal and abyssal. The *Spumellaria* and *Acantharia* predominate at the surface, the *Nassellaria* and *Phaeodaria* at abyssal depths; the zonal fauna being a mixed one. It is probable that the young of a given species are found at a greater depth than the adult. The organic skeletons of *Acantharia* perish at death, but the siliceous skeletons of *Spumellaria* and *Nassellaria* (= *Polycystina* of Ehrenberg), and of *Phaeodaria*, to a very slight extent, occur in marine deposits. They make up often more than three-quarters of the Radiolarian ooze which has been dredged in the Pacific and Indian Oceans at depths of 2-3000 fathoms. In *Globigerina* ooze (p. 893 *post*) they are frequently present in great numbers. Nor are they wanting in the deepest and most extensive of oceanic deposits, the Red Clay, which is probably derived to a great extent from the decomposition of their shells. They are also found in varying proportions in muds near the shores. The same groups occur fossil, the *Phaeodaria* being represented by the family *Dictyochida*, which has a perfectly solidified skeleton. Simple *Spumellaria* and *Nassellaria* have been detected in various Palaeozoic strata. Among Mesozoic formations they are found principally in Jurassic strata, in quartzites of various kinds (fossilised Radiolarian ooze) and in coprolites, scantily in the Chalk and Trias. The Spumellarian *Sphaeroida* and *Discoidea* constitute the minority, the Nassellarian *Cyrtoida* the majority; the skeletons are simple and massive, somewhat larger than the Radiolaria of the Tertiary strata. The deposits of the latter are apparently of Miocene age, and contain either living species or species akin to them. They are found plentifully in Barbados as marls, sometimes almost pure Radiolarian ooze, sometimes *Globigerina* ooze, or containing clay, pumice, &c.; in the Nicobar Islands as a Radiolarian clay; and in the Mediterranean round its coasts, both South European and North African (Oran to Tripoli), and in its islands, as marls, chalky deposits, powdery tripoli, sometimes coherent as whetstone or polishing slate.

Haeckel classifies the Radiolaria as follows:—

A. Holotrypasta s. Porulosa: central capsule with innumerable fine pores: spherical or derived from a sphere.

I. *Spumellaria* s. *Peripylea*: pores of capsule evenly distributed; skeleton siliceous or wanting; contains (i) *Collodaria*, with no skeleton, *Colloidea*, e. g. *Thalassicolla*, *Collozoum*, or a spicular skeleton, *Beloidea*, e. g. *Physematium*, *Sphae-*



rozoum; (ii) *Sphaerellaria* with a lattice or spongy shell always complete, spherical in *Sphaeroidea*, which contains the colonial *Collosphaerida* among other forms, cylindrical or elliptical in *Prunoidea*, discoidal in *Discoidea*, lent-elliptical in *Larcoidea*.

II. *Acantharia* s. *Actipylea*: pores in groups or lines, skeleton composed of acanthin in the form of radial spines, with or without a lattice-shell; contains (i) *Acanthometra* with spines, lattice-shell if present incomplete, the former indefinite in number and irregularly arranged in *Actinelida*, or twenty and regularly arranged in *Acanthonida*; (ii) *Acanthophracta* with twenty spines regularly arranged, and complete lattice-shell; subdivided according to character of shell and size of spines.

B. Merotrypasta s. *Osculosa*: central capsule with one principal aperture, and with or without accessory openings; derived from an egg-shape, or perhaps bilateral.

III. *Nassellaria* s. *Monopylea*: a porous area = porochora at one pole of main axis with an intracapsular podocoene; skeleton siliceous: contains (i) *Plectellaria*, without shell, *Nassoidea* (*Cystidium*, *Nassella*), or with an incomplete one, either a basal tripod without ring, *Plectoidea*, or a sagittal ring usually without tripod, *Stephoidea*; (ii) *Cyrtellaria*, with a complete lattice-shell or cephalis, bilocular with sagittal constriction, *Spyroidea*, multilocular with two or more constrictions and lobes, *Botryodea*, or simple, *Cyrtoidea*.

IV. *Phaeodaria* s. *Cannopylea* s. *Pansolenia*, including *Tripylea* of R. Hertwig; membrane of central capsule double; an astropyle with or without parapylae; a phaeodium surrounding astropyle; skeleton siliceous: contains (i) *Phaeocystina*, with skeleton wanting, *Phaeodinida* (*Phaeocolla*, *Phaeodina*), or composed of scattered pieces, *Cannorhaphida*, or hollow radial tubes, *Aulacanthida*; (ii) *Phaeosphaeria*, a simple lattice-shell, or one of hollow tangential tubes with nodal septa, single or double; (iii) *Phaeogromia*, a simple spherical, ovate or polyhedral shell, with large mouth opposite astropyle surrounded by teeth or feet, diatomaceous, *Challengerida*, alveolate, *Medusettida*, latticed, *Castanellida*: or porcellanous with fine needles imbedded in a punctate cement, *Circoporida*, *Tuscarorida*; (iv) *Phaeoconchia*, a bivalved lattice-shell, thick and firm, *Concharida*, or thin, fragile, scarcely latticed, with a conical cupola or helmet-shaped galea at the centre of each valve, and with hollow tubes, *Coelodendrida*, *Coelographida*.

The number of genera and species known is very large.

Bütschli, Bronn's Klass. und Ordn. des Thierreichs, i. Protozoa, pp. 332-478; Haeckel, 'Report on the Radiolaria,' Challenger Reports, xviii. 1887; Id. 'Die Radiolarien,' Berlin, 1862; Brandt, 'Die Kolonie-bildende Radiolarien,' &c., Fauna und Flora des Golfes von Neapel, xiii. 1885; R. Hertwig, 'Organismus der Radiolarien,' Dk. Med. Wiss. Ges. Jena, ii. 1880; Id. 'Zur Histologie der Radiolarien,' Leipzig, 1876.

*Coelothamnus Davidoffii* and structure of skeleton, especially in *Cyrtida*, Bütschli, Z. W. Z. xxxvi. 1882; *Thalassicolla coerulea*, Eberth, A. M. A. xxx. (1), 1887.

*Extracapsular bodies; spore-formation; phosphorescence and other points of physiology*, Brandt, op. cit. supra.

*Regeneration from central capsule*, Schneider, Archiv für Anat. und Physiol. 1867, p. 509.

*Yellow cells*, Brandt, op. cit. *supra*, pp. 65-71; Id. Mitth. Zool. Stat. Naples, iv. 1883, p. 220, p. 235; Geddes, Nature, xxv. 1881-2, p. 303.

*Distribution and Fossil forms*, Haeckel, Challenger Reports cited *supra*, pp. cxlvi-clxxv. with lit. quoted.

## CLASS FORAMINIFERA.

### (*Reticularia*; *Thalamophora*.)

*Rhizopod Protozoa with long branching and anastomosing pseudopodia which show well-marked granule-streams. The protoplasm is of a uniform character throughout the body; the nucleus single; contractile and non-contractile vacuoles are very rare. A test or shell is invariably present either chitinoid, calcareous or adventitious; it presents many varieties of shape and structure. Reproduction is typically effected by the multiplication of the nucleus, the separation of a portion of protoplasm round each nucleus so formed, and its inclosure by a test. Chiefly marine; a few freshwater.*

The test is the most prominent feature of the Foraminifera. It is chitinoid in the *Gromidae*; very delicate in *Lieberkühnia*, stouter but flexible in *Gromia* itself, resistant in *Microgromia*, and in *Diaphoropodon* incrustated with diatom shells, &c. It is hyaline or somewhat yellow; ovate with a single terminal aperture, except in *Shepherdella*, where it is a tube with an aperture at both ends. There is reason to suppose that it is porous in *Diaphoropodon*<sup>1</sup>.

A calcareous test is characteristic of the *Miliolidae*, *Textularidae*, *Cheilostomellidae*, *Lagenidae*, *Globigerinidae*, *Rotalidae* and *Nummulinidae*. In the *Miliolidae* its substance is compact in texture, homogeneous with a polished white or 'porcellanous' appearance by reflected light, in thin shells, or in thin sections viewed by transmitted light, amber-coloured. Young specimens are opalescent and diaphanous. In the other families above-named the substance of the test is traversed by fine vertical pores, varying in diameter and sometimes of two different sizes in the same test, e.g. in *Orbulina* and some other *Globigerinidae*, often laminated and in thin tests or sections transparent or hyaline. When the test is thin, and its pores relatively far apart and wide, it has a vitreous aspect; when thick, the pores fine and close set, it is milky and semiopaque. Some are perfectly opaque like *Calcarina*, and this is always the case if they are dead and have been lying long in sea-water. Owing to the absence of pores the Miliolid test is often termed 'imperforate,' that of the other

<sup>1</sup> The test of *Microgromia* withstands the action of concentrated acids and alkalis; it is perhaps silicified. The short hyaline simple processes fringing the body of *Diaphoropodon* appear to be pseudopodial (Archer, Q. J. M. ix p. 396).

families where pores are present, 'perforate,' designations sometimes employed as classificatory. There is an organic basis, more or less plentiful, visible after careful decalcification, and a distinct chitinous membrane of varying thickness lines the cavity of the test, its passages and pores<sup>1</sup>. The principal mineral constituent is Calcium carbonate, as Calcite in the perforate test, but possibly in the form of Arragonite in the imperforate. Among *Miliolidae*, *Biloculina* has been found to contain as much as 7-10 per cent. of Silica, and *Orbitolites* about 10 per cent. of Magnesium carbonate with a trace of Silica. In the perforate series it has been observed that the tests of pelagic *Globigerinae* are entirely soluble in acid; and that those of two Nummulids, *Amphistegina Lessonii* and *Operculina complanata*, contain 5 per cent. of Magnesium carbonate, with traces of phosphates, Silica, Ferric and Aluminic oxides. Grains of sand are in some instances attached to the outside of the test, e. g. frequently in the Miliolid *Nubecularia*; and in the larger *Textularinae* the quantity of sand thus added may be very great, the perforate calcareous basis sometimes disappearing. The perforate *Polytrema* and *Carpenteria*, especially the latter, use spongespicules as a foundation for the calcareous crust. In species which are able to live in brackish water the amount of calcareous matter diminishes until in one instance, *Miliolina* (= *Quinqueloculina*) *fusca*, the test becomes chitinous with minute impacted sand-grains; so too in *Entzia* from a salt-pool at Deva in Transylvania. The tests of *Miliolina* from abyssal depths (3950 fathoms) in the North Pacific, where the bottom is a Radiolarian ooze, are reduced to delicate homogeneous siliceous films.

The calcareous test affords many varieties of shape. It may consist of a single or of many chambers; in other words, it is mono- or polythalamous, a distinction which has been used for classificatory purposes, but has no significance so far as the intimate structure of the organism is concerned (*infra*, p. 891). It is nearly always free, seldom attached, and its growth as a rule follows a definite plan. Sometimes however it is really irregular, though outwardly symmetrical, as in the lenticular Nummuline *Archæodiscus*, which consists of a tube coiled on itself in

<sup>1</sup> As a rule no signs of structure are to be discerned in the test save the lamination of many perforate forms. In a few instances, the perforate *Amphistegina*, *Operculina*, *Heterostegina*, *Cycloclypeus*, it is composed of vertical hexagonal prisms traversed each by a pore; and its outer or secondarily deposited layers in *Orbulina*, *Globigerina*, &c., are said to be made up of vertical wedge-shaped masses. The siliceous skeletons of diatoms, sand-grains, &c., have been detected in the tests of the perforate *Amphistegina* and *Orbulina* during decalcification (Folin, C. R. 102, 1886, pp. 1575-6). The specific gravity of the imperforate test is higher than that of the perforate; the former varies from 2.7 to 2.722, the latter from 2.626 to 2.674 (Sollas, Sci. Proc. Royal Dublin Soc. iv. 1885, p. 390). Little is known as to the way in which new chambers are added. The protoplasm grows in amount and protrudes from the last chamber, and the walls of the new chamber are at first very thin; the pores are evident at an early period; see Max Schultze, *Organismus*, &c., pp. 29-30. Growth in size must take place by resorption within and addition without. According to Moebius (*Beiträge*, &c., p. 83), the pores in the arborescent stem of *Carpenteria raphidodendron* are formed soon after the calcareous matter is first laid down.

varying directions, but inclosed by a thick and finely perforated calcareous mass; or it becomes irregular, and this is especially the case when it is attached, e. g. in the imperforate *Nubecularia*, the perforate *Carpenteria*, where in *C. raphidodendron* it is arborescent. But in most instances of this kind growth is at first regular. Exceptions to this rule however occur among the Rotalid *Tinoporinae*, e. g. in the encrusting or arborescent *Polytrema*, or in the Lagenid *Ramulina*, with chambers connected to one another by long tubes. The single-chambered test may be more or less spherical, as in the imperforate *Squamula*, the perforate *Orbulina*, vasi-form, as in the perforate *Lagena*, or plano-spiral, as in the imperforate *Cornuspira* and the perforate *Spirillina*. When the test is polythalamous, its chambers may follow one another in a more or less straight or arcuate and single series, e. g. *Nodosaria*, seldom in a bi- or tri-serial series, as is sometimes the case in *Polymorphina*, or they are disposed in a spiral with the elements lying either in the same plane, e. g. in *Biloculina*, the nautiloid *Polystomellinae* and *Nummulites*, or in a more or less helicoid or trochoid manner as is generally the case. Successive chambers or coils may inclose their predecessors, i. e. the shell becomes involute, e. g. in the imperforate *Biloculina* and the perforate *Hastigerina*<sup>1</sup>. Spiral growth may give way to a cyclical, due to the excessive widening in a planospiral test of the peripheral chambers, which meet sooner or later round the first formed portion of the shell, as in some species of *Orbiculina* and the genus *Orbitolites*, among imperforate forms, and the *Cycloclypeinae* among perforate<sup>2</sup>. Or the axis of convolution may be lengthened out, as in the *Alveolinae* and *Fusulininae* respectively, in the imperforate and perforate series, the chambers consequently attaining a great width and the shell a fusiform

<sup>1</sup> The term 'spiral axis' applied to a coiled test denotes the longitudinal axis of the convolutions; 'plane of convolution' a vertical plane coiled like the test; 'axis of convolution' a line drawn through the point at which the test commences, and round which it is imagined to be coiled. See on the subject of the spiral coiling, von Möller, *Mém. Imp. Acad. St. Petersburg* (7), xxv. No. 9, pp. 27-40. The perforate family *Cheilostomellidae* is remarkable for the degree to which involution is carried. In the extinct *Ellipsoidina* every new chamber completely incloses its predecessors, all being connected at their bases; i. e. the test resembles a number of flasks standing one within the other. So, too, in *Cheilostomella*, but every new chamber has its aperture turned in the opposite direction to its immediate predecessor; whilst in *Allomorphina* the chambers are disposed in cycles of three, the last chamber leaving a portion of its two predecessors exposed.

<sup>2</sup> The cyclical *Orbitolites* has a very perfect series of species, showing its evolution from *Orbiculina*, which is itself derived from *Peneroplis*. The Orbiculine portion of the test is extremely large in *O. tenuissima*, and is very decidedly excentric, features very much less marked in *O. marginalis*, whilst in *O. duplex* and *O. complanata* the excentricity is lost, and the cyclical mode of growth established almost from the first, the last named being the most advanced. There is also in the two last named species a complication in the structure of the chamberlets, *O. duplex* leading from the simple type of *O. marginalis* to the complicated type of *O. complanata*. See W. B. Carpenter, 'Challenger Reports,' vii. 'On the genus *Orbitolites*.' The spiral origin of the test is indicated plainly but slightly in the perforate *Cycloclypeus*, and apparently not at all in *Orbitoides*. The most remarkable feature in *Cycloclypeus* is the addition of a fresh calcareous lamina to each surface of the test when a new cycle of chamberlets is formed; and in *Orbitoides* the presence of irregularly arranged chambers on either aspect of the disc.

FORAMINIFERA.

aspect, successive coils inclosing their predecessors completely. The imperforate *Keramosphaera* is spherical, and consists of chambers arranged in concentric layers; there is no corresponding form known in the perforate series. An altogether irregular arrangement of chambers obtains in the perforate *Tinoporinae*, and irregular layers of chambers are found on each side of the disc in *Orbitoides*.

Dimorphism exists in some cases, but the term has been applied in two different senses. In one it denotes that a given test follows in its individual growth two different types of structure, in the other that it is found under two different forms. The first mode is exemplified in the Miliolid *Hauerininae*, some *Textularidae*, and *Lagenidae*, e.g. *Hauerina*, with its first chambers arranged as in *Miliolina*, their successors in a planospiral with more than two in each turn of the coil. Trimorphism in the same sense is very rare. The second mode has been observed in *Nummulites* and its congener *Assilina*. The tests, e.g. of *Nummulites*, occur in pairs, one constantly smaller than the other and possessed of a large primordial chamber, the other of larger size but with a small primordial chamber or none at all recognisable. The *Miliolininae* combine both modes. One set of forms is small, the other large; the former have a large, the latter a small primordial chamber, with, moreover, the first chambers differently grouped to their successors which are typical. The initial chambers, moreover, in one and the same species may be disposed in different ways, leading to a polymorphism. The significance of these facts is not known.

As to structure, the following points may be noticed. The terminal aperture of the test is rarely absent as in many specimens of *Orbulina*; it may be simple, its shape sometimes depending on that of the test, sometimes independent of it; or it may be radiate, owing to the projection across it of calcareous bars; finally, it may be replaced by pores. In *Lagena* great variety prevails; it may be situated at the extremity of a tube (ectosolenian), or the tube is prolonged inwards into the test (entosolenian); whilst in other examples the two modes may be combined (ecto-ento-solenian), and more rarely a second aperture is present<sup>1</sup>. The spherical or pyriform chambers of *Ramulina* have several tubular orifices, and in the arborescent *Carpenteria raphidodendron* and *Polytrema* the branches terminate in simple apertures. In a few chambered tests each chamber has its own separate aperture, e.g. in some species of *Globigerina*; and in *Cymbalopora* not only is this the case, but accessory apertures may be present as well. The chambers in polythalamous tests may be separated from one another by slight constrictions, by imperfect septa, or by perfect but porous septa. They may in some instances be subdivided into chamberlets by vertical partitions, imperfect in the imperforate *Orbiculina*,

<sup>1</sup> Gruber has described an entosolenian *Gromia Lagenoides*; Nova Acta, xlvi. p. 495.

*Orbitolites*, *Alveolina*, perfect in the perforate *Cycloclypeinae*. In recent species of *Alveolina* the chamberlets in turn are subdivided. The septa dividing the chambers in the imperforate Foraminifera and the simpler perforate, are single and formed by a portion of the outer wall of the preceding chamber; in the higher perforate forms, e.g. larger species of *Rotalia*, in *Polystomella*, they are double, a second layer being added to the surface of the old chamber at the formation of a new chamber. The first, primordial, or embryonal chamber differs from its successors; it is globular, ovate or lens-like. The difference is naturally most marked in complicated shells. In some *Rotalidae* and *Nummulinidae* there is a supplemental, exogenous, or secondary skeleton in addition to the chamber walls proper. This secondary deposit may fill up the depressions between successive chambers and the central umbilical cavities due to the increasing size of successive coils, or it may coat the entire test as in *Calcarina* and *Heterostegina*. Small projecting masses of it are found between the edges of the chamberlets in the *Cycloclypeinae*. It may grow out into spines between the chambers of the larger species of *Rotalia*, or from the surface in general as in *Calcarina*. A system of more or less complicated 'interseptal' canals opening superficially is usually developed in connection with this skeleton between the convolutions and septa: by its means the protoplasm of the more deeply situated parts communicates with the surface. The surface of the test may be ornamented with pits, areolae, ridges or bands; it is sometimes spinulose, in *Globigerinidae* especially, the spines attaining a great length and being moveable in *Hastigerina*. With few exceptions the test itself is colourless; it is red in *Polytrema* and *Globigerina rubra*.

An adventitious skeleton is characteristic of the two families *Astrorhizidae* and *Lituolidae*. The material of which it is composed is selected and is in most instances sand-grains, which are loose with very little cement indeed in *Astrorhizinae*, in others generally cemented firmly together. The nature of the cement varies; it is chitinous, and the test flexible in *Rhizammina* or brittle in *Rheophax membranacea*; as a rule it consists of Ferric oxide and Calcium carbonate in varying proportions, the former being especially predominant in some *Lituolidae*, viz. 16.3 per cent. in *Haplophragmium latidorsatum*, and 9.4 per cent. in *Cyclammina cancellata*. It is very rarely siliceous, e.g. in *Rheophax nodulosa*. The surface of the test is generally rough, but in the *Trochammininae* it is smooth and polished, being composed of a large amount of cement with very fine sand-grains. Mud coating a chitinous membrane is found in the *Astrorhizine Pelosina*; so too in *Dendrophrya*, but the chitinous membrane is beset with sand-grains. Sponge-spicules felted together, mixed with fine sand but not united by cement, characterise the test of the *Pilulininae*. Sponge-spicules are also preferentially selected by *Haliphysema* mixed with other foreign

bodies and united by a calcareous cement; they are used also by some *Lituolinae*. The Trochammine *Carterina* is unique in forming proper fusiform calcareous spicules which with sand-grains and a calcareous cement make up its Rotaline test. The character of the sea-bottom often influences the composition of the test. Foraminiferal tests are used where *Globigerina* ooze prevails; the shells of Radiolaria, frustules of Diatoms where they abound to the exclusion of other material. *Ammodiscus incertus*, from a bottom of Radiolarian ooze, has a siliceous cement; *Trochammina inflata* loses its calcareous cement and becomes chitino-arenaceous when living in brackish water, and in the variety *T. macrescens*, the test is a flexible membrane with scarcely any calcareous investment.

As to shape, the *Lituolidae* are for the most part isomorphous with calcareous Foraminifera; even *Loftusia* finds a representative in *Alveolina* and *Parkeria* in *Keramosphaera*. With the exception of some *Endothyridinae*, an extinct sub-family, all are imperforate. The test is sometimes monothalamous, e. g. some species of *Rheophax*, *Thuramina*, &c., but more generally polythalamous. The septa are often imperfect in some *Lituolinae*, e. g. in *Lituola* they are labyrinthic. The walls of the test in the *Loftusinae*, e. g. *Cyclamina*, are thick and cancellated, i. e. traversed by passages, with the exception of a thin superficial layer. Some forms occur both free and adherent; some are always adherent. Among the latter *Webbina*, which has either a simple spherical chamber or an oval chamber with a tube, or several oval chambers connected by tubes, has no wall on the attached side. The *Astrorhizidae* present peculiar types of shape. *Psammosphaera* is a globe with interstitial apertures here and there, *Sorosphaera*, a collection of such globes; in *Storthosphaera* the orifices are slightly tubulated. Globular or oval forms with a single distinct aperture are seen in *Saccamina*, *Pelosina*, *Pilulina*, *Technitella*. The first-named occurs sometimes in groups, the members of which may be connected by tubular stolons. Or the test is a tube closed at one end which may or may not be dilated into a chamber, straight in *Iaculella*, sinuous or branched and sometimes adherent in *Hyperammina*. A simple tube, open at each end, is seen in some species of *Astrorhiza*, in *Bathysiphon* and *Marsipella*. In *Rhabdammina* there is a central chamber, sometimes scarcely marked, with two or more tubular arms typically radiating from it. This central chamber becomes large, the arms more or less numerous, irregular in shape, and sometimes branching, in some species of *Astrorhiza* and in *Aschemonella*; in the latter several chambers may be connected together irregularly by tubes. *Dendrophrya* has the chamber adherent, the arms branched, spreading or erect. *Syringammina* consists of a rounded mass of branching sand-tubes, radiating from a common centre and connected at intervals by lateral branches; the terminal apertures of the tubes are filled with loose sand-grains. The extinct *Syringosphaera* and *Stoliczkaria* have a similar

structure. *Rhizammia* has a free branching tube open at the ends; so too *Sagenella*, but the branches anastomose and the test creeps over some foreign object. The two genera *Botellina* and *Haliphysema* stand by themselves. As to the former, the test is probably attached; it is more or less straight, expanded, and thin at the free end, where there are interstitial apertures; the rest of the tube is thick-walled and traversed by irregular sandy partitions. *Haliphysema* has an expanded base from which spring one or more columns, simple or branched, and somewhat swollen at the extremity.

The protoplasm is typically of a uniform granular character throughout; but *Shepherdella* and *Lieberkühnia* are said to have a delicate clear superficial layer. Currents in it have been observed in some forms. It is often colourless, but it is brown in many *Miliolidae*, olive-green in many arenaceous forms from the deep sea, and *Orbitolites tenuissima*, greenish in *O. complanata*, reddish or red-brown in *O. duplex*, and many others. But the last-named colour is perhaps derived from the food, which consists chiefly of Diatoms<sup>1</sup>. The pseudopodia are typically fine filaments which branch, anastomose, and extend to a great distance. They show currents of granules flowing outwards and backwards simultaneously in the same pseudopodium. When the test is imperforate they originate as a rule from its aperture alone, whether single, double, or multiple; in *Microgromia* and *Lieberkühnia* from a pseudopodial peduncle or compact process extended from the mouth of the test. In the *Gromidae*, except *Microgromia*, there are also pseudopodia given off from the surface of the test, probably through perforations in it in *Diaphoropodon*, but in *Lieberkühnia* and *Gromia* itself, where they are plentiful, and *Shepherdella*, where they are few, from a layer of protoplasm which flows from the aperture round the test. Those which radiate from the surface of the test in *Diaphoropodon* are fine, straight, linear, short; those which originate from the mass of protoplasm at the mouth of the test form a dense radiant bundle and branch slightly, but if the organism is disturbed some of them become of great length and tufted at several points. The protoplasm in all perforate genera forms a superficial coat from which the pseudopodia are given off, and issues not only from the aperture but the pores of the test, as well as from the interseptal canals when present, a rule to which the genus *Lagena* is possibly an exception; *L. elegans* certainly is so (*Bütschli*). In the pelagic *Hastigerina Murrayi*, and probably in some other pelagic species, this coat is filled with large non-contractile vacuoles, such as are seen in the

<sup>1</sup> The colouring matter exists either in the form of minute particles, or collected in distinct vesicles, but the latter may be symbiotic algae. See p. 894 *infra*. The oldest chambers are the most intensely coloured, the newest being generally colourless. The colour disappears more or less completely on deprivation of food, and is restored when it is plentiful. The chemical reactions of the reddish colour are like those of Diatomin; see Max Schultze, 'Organismus,' pp. 19-20.



extracapsular protoplasm of many Radiolaria. The pseudopodia are organs of locomotion as well as of alimentation. Foreign bodies when sufficiently small may be drawn within the test; but they are very generally, in many instances indeed necessarily, digested outside it. Minute non-contractile vacuoles have been observed in *Shepherdella* and *Spirillina*; a single contractile vacuole in some species of *Gromia*, in *Microgromia* and *Diaphoropodon*. It is said that the vacuoles of *Lieberkühnia* eventually come to the surface and burst. Vacuoles which change in shape and disappear, whilst others appear in their stead, have been observed in some marine genera, e. g. the Miliolid *Biloculina* (Bütschli).

All Foraminifera properly examined have been found to possess a nucleus, and at first one only—a fact to be carefully noted, as showing that polythalamous genera are neither truly segmented nor colonial<sup>1</sup>. In them the nucleus appears to wander by degrees into the outer chambers from the primordial chamber where it is primitively situated. Both mono- and poly-thalamous genera however become multinucleate sooner or later, and the nuclei are thereupon scattered through the chambers if there is more than one. The increase of the nuclei in number is probably connected with reproduction (*infra*). The nucleus has a membrane with contents usually described as homogeneous or finely granular, but in well-prepared specimens there is a distinct chromatin network, with one or more nucleoli (Bütschli). In *Trochammina* (*Rotalina*) *inflata*, and in an *Ovulina*, one half of the nucleus has been found to consist of chromatin, the other of a non-staining substance.

Binary fission has been observed only in *Lieberkühnia* and *Microgromia*<sup>2</sup>. In the former it is transverse, and the delicate test undergoes division with the body; in the latter it is either transverse or longitudinal. When it is transverse the hinder part quits the test and becomes either amoeboid or ovate and biflagellate. When longitudinal, both parts are in connection by their pseudopodial peduncles; one quits the test but remains a member of the colony; it sometimes undergoes a previous subdivision into two. Portions of the disc in *Orbitolites*, accidentally broken off, continue to live and form new and completely concentric annuli. A mode of reproduction to be regarded as spore-formation(?) has been observed in various calcareous Foraminifera—*Miliolina*, *Peneroplis*, *Orbitolites complanata*, *Cristellaria*, *Spirillina*, and a Rotalid, representatives of both imperforate and perforate genera. There appear within the adult

<sup>1</sup> The monothalamous *Lieberkühnia*, *Haliphysema* and *Spirillina* are known only in the multi-nucleate state.

<sup>2</sup> It is not likely that abortive attempts at fission are indicated in the double shells seen sometimes in *Lagena*, the partially divided coils of *Polystomella*, the bifid discs of *Orbitolites complanata*, or the half-discs set on the normal discs in that Foraminifer. They are probably simply irregularities of growth. To what an extreme such irregularity may be carried, see von Roboz' account of *Calcituba* in SB. Wien. Acad. 88, Abth. 1, 1884.

minute young with calcareous tests, single-chambered in *Miliolina*, *Spirillina* and *Peneroplis*, three-chambered in the Rotalid, with the first ring of chambers complete in *Orbitolites*. Similar young of *Miliolina* and *Rotalia* have been found free, and been proved to be uninucleate by Hertwig, the nucleus lying in the primordial chamber of the *Rotaliae*. There can be little doubt that the young in question take origin by the multiplication of the nucleus, the separation of protoplasm round the nuclei thus formed, and the deposition of a test; they are then set free at the aperture of the parental test, or, if this is represented by pores, as in *Peneroplis*, by solution of the walls of the chambers containing them<sup>1</sup>.

A colonial state occurs in *Microgromia socialis*, where a number of individuals remain united by their pseudopodia. When the latter contract, as they do on irritation, the tests are drawn into a heap, and in this condition the organism was described by Archer as *Cystophrys Haeckeliana*, in its expanded state as *Gromia socialis*. Young *Miliolinae* were observed by Hertwig associated to the number of 30–40 by a protoplasmic mass, from which pseudopodia streamed in all directions. Conjugation has not been observed, unless the apposition of young *Miliolinae* in twos, recorded by Gervais, is an instance.

The majority of Foraminifera are marine, but some of the marine species are capable of living in brackish water, with very slight admixture of salt, and two (*Polystomella striatopunctata*, *Nonionina depressula*) have been gathered even in perfectly fresh. *Microgromia* and *Diaphoropodon* are entirely freshwater, *Lieberkühnia* and *Gromia* inhabit both fresh and salt. One species, *Entzia tetrastomella*, has been found in salt pools in Transylvania. The only terricolous form known, *Gromia terricola*, was

<sup>1</sup> Ray Lankester found in the anterior part of *Haliphysema Tumanowiczii* nucleated egg-like bodies (Q. J. M. xix. p. 482), and Saville Kent describes in the same Foraminifer minute amoebiform young, naked pyriform bodies, and every stage to the adult (A. N. H. (5), ii. p. 76). It is possible that the 'ova' described by some older authorities in various genera are young in an early stage. The protoplasm of the parent may or may not be completely used up in the reproductive process. In *Orbitolites* the young lie in the peripheral annulus, the outer wall of which is described by W. B. Carpenter as very thin, and its cavity undivided by septa into chamberlets. The number of young is sometimes very great, e. g. in a *Peneroplis Proteus* described by Schacko it was 118, all contained in the fourteen terminal chambers. Many specimens of the Globigerinid *Orbulina*, which has the form of a perfect sphere, with, in some instances, an aperture, contain adherent to the inner surface a *Globigerina* with a number of chambers, up to 13–14, the larger chambers being spinulose. Such inclosures are most common in small and middle-sized specimens, whilst in large they are either absent or scarcely indicated; they are found both in recent and fossil specimens. Three theories have been proposed to account for the phenomenon: (1) that *Orbulina* is the terminal chamber of a *Globigerina* which has undergone complete involution, and is gradually absorbed; (2) that the *Globigerina* is developed within the *Orbulina* from a germ which has not been set free (Schacko, A. N. 49 (1), 1883, p. 437); (3) that the *Orbulina* is the initial, i. e. primordial chamber of a *Globigerina*, other chambers having been developed within it, and the case being one of dimorphism (Schlumberger, A. N. H. (5), xiv. 1884, p. 70). The figures and descriptions given by Shacko appear to be directly contradictory of Schlumberger's theory. Siddall has described curious disruptive phenomena in *Shepherdella*, which appear to be reproductive see his paper, Q. J. M. xx. 1880.

discovered by Leidy amidst damp moss in the cracks of a pavement in Philadelphia. In the sea the Foraminifera are universally distributed and at all depths, arenaceous forms proper, i. e. *Astrorhizidae*, being for the most part inhabitants of the deep sea, where also the *Lituolidae* attain their highest development in size and complexity. The largest and most specialised calcareous genera are found in the shallow waters of tropical and sub-tropical seas. A few calcareous forms are pelagic, principally species of *Globigerina*, *Orbulina*, *Pulvinulina*, *Pullenia*, and the genus *Hastigerina*, all members of the family *Globigerinidae*. It is their tests which, together with those of some non-pelagic species, in small proportions however, make up the *Globigerina* ooze, or modern chalk, which is undergoing deposition at the present time over immense surfaces of the sea-bottom, at depths ranging from 250 to 2900 fathoms, especially from 1000 to 2000. There is reason to suppose that pelagic forms, with the exception probably of *Hastigerina*, are capable of living also at the bottom. Foraminifera are also met with in the two other deep-sea deposits, Radiolarian Ooze and Red Clay. Their fauna is approximately identical according to Brady, in some instances differing little from that of *Globigerina* ooze, though naturally in relatively smaller proportion to the characteristic materials of the two deposits in question. The tests of the pelagic forms however which they contain are worn and corroded. In two dredgings made by H.M.S. 'Challenger' in the Pacific, both in mid-ocean, arenaceous species occurred almost exclusively; in two others minute and highly ornamented *Lagenae* were abundant. Foraminifera are common in marine geological deposits, and a large number of living genera make their appearance at an early period—*Textularia*, *Lagena* and *Nodosaria* in the Silurian, *Cornuspira*, *Lituola*, *Trochammina*, *Calcarina*, *Nummulites*, &c., in the Carboniferous, *Miliolina* and *Globigerina* in the Trias, a very large number of forms in the Chalk, and especially in the Tertiary period. *Alveolina*, *Operculina* and *Nummulites* are genera which, though living at the present day, were particularly numerous in Eocene times; and the last-named especially contributes largely to the building up of limestones of that age in Central Europe, Central and Southern Asia, and Northern Africa. Many arenaceous genera (*Astrorhizidae* and *Lituolidae*), still living in the deep sea, are found in the Lias and attain their maximum development before the Cretaceous period. Of extinct forms, one *Eozoon*, of doubtful animal nature however, is found in Pre-Cambrian strata. It is supposed to have consisted of tiers of more or less oval chambers with perforated walls, connected by vertical canals and an intervening supplemental skeleton with interseptal canals; the chambers in each tier have usually wide openings into one another; the whole structure covered surfaces a foot square with masses 5-6 in. thick. Among *Lituolidae* the *Endothyrinae* extend from the Carboniferous into the lower Oolite; *Parkeria* is confined to

the Greensand, *Loftusia* comes from the Carboniferous limestone of British Columbia and Eocene strata in Persia. *Fusulina* is Carboniferous and Permian; *Orbitoides* occurs in Cretaceous strata, in Eocene, where it is very frequent in Nummulitic limestone, whilst in Miocene it is rare. Chalk is a fossilised *Globigerina* ooze; in some specimens of it *Globigerinae* form 90 per cent. at least of the bulk. They are found also in some of the Barbadian marls. The majority of Foraminifera are of moderate size, below  $\frac{1}{2}$  in.; many are microscopic; *Cycloclypeus Carpenteri*, the largest living species, measures rather more than 2 in. across the disc; *Parkeria* and species of *Orbitoides* and *Nummulites* attain a diameter of 2 in.; *Loftusia* is fusiform and 3 in. long. A symbiotic *Zooxanthella* has been observed in *Globigerina echinoides*, brownish cells in a *Peneroplis*, minute nucleated cells in *Orbitolites complanata*, as well as others of larger size, possessed of a distinct membrane, within which the cell undergoes fission. Diatoms retaining their soft parts have been found by Bütschli in the last-named species.

Carter has described, under the designation '*Testamoebiformia*,' three organisms from the Gulf of Manaar (between South India and Ceylon), two adherent, creeping, with calcareous tests, and of these *Holocladina* is root-like, *Cystoedictyina*, retiform; the third *Ceratestina*, with subglobular chitinous chambers connected by stolons. Nothing is known of the living organism. See A. N. H. (5), v. 1880, p. 446.

The *Dactyliporinae*, which have been usually classed as Foraminifera, are now regarded as Calcareous Algae; Brady, 'Report,' &c., Challenger Reports, ix. p. 59.

Structures known as Coccoliths and Rhabdoliths are generally found in *Globigerina* ooze and also fossilised in chalk. A Coccolith consists of a flat disc, or of two concave-convex discs, fitted into one another, composed of Calcium carbonate and an organic basis. A Rhabdolith with the same composition has a rod-like form, the actual shape of the rod varying much. Both occur associated in spherical masses, Coccuspheres and Rhabdospheres, which are found floating at the surface of the ocean as well as at the bottom. By some they are regarded as Calcareous Algae; but it has been suggested that they are not unlike the forms assumed by calcareous matter when precipitated in an organic matrix. See Wallich, A. N. H. (3), viii. 1861; (4), xix. 1877; O. Schmidt, SB. Wien. Akad. lxii. Abth. 1, 1870; Carter, A. N. H. (4), vii. 1871; Wyville Thomson, 'Voyage of the Challenger,' The Atlantic, London, 1877, i. p. 220-2, figs. 49, 50.

It may be noted here that the term 'Foraminifera' was originally employed by D'Orbigny in allusion, not to the pores of the perforate test as is commonly supposed, but to the one or more pores in the divisions or septa between the chambers in the species known to him. D'Orbigny regarded the Foraminifera as a subdivision of Cephalopoda. See A. Sc. N. (1), vii. 1826, p. 245.

Brady classifies the Foraminifera as follows:—

Fam. 1. *Gromidae*. Test chitinous; smooth or encrusted with foreign bodies; imperforate; with a pseudopodial aperture at one or both extremities; pseudopodia long, branching, reticulate; with a single terminal aperture, *Lieber-*

*kühnia*, *Microgromia*, *Gromia*, *Diaphoropodon*; with an aperture at each end of the test, *Shepherdella*.

Fam. 2. *Miliolidae*. Test imperforate, normally calcareous and porcellanous, sometimes encrusted with sand; under starved conditions (e. g. in brackish water) becoming chitinous or chitino-arenaceous; at abyssal depths occasionally consisting of a thin homogeneous siliceous film; contains *Nubecularinae*; *Miliolininae*; *Hauerininae*; *Peneroplidinae*, e. g. *Cornuspira*, *Peneroplis*, *Orbitolites*; *Alveolininae*; *Keramosphaerinae*.

Fam. 3. *Astrorhizidae*. Test invariably composite, usually of large size and monothalamous; often branched or radiate, sometimes segmented by constriction of the walls, but seldom or never truly septate; polythalamous forms never symmetrical; contains *Astrorhizinae* with thick walls to test composed of loose sand, or mud, slightly cemented, e. g. *Astrorhiza*, *Pelosina*, *Syringamina*; *Pilulininae* with monothalamous test, composed of loosely felted sponge-spicules and fine sand without any cement, *Pilulina*, *Technitella*, *Bathysiphon*; *Saccamininae* with thin spherical chambers composed of firmly cemented sand-grains, *Psammosphaera*, *Sorosphaera*, *Saccamina*; *Rhabdamminae*, test composed of firmly cemented sand-grains often with sponge-spicules intermixed; tubular, straight, radiate, branched or irregular; free or adherent; with one, two, or more apertures; rarely segmented, e. g. *Jaculella*, *Marsipella*, *Rhizammina*, *Sagenella*, *Haliphysema*.

Fam. 4. *Lituolidae*. Test arenaceous, usually regular in contour; septation of polythalamous forms often imperfect; chambers frequently labyrinthic. Comprises sandy isomorphs of the simple porcellanous and hyaline types together with some adherent species; contains *Lituolinae*; *Trochammininae*; *Endothyrinae* (extinct); *Loftusinae*—*Cyclammina*, *Loftusia*, *Parkeria*.

Fam. 5. *Textularidae*. Tests of the larger species arenaceous, either with or without a perforate calcareous basis; smaller forms calcareous and conspicuously perforate. Chambers arranged in two or more alternating series, in a spiral, or confused; often dimorphous; contains *Textularinae*; *Bulimininae*; *Cassidulininae*.

Fam. 6. *Chilostomellidae*. Test calcareous, finely perforate, calcareous. Segments following each other from the same end of the long axis (*Ellipsoidina*) or alternately at the two ends (*Chilostomella*), or in cycles of three (*Allomorphina*), more or less embracing. Aperture a curved slit at the end or margin of the final segment. See note 1, p. 886.

Fam. 7. *Lagenidae*. Test calcareous, very finely perforated; either monothalamous, or consisting of a number of chambers joined in a straight, curved, spiral, alternating or rarely branching, series. Aperture simple or radiate, terminal. No supplemental skeleton nor canal system; contains *Lageninae*; *Nodosarinae*; *Polymorphininae*; *Ramulininae*.

Fam. 8. *Globigerinidae*. Test free, calcareous, perforate; chambers few, inflated, arranged spirally; aperture single or multiple, conspicuous. No supplemental skeleton nor canal system. All the larger species pelagic in habitat; e. g. *Globigerina*, *Orbulina*, *Hastigerina*.

Fam. 9. *Rotalidae*. Test calcareous, perforate, free or adherent. Typically spiral and 'Rotaliform', i. e. coiled so that the whole of the segments are visible on the superior surface, those only of the last convolution on the inferior or apertural side, sometimes one face being more convex, sometimes the other. Aberrant forms evolute, outspread, acervuline (i. e. irregularly massed) or, irregular. Some of the

higher forms with double chamber walls, supplemental skeleton and interseptal canal-system: contains *Spirillininae*; *Rotalinae*, e.g. *Cymbalopora*, *Carpenteria*, *Rotalia*, *Calcarina*; *Tinoporinae*, test composed of irregularly heaped chambers with or without a distinctly spiral primordial portion; for most part no general aperture; e.g. *Tinoporus*, *Polytrema*.

Fam. 10. *Nummulinidae*. Test calcareous and finely tubulated; typically free, polythalamous and symmetrically spiral; higher forms with a supplemental skeleton and more or less complex interseptal canal system; contains *Fusulininae*; *Polystomellinae*; *Nummulitinae*, e.g. *Amphistegina*, *Operculina*, *Heterostegina*, *Nummulites*; *Cycloclypeinae* — *Cycloclypeus*, *Orbitoides*; (?) *Eozoöininae*, test forming irregular, adherent, acervuline masses; *Eozoon*.

Bütschli, Bronn's Klass. und Ordn. des Thierreichs, Protozoa, i. pp. 3-260 under 'Rhizopoda,' together with *Amoebina* and *Proteomyxa*; Brady, 'Report on Foraminifera,' Challenger Reports, ix. 1884 with lit. pp. 1-42 d; cf. Id. Q. J. M. xix. 1879; xxi. 1881; Moebius, Beiträge zur Meeresfauna der Insel Mauritius, &c., Berlin, 1880, pp. 65-108; Carpenter, W. K. Parker, and T. Rupert Jones, 'Introduction to the Study of the Foraminifera,' Ray Soc. 1862, with lit. pp. xvii-xxii; Max Schultze, 'Organismus der Polythalamien,' Leipzig, 1854.

*Lieberkühnia*, W. B. Carpenter, 'Introduction,' *supra*, pp. 29, 63; Maupas, A. N. H. (5), x. 1882; as *Gromia paludosa*, Cienkowski, A. M. A. xii. 1876, p. 32; Gruber, Nova Acta, xlvi. 1884, p. 484; with *Shepherdella*, Siddall, Q. J. M. xx. 1880; *Gromia terricola*, Leidy, Freshwater Rhizopoda of N. America, U. S. Geological Survey of the Territories, xii. 1879, p. 277; *Microgromia*, Hertwig and Lesser, A. M. A. x. 1874, suppl. p. 8; Cienkowski, *ibid.* xii. 1876, p. 34; Archer, Q. J. M. xvii, 1877, p. 115 and A. N. H. (5), viii. 1881, p. 230; *Diaphoropodon*, Archer, Q. J. M. ix. 1869, p. 394. *Various marine forms*, Gruber, 'Protozoen des Hafens von Genua, Nova Acta, xlvi. 1884; *Calcutuba*, von Roboz, SB. Wien. Akad. 88, Abth. 1, 1884; *Orbitolites tenuissima*, W. B. Carpenter, Ph. Tr. 174, 1883; Id. 'On species of *Orbitolites*,' Challenger Reports, vii. 1883; *Keramosphaera*, Brady, A. N. H. (5), x. 1882. *Syringamina*, Brady, P. R. S. xxxv. 1883; *Haliphysema*, p. 808, *ante*. *Cycloclypeus* and *Orbitoides*, Martin, Niederländ. Archiv f. Zoologie, v. 1879-80.

*Foraminifera of marine deposits*, Brady, Challenger Reports, ix. *supra*, pp. 753-85; *pelagic*, Id. *ibid.* pp. ix-xv; cf. *on Hastigerina*, Murray, P. R. S. xxiv. 1875-6, p. 534, and R. Hertwig, J. Z. xi. 1877, p. 342; *of brackish water*, Brady, A. N. H. (4), vi. 1870; *of salt pool*, = *Entzia*, von Daday, Z. W. Z. xl. 1884, cf. A. N. H. (5), xiv.

*Fossil Foraminifera*: T. Rupert Jones, Catalogue, British Museum, 1882; Zittel, Handbuch der Palaeontologie, Abth. 1, Palaeozoologie, i. 1876-80; Bütschli, Bronn's Thierreich (*supra*), pp. 242-60; *liassic*, Häusler, N. Jahrbuch für Min. Geol. Palaeont. 1883, (1); *Swiss Jurassic*, Id. Quart. Journal Geol. Soc. xxxix. 1883; *of London Clay*, Sherborne and Chapman, Journal R. Micr. Soc. (2), vi. 1886; *Eozoon*, Cogan, Dawson, Carpenter, Quart. Journal Geol. Soc. xxi. 1865; Carpenter, King and Rowney, *ibid.* xxii. 1866; Moebius, Palaeontographica, xxv. 1878; Id., Dawson, Carpenter, Nature, xx. 1879; Dawson, Amer. Journal of Science and Arts, (3), xvii. 1879; Moebius, *ibid.* xviii. 1879. *Syringosphaeridae*, Martin Duncan, Sc. Results of Second Yarkand Mission, Calcutta, 1879; *Stoliczkaria*, Id.

Quart. Journal Geol. Soc. xxxviii. 1882. *Parkeria*, *Loftusia*, W. B. Carpenter and Brady, Ph. Tr. 159, 1869; *Loftusia*, Dawson, Quart. Journal Geol. Soc. xxxv. 1879; cf. Carter, A. N. H. (4), xix. 1877. *Orbitoides*, Martin, *supra*.

*Dimorphism*: Brady, Challenger Reports, ix. *supra*, p. viii; Munier-Chalmas on *Nummulites* and *Assilina*, Bull. Soc. Géol. France (3), viii. 1881; De la Harpe, *ibid.* ix. 1882; Munier-Chalmas and Schlumberger on *Miliolinae*, A. N. H. (5), xi. 1883; Id. 'Miliolides trématophorées,' Bull. Soc. Géol. France, (3), xiii. 1885.

*Chemical composition of test*: Brady, Challenger Reports, ix. *supra*, pp. xvi-xxi. *Structure of protoplasm*, Bütschli, M. J. xi. 1886. *Nuclei*: Id. *ibid.*: R. Hertwig, J. Z. x. 1876, xi. 1877, pp. 345-7; F. E. Schulze, A. M. A. xiii. 1877, p. 9; Gruber, Z. W. Z. xl. 1884, pp. 127-8; *Multinucleate Gromia*, Max Schultze, A. M. A. ii. 1866, p. 140.

*Reproduction*: W. B. Carpenter, &c., 'Introduction,' *supra*, pp. 37-8 with ref.; Id. on species of *Orbitolites*, Challenger Reports, vii. p. 16; *Peneroplis* (and *Orbulina*), Schacko, A. N. 49, 1883; *Cristellaria*, Brady, Challenger Reports, ix. *supra*, p. 543.

*Conjugation* (?), Gervais, C. R. xxv. 1847, p. 467.

*Symbiotic algae*, &c., Bütschli, M. J. xi. 1886, pp. 93-9.

## CLASS AMOEBINA.

*Rhizopod Protozoa with lobose, digitiform or filose pseudopodia, sometimes branched, rarely anastomosing, either locomotor and alimentative in function or the latter alone, sometimes perhaps tactile. The presence of a hyaline border ('ectosarc') depends on the density of the protoplasm. The body is either naked, enveloped in a complete gelatinoid or chitinoid coat, or lodged in a monothalamous test with one or two apertures, in composition either gelatinoid, chitinoid, encrusted with foreign bodies, or made up of chitinoid or siliceous plates cemented together. Non-contractile vacuoles are sometimes present in numbers; contractile vacuoles, sometimes absent, are usually single, or limited to a few. There may be one, two, or many nuclei. Freshwater, terricolous, rarely marine, saprophytic, or parasitic.*

It has been shown that in the naked Amoebina with dense protoplasm, a superficial thin layer undergoes coagulation by contact with the water in which the animal lives, but that it is continually dissolved in locomotion and as continually formed anew. The degree to which it is specialised is variable in different species; when more resistant than usual it causes puckers and lines on the surface, e.g. in *Amoeba verrucosa*, and conular eminences at the bases of the pseudopodia, e.g. *A. tentaculata*. In a few instances however a permanently differentiated layer or cuticle is met with. *Zonomyxa* has a chitinoid (?) resistant membrane which is stretched out to invisible thinness where the protoplasm is in motion or protruded as pseudopodia; *Amphizonella violacea* is clothed with a gelatinous coat pierced by the pseudopodia; *Trichosphaerium*, with an invest-

ment of short spines set on a thin membrane, rounded gaps here and there giving exit to the pseudopodia. The marine *Amoeba obtecta* inhabits a cup-shaped gelatinous theca. The test of those Amoebina which possess one is always monothalamous, when chitinoid either colourless, yellow or brown, according to thickness. It has a single aperture, except in three genera, *Diplophrys*, *Ditrema* and *Amphitrema*, with two at opposite poles. Pores at the base of the test for the escape of water have been observed in two instances, in *Hyalosphenia papilio* and *Nebela bursella*. The test is cup-shaped in *Cochliopodium*, more or less hemispherical, with the aperture limited by an inwardly turned rim in *Arcella*, usually globular, oval or pyriform. Owing to compression, or to obliquity of the mouth, it may become bilateral; in *Diffugia spiralis* and *Pleurophrys* (= *Pseudodiffugia*?) *Helix* it is usually said to form a half-coil. As to the former, however, Leidy states that it is retort-shaped, and an internal septum stretched across the neck of the retort gives the appearance of a spiral twist. The simple chitinoid shell may be very thin, flexible and closely applied to the body (*Pamphagus*, *Diplophrys*?), thicker, but not rigid (*Cochliopodium*), stiff (*Ditrema*), and the body not in complete contact with it (*Hyalosphenia*, *Platoun*), as is nearly invariably the case in the genera to be mentioned. In *Quadrula* it consists of transverse rows of squarish chitinoid plates, and in *Arcella* of two membranes, an inner thin, homogeneous, and an outer composed of hexagonal prisms, placed vertically, and filled with water. *Diffugia*, *Amphitrema*, &c., have foreign bodies of very various kinds (diatom-frustules, sand-grains, &c.) attached to the outer surface of the chitinoid membrane, or held together by a cement, either gelatinous or siliceous(?). In *Euglypha* and its allies the plates composing the test appear to be silicified; they are probably held together by a chitinoid cement. The plates of the row surrounding the mouth are pointed and serrated, and that aperture has consequently a margin strongly denticulated in *Euglypha*; it is beaded in *Trinema*, but as a rule it is smooth. The remaining plates of the test are oval, or hexagonal, disposed in regular longitudinal lines and sometimes overlapping, exceedingly minute in *Cyphoderia*, and implanted in a chitinoid membrane<sup>1</sup>. The test is sometimes furnished with processes, or tubercles, with a crest or with spines, coarse or fine, and in *Placocista* moveable.

The protoplasm varies much in density in the naked Amoebina or *Nuda*. When it is fluid the granules, &c., which it contains are distributed

<sup>1</sup> *Nebela* (Leidy) is remarkable for the very varied shape of the siliceous elements of its test: they are round or oval discs, or rod-like bodies, varying in length and size, sometimes intermingled, imbedded in a chitinoid membrane (Taránek). They were supposed by Wallich (A. N. H. (3), xiii. pp. 233-4) to be derived possibly from metamorphosed diatom-frustules. The cementing material between the sand-grains, &c. of the test in *Diffugia* sometimes stains readily. There appears to be a diversity of opinion as to the chitinoid or siliceous nature of the plates in some instances, e. g. in *Quadrula*.



throughout its whole substance, and it may or may not show a hyaline edge at the spot which is extending onwards in locomotion. But with an increase in density, the granules, &c., are confined to the more central portion and leave a more or less pronounced hyaline border. Hence a distinction into an outer ectosarc and an inner endosarc<sup>1</sup>. In the *Testacea* the granules are frequently aggregated in a middle zone. Their protoplasm also, when the test is rigid, does not under ordinary circumstances fill it, but a connection is maintained between the two by contractile threads which retract the animal when it is molested. The configuration of the pseudopodia appears to depend on the density of the protoplasm. In the *Testacea* they are emitted only at the aperture or in amphistomatous genera at both apertures, from a mass of clearer protoplasm, and they are either few and digitiform, occasionally containing granules and sometimes slightly branched, e.g. in *Arcella*, *Diffugia*, &c., or they are filose, i.e. filamentous, and generally somewhat numerous, simple or branched, rarely widely extended as in *Pamphagus*, and seldom undergoing anastomosis<sup>2</sup>. In the *Nuda* they are subject to much variation. When the protoplasm is fluid it not infrequently flows as a whole in one direction; or the pseudopodia are broad, more or less irregular lobes, seldom, as in *Amoeba Proteus*, digitiform, and the granules and other contents of the protoplasm flow into them. A steady onward flow is also observable in the locomotion of species with very dense protoplasm and a well-defined ectosarc, e.g. *Hyalodiscus* with the ectosarc as a border on the advancing side; *Amoeba verrucosa* and *A. terricola* with an uneven advancing edge or knob-like projections and wrinkled surface. So too in *A. tentaculata* and *A. actinophora* with coagulated surface, in *Zonomyxa* and *Trichosphaerium* with differentiated cuticular structures (*supra*). But the four last-named have also special pseudopodia, purely ectosarcal except in *Zonomyxa*, of no use however as organs of locomotion, but serving solely as nutritional, and perhaps also as tactile organs. In *A. tentaculata* they protrude from the ends of conular eminences, are short, pointed, and display curving motions; they are retracted in locomotion or persist tentacle-like on the advancing margin. They are short and digitiform in *A. actinophora*, and put forth at one spot or near together; hence the *Amoeba* has the look of a *Cochliopodium*. In *Trichosphaerium* they are elongated, cylindrical, and issue from gaps in the cuticle; in *Zonomyxa* branched and stretching the cuticle wherever they protrude until it becomes indistinguish-

<sup>1</sup> Gruber insists strongly on the fact that there is but *one kind* of protoplasm in an *Amoeba*, and that when the granules, &c. either do not follow at once the forward movement of the body, or are confined to a central part, the cause is not the existence of different layers, but the greater density of the protoplasm. See Z. W. Z. xli. pp. 196, 201; Biol. Centralblatt. vi. p. 5.

<sup>2</sup> *Amphitrema stenostoma* is said by Nüsslin to emit both digitiform and filose pseudopodia, one at one end of the test, the other at the other end, simultaneously. The digitiform alone are used in locomotion. Z. W. Z. xl. pp. 718-9.

able. *Amphizonella* with a gelatinous envelope retains a more or less globular shape; its motions are very slow; its digitiform pseudopodia perforate the envelope at any point. With a protoplasm of medium density and ectosarc as a well-marked hyaline border, the pseudopodia may have the form of small lobes with hyaline borders, or of conical and pointed ectosarc processes, occasionally of some length. Locomotion is effected solely by their means or in combination with lobular protrusions. In *Amoeba lucida* the extremities of the pseudopodia are apt to become spirally twisted. Noticeable peculiarities are, the termination in the Testacean *Petalopus* of the pseudopodia in plate-like ends, their transformation in the naked *Plakopus* and *Amoeba cellarum* into protoplasmic membranes uniting together so as to include funnel-shaped spaces, the villiform protoplasmic processes covering both body and pseudopodia in some specimens of *Dactylosphaerium vitreum*, and the somewhat similar rigid spinules of *Deinamoeba* (Leidy). The last-named is occasionally invested with a gelatinous coat, beset with minute vertical rods, possibly of Bacterial nature.

Very many *Nuda* possess while in motion, especially flowing motion, a patch of villous processes at the posterior extremity of the body. If the protoplasm is very fluid, the villi are fine and cilia-like, but are seldom seen; if somewhat dense, they are pointed and filamentous; if denser still, stout and blunt. Their significance is unknown. The genus *Ouramoeba* of Leidy is characterised by having in the same position motionless trailing filaments, cylindrical, tubular, sometimes branched or jointed, aggregated in bundles. It is possible that they are the mycelium of a fungus. Indeed, many *Amoebae* contain rod-like bodies of varying length, especially aggregated round the nuclei, and the only probable explanation of their nature is that they are symbiotic fungi<sup>1</sup>.

The protoplasm may contain colouring matters, sometimes derived from the diatom or chlorophyll of the food, sometimes intrinsic like the green or yellow globules of *Dactylosphaerium*, the green, brown, or red

<sup>1</sup> Korotneff states that the appendages of his *Longicauda*, = *Ouramoeba*, *amoebina*, undergo changes under unfavourable circumstances, the contents of the filaments becoming segmented into small squarish highly refractile bodies (? spores); A. Z. Expt. viii. 1879-80, p. 472. In Leidy's *O. vorax* the filaments are said to be cylindrical tubes, in *O. botulicauda* they consist of a series of elliptical joints, 1-4, adapted end to end. Leidy says they resemble mycelial filaments; see his Pl. ix. in the Fresh-water Rhizopoda, &c. Gruber thinks they are fungoid, and mentions that he has seen the fungoid filaments of *Amoeba binucleata* protruded in bundles under the action of chromic acid; Z. W. Z. xli. p. 211.

Rod-like bodies, probably of fungoid nature, are very common in *Amoebae* and *Pelomyxa*; see especially Gruber, Z. W. Z. xli. p. 210. The 'Glanz-körper' or 'glittering bodies' of *P. palustris*, are probably of parasitic origin (? Chytridian), and the source of the amoeboid and flagellate spores seen by Greeff, Korotneff, and Weldon (cf. Ray Lankester, Encycl. Brit., ed. ix., xix. p. 842). According to Leidy they are present in *P. villosa*, but Gruber did not observe them in that species, nor Korotneff in *P. parvialveolata*. Gruber found very similar bodies in *Amoebae*, particularly in *A. quinta*; see Z. W. Z. xli. pp. 191, 209. Bütschli says he has seen spore-like bodies with membrane and nucleus, in *Pelomyxa (palustris?)*; see his Protozoa, Bronn's Thierreich, i, note, p. 159.

granules of *Plakopus*, the violet granules of *Amphizonella violacea*, or vacuoles of *Zonomyxa*, the oil-globule, amber or red in colour, of *Diphrys*, or the chlorophyl bodies of some species of *Diffugia*, *Hyalosphenia papilio*, *Heleopera picta*, *Arcella artocrea*, *Ditrema flavum*, *Amphitrema Wrightianum*<sup>1</sup>. Other solid elements are fatty granules, glycogen, and, when chlorophyl is present, starch (?), concretions rounded or crystalline in many *Amoebae*, probably of an *excretory* character, mud or sand taken up by *Amoebae* with fluid protoplasm and by *Pelomyxa*, elliptical siliceous bodies secreted by the organism in *Amoeba granulosa*, together with food or its faecal residue. The food, which is either ingested by the pseudopodia, or by the flowing round it of the protoplasm, consists of Diatoms, algae, dead portions of plants, or minute animals; it is sometimes inclosed in a vacuole, sometimes in direct contact with the protoplasm<sup>2</sup>. The latter may be expelled, sometimes inclosed in a vacuole, at any point, but frequently at the posterior end of the moving body in *Nuda*, or at the mouth of the test in *Testacea*. Some *Amoebae*, *Arcella* and *Diffugia proteiformis* possess the power of evolving and reabsorbing at will in the protoplasm bubbles of a gas, apparently Carbon dioxide, by means of which they float to the surface of the waters they inhabit. Non-contractile vacuoles are present in numbers in some *Amoebae*, in *Pelomyxa*, &c. Occasionally they have been observed to disappear slowly, others appearing at another spot as in *Zonomyxa*. Contractile vacuoles may be entirely absent, as in *Pelomyxa* and some others. Their number when present is liable to variation. *Amoebae* very generally have 1-3; many *Testacea* a single large one; others several, in the posterior part of the body, which travel to the mouth of the test to burst. *Arcella* may have as many as twelve in a ring round the body.

The nucleus is vesicular, i. e. provided with a membrane, nuclear fluid and chromatin. The modes in which the chromatin is arranged are very various, and in *Amoebae*, at any rate, have been asserted to characterise the species (Gruber). As to number, some *Nuda* and many *Testacea* are

<sup>1</sup> The old question recurs, do these chlorophyl bodies belong to the organism, or are they symbiotic algae? *Diffugia pyriformis* and *D. lobostoma* are both stated by Leidy to be sometimes colourless, and other species of *Diffugia* may be occasionally green-coloured. The other five species named in the text are always green. When encystation takes place, the chlorophyl granules are included in the encysted mass. But attention may be drawn to fig. 12, Pl. xxi, and figs. 8, 10, Pl. xxvi, of Leidy's monograph, where *Hyalosphenia* and *Heleopera* are respectively shown with tests empty save of scattered chlorophyl bodies. Two explanations only of this fact are possible, (1) that the chlorophyl bodies simply persist for a time after death, (2) that they are algae surviving as symbiotic algae do after the death of their host. The small size of the bodies in question forbids the supposition that they represent the contents of a cyst segmented. It may be noted that some *Nuda* have a great propensity to ingest green algae in quantity, e. g. the *Amoeba binucleata* of Gruber, *Zonomyxa* before its encystation.

<sup>2</sup> *Diffugia pyriformis* perforates and sucks out by means of its pseudopodia the cells of *Spirogyra*; Stokes, Amer. Monthly Micr. Journal, iii. 1882, p. 93. So, too, a naked form (? Amoebine) described by Maupas, A. Z. Expt. ix. 1881, p. 358, and C. R. 89, 1879, p. 252.

constantly uninucleate; *Arcella* and one *Amoeba* (*A. binucleata*) are typically binucleate; some *Amoebae*, *Pelomyxa*, *Zonomyxa*, invariably multinucleate; and in this case the number of nuclei may be constantly limited, e.g. to not more than eight in *Amoeba tertia*, or it may be indefinite and reach a high figure, e.g. some hundreds in *A. quinta* and *Pelomyxa palustris*. But both uni- and bi-nucleate forms may become multinucleate, e.g. *Arcella*, with 6, or even 40, *Diffugia proteiformis* with 40, and the increase is doubtless connected, as in Foraminifera, with reproduction.

Binary fission has been observed in some *Nuda*, and is probably universal among them. Among *Testacea*, in *Pamphagus* (= *Lecythium*) longitudinal fission takes place and includes the delicate test; similarly transverse fission in *Diplophrys Archeri*. But in those *Testacea* where the test is rigid, a process of modified fission or gemmation occurs, observed in all its details in *Euglypha alveolata* by Gruber. A number of concavo-convex plates lay round the nucleus at the base of the test, which was entirely filled by protoplasm: the latter slowly protruded from the aperture of the test, and the loose plates passed by degrees up its sides out of its aperture, and arranged themselves on the surface of the swelling mass of protoplasm. As soon as this mass had attained the same size as the individual from which it was derived, the nucleus of the latter became greatly elongated, and its chromatin filaments arranged in parallel longitudinal lines; it then underwent fission, and one part passed into the new individual. When the transfer was completed, lively currents in the protoplasm were set up in and between the two *Euglyphae*. On their cessation the protoplasm was somewhat retracted from the walls of the tests, pseudopodia were extruded at the line of junction between their apertures, and then came separation. A similar process was observed, incompletely however, in *Cyphoderia*. From the fact that tests are often seen in apposition by their mouths, that loose plates have been seen within empty tests, e.g. in *Quadrula*, Gruber believes that the process, as witnessed in *Euglypha*, is general among *Testacea*, the material of the new test, whether plates, chitinous prisms or foreign bodies, being furnished by the parent. Individuals of *Arcella* are frequently seen in apposition, the shell of one being colourless, or nearly so, indicating its newness. But it is possible that in *Arcella*, and certain that in *Platoum stercoreum*, the new test covering the protoplasmic protrusion is formed by the protrusion itself. Whether conjugation ever really occurs is doubtful; but individuals of *Arcella* and of *Diffugia globulosa*, with tests evidently old, have been found united aperture to aperture. And in the first-named the production by gemmation (?) within the test of amoeboid young, with nucleus and contractile vacuole, and their subsequent escape, has been seen to follow this union (Bütschli). Similar amoeboid bodies, produced by gemmation or repeated fission in *Arcella*, have been traced until they acquired

the characteristic test (Buck, Cattaneo). Conjugation of *Amoebae* has been said to occur<sup>1</sup>.

The formation of colonies, similar to those of *Microgromia* (p. 892, *ante*), takes place in a few instances. In *Pamphagus* (= *Lecythium*) the individuals formed by fission may remain united by a protoplasmic mass from which radiate pseudopodia; or free individuals may fuse, two or more together (= *Gromia socialis*, F. E. Schulze). *Platoun stercoreum* emits from the aperture of the test a mass of protoplasm, which acquires a test itself; new individuals then bud from the bridge uniting the two. So too in the *Plectophrys* of Entz. The colonies (= *Cystophrys ocula*) of *Diplophrys Archeri* are probably produced by fission. Encystation is general. In *Amoebae* stalked brown resting cysts and delicate digestive cysts have been recorded. *Cochliopodium bilimbosum* forms a thick cyst with outer gelatinous layer. *Diplophrys Archeri* has a double cyst, an inner smooth membrane, and an outer tuberculate. The *Testacea*, as a rule, encyst within the test, the aperture of which either collapses (*Placocista*) or is closed by a diaphragm, sometimes laminated, sometimes containing foreign bodies, e. g. diatom-frustules, algal cells, residues of food, &c. The organism itself contracts, and may have a single-walled cyst or a double, both forms occurring in the same species. In the double cyst of *Euglypha* the outer cyst is ovate and composed of hexagonal plates, the inner globular and tuberculate. *Platoun* may quit the test to undergo encystation, and a number of individuals may fuse and then encyst like a single individual.

The Amoebina appear to be cosmopolitan. They are chiefly freshwater; *Amoebae* usually living in mud, &c., Testaceous genera on stones and water plants. Very many of the freshwater forms are found in damp moss; *Amphizonella violacea* and a few *Amoebae* in earth or sand. *Amoebae* occur in putrifying solutions, Testaceous forms rarely do so. A few *Amoebae* are parasitic, both in Vertebrates and Non-Vertebrates. *Endamoeba Blattae* is a constant inhabitant of the large intestine of the cockroach. An *Amoeba* has been found associated with a skin disease of sheep in Australia, and in inflammation of the colon in man<sup>2</sup>. *Phoner gates vorax* (= *Pamphagus*) may live as a parasite in *Cyclops*, Rotifers, Infusoria, and leaves of plants.

<sup>1</sup> Gruber mentions (Z. W. Z. xli. p. 215) that an *Amoeba verrucosa* very commonly contains within it a small specimen of its own species which apparently undergoes no change. For a summary of the accounts given of the formation of amoeboid spores, &c., in different *Amoebina*, see Bütschli's Protozoa, pp. 156-61, and the original authorities to which he refers. It is probable that many of them at least are cases of parasitism, probably of *Chytridiacea* or *Schizomycetes*. *Phoner gates vorax* is said by Buck (Z. W. Z. xxx. pp. 29, 31) to give origin to spores by which animals or plants may be infected. See also note 1, p. 900, *ante*.

<sup>2</sup> The parasitic *Amoeba*, described by Grassi (Rendic. d. R. Ist. Lomb. (2), xiv. 1881, and Atti Soc. Ital. Sc. Nat. xxiv. 1882), from *Sagitta*, &c., like the *Protomyxomyces* of Cunningham (Q. J. M. xxi) are probably Mycetozoa judging from their reproductive phenomena.

Hallez has described by the name of *Arcyothrix Balbianii* an Amoebine found by him in a vessel containing ova of *Ascaris megalcephala*, kept at 25°C. It moves upon a pedal disc, is in shape irregularly globular, has non-contractile vacuoles and one contractile, with pseudopodia of two kinds, an anterior, digitiform, by which food is captured, and two posterior. The latter are of great length and extreme tenuity, beset with minute varicosities, and as a rule bifid. They are usually directed in opposite directions, and Hallez thinks they serve like a moveable net to retain the food. See Mém. de la Société des Sc. &c., Lille, (4), xiv. 1885. With *Arcyothrix* may be compared *Podostoma filigerum*, a freshwater amoeboid form, which possesses, in addition to ordinary pseudopodia, one or two long vibratile processes used for catching food. See Claparède and Lachmann, Études sur les Infusoires, &c., Paris, i. 1858-9, p. 441; Cattaneo, Atti Soc. Ital. Sc. Nat. xxi. 1879.

*Catallacta*. Under this name Haeckel has described a marine organism, *Magosphaera planula*, found by him in 1870 on the coast of Gisoe, a Norwegian island some miles S. W. of Bergen. His account may be briefly summarised as follows. (i) *Egg-like stage*, in the form of spherical cysts 0.7mm. in diameter, attached to the stem of the Alga *Cladophora*. The cyst-membrane is tough, indistinctly laminated, and at the point of attachment either thin or perforated. The contained protoplasm is yellowish; there is a vesicular nucleus surrounded by a zone of granules, often disposed in radiating processes. (ii) *Segmentation stage*. The nucleus and protoplasm undergo binary fission with successive stages, 2, 4, 8, &c., until thirty-two cells are formed. The cells, at first globular, become polygonal from mutual pressure, and are arranged in a single layer. Their outer surfaces give origin to pseudopodial processes which are finally converted into cilia. The sphere now rotates within the cyst. (iii) *Volvox stage*. The sphere is free-swimming, 0.7mm. in diameter. Its constituent cells are pear-shaped, their outer surfaces convex and ciliated, their inner ends attenuated and united centrally; they are imbedded in a clear structureless jelly. Each cell has at its base a slowly pulsatile vacuole. The vesicular nucleus surrounded by granules is median in position. (iv) *Peritrichous Infusorian stage*. The cells are detached, and swim about by means of their cilia. The body of the cell shortens, lengthens, bends from side to side. The contractions of the vacuole are more rapid. The ciliated disc is seen to be vertically striated, and particles of carmine brought to it by the cilia are ingested. (v) *Amoeba stage*. The cells become amoeboid. The Amoeba is characterised by its sharp-pointed pseudopodia protruded singly or in bundles. From time to time a pseudopodium elongates and vibrates slowly. There is a hyaline ectosarc. Carmine particles are ingested at any point of the surface. Haeckel did not succeed in tracing the life-history beyond this stage. But he found creeping over the *Cladophora* Amoebae of various sizes, with pseudopodia of identical character. The nucleus of the larger Amoebae was as large as that of the egg-like stage. The contractile vacuoles were increased in number, the largest specimen observed having five. The Amoebae in question were crammed with diatom-frustules, chlorophyl-bodies, &c. Haeckel supposes that they encyst, and the life-history, as above-detailed, recommences. If this supposition is correct, the dominant phase is an Amoeba, and *Magosphaera* can scarcely be classed with *Flagellata* as it is by Saville Kent. The organism does not appear to have been seen by any subsequent observer. See Haeckel, J. Z. vi. 1871;

Saville Kent, *Manual of the Infusoria*, i. p. 322-4; Allman, *J. L. S.* xiii. 1887, p. 435.

The Amoebina may be classified as follows:—

1. *Nuda* s. *Gymnamoebae*: devoid of a test; in some instances there is a coagulated superficial pellicle, or a complete gelatinoid, chitinoid, or spinulose coat; pseudopodia lobose, pointed, &c.

*Amoeba* (with *Lithamoeba*, *Ouramoeba*, and *Endamoeba*); *Deinamoeba* s. *Chaetoproteus*, covered by minute spicule-like processes; *Hyalodiscus*, no pseudopodia, but the disc flows onwards without change of shape; *Plakopus*, with membranous expansions united together, so as to include spaces, sometimes resembling *Hyalodiscus*<sup>1</sup>; *Dactylosphaerium* with rounded body, digitiform pseudopodia, and green or yellow bodies; ? *Podostoma*, resembles *Dactylosphaerium*, but has two vibratile pseudopodia produced temporarily for the inception of food; *Pelomyxa* (= *Pelobius*), pseudopodia broad, and wave-like, non-contractile vacuoles, and nuclei numerous, gorged more or less with mud, sand, food; *Amphizonella*, a gelatinous envelope pierced by the digitiform pseudopodia, inert; *Zonomyxa*, an elastic chitinoid investment, pseudopodia more or less branched, minute violet vacuoles, many slowly (?) contractile vacuoles and nuclei; *Trichosphaerium* (= *Pachymyxa*), a coat of vertical rods implanted in a membrane, with gaps for the long cylindrical pseudopodia, multinucleate, marine.

2. *Testacea* s. *Lepamoebae*: a test either chitinoid and then flexible or rigid, in some incrustated with foreign bodies, or composed of chitinoid or siliceous plates cemented together or borne by a chitinoid membrane.

(i) *With digitiform, sometimes slightly branched pseudopodia* (= *Arcellina*, Bütschli).

*Cochliopodium*, a flexible cup-shaped chitinoid test, closely adherent to body; *Arcella*, a semi-globular, rigid, complex test (p. 898), dark-brown, with aperture limited by a horizontal flange or rim, ? young forms *Pyxidicula* and *Pseudochlamys*; *Centropyxis* (= *Echinopyxis*), test chitinoid, but aperture and fundus excentric in opposite directions, smooth or spinose, dark-coloured; *Hyalosphenia*, test ovoid or pyriform, compressed, chitinoid, structureless, colourless or yellowish; *Quadrula*, test pyriform, compressed, colourless, composed of squarish chitinoid (? siliceous) plates in transverse rows; *Nebela*, test pyriform, compressed, with or without appendages, typically composed of a chitinoid membrane with large and small oval or rod-like siliceous plates, sometimes intermixed; *Heleopera*, test ovoid, compressed, chitinoid with a reticulation of dotted lines; *Diffugia*, test of variable shape, globular to elliptical, often provided with processes, commonly compressed, aperture terminal or sub-terminal, composed of very various foreign bodies cemented together,—such as sand-grains, diatoms, frustules, or of a chitinoid membrane with scattered foreign bodies, or oval and rod-like bodies (as in *Nebela*); *Lecquereusia* = *Diffugia spiralis*, retort-shaped, with internal septum (p. 898); *Petalopus*, ? a test, pseudopodia ending in plate-like expansions; *Arcellina*, test chitinoid, with a produced aperture and pores opening each on the summit of a tubercle, (?) globular, ovate, as large as a hemp-seed, marine.

<sup>1</sup> *Plakopus* and *Hyalodiscus* are supposed by Leidy to be identical; so too by Mereschkowski (*A. M. A.* xvi. pp. 194-5). Zopf believes them to be the same as Klein's *Vampyrella pedata*, a *Proteomyxan*.

(ii) *With flose pseudopodia, sometimes branched, rarely anastomosing (= Euglyphina, Bütschli).*

(a) A single aperture: *Pamphagus* (= *Plagiophrys*, *Lecythium*, *Phonergates*?), test spheroidal or ovate and compressed, chitinous, flexible, colourless, adapted to the body; *Pseudo-diffugia* (= *Pleurophrys*?), test thin, chitinous, with a variable proportion of fine sand, &c.; *Platoum* (= *Troglodytes*, *Chlamydothrys*), test chitinous, vasiform, elliptical or round in section, somewhat flexible, freshwater, damp earth, and putrifying substances; *Plectophrys*, like *Platoum*, but test fibrous; *Cyphoderia*, test retort-shaped, chitinous, with minute oval plates; *Campascus*, similar to *Cyphoderia*, but incrustated with fine sand and two basal horn-like processes; *Euglypha*, test composed of oval or hexagonal siliceous plates disposed in longitudinal rows, with or without minute spines, ovoid, sometimes compressed; *Placocista*, test oval, hyaline, colourless, composed of overlapping oval plates, compressed, edges and base beset with moveable spines; *Assulina*, test compressed, oval or spherical, composed of oval or hexagonal plates, brown, aperture transversely elliptical, with ragged edges; *Trinema*, test hyaline, pouch-like, with oblique longitudinal axis, and sub-terminal beaded aperture, homogeneous, or composed of oval plates, with frequently beaded borders; *Sphenoderia*, test globular or oval, sometimes slightly compressed, with a short broad neck, composed of overlapping oval, or large hexagonal plates.

(b) With two apertures, i. e. amphistomatous: *Diplophrys*, globular or fusiform, test, if present, very delicate, sometimes with foreign bodies, one or more yellow or red oil-globules, sometimes colonial, freshwater, and in dung; *Ditrema*, test hyaline, yellowish, thick and rigid, edges of apertures somewhat inflected; *Amphitrema*, test oval, incrustated with foreign bodies.

Bütschli, Bronn's Klass. und Ordnungen des Thierreichs, i. 'Protozoa' (under Rhizopoda), pp. 3-229; Leidy, 'Freshwater Rhizopoda of North America,' U. S. Geological Survey of the Territories, Washington, xii. 1879, pp. 23-232; *Summaries*, by Archer, in Q. J. M. xvii. 1877<sup>1</sup>.

*Pelomyxa villosa*, *Amoebae*, 'Studien über Amöben,' Grüber, Z. W. Z. xli. 1884; *Amoeba tentaculata*, *A. actinophora*; 'Beiträge,' &c., Id. ibid. xxxvi. 1882, cf. A. N. H. (5), ix., and Wallich, 'Critical Notes,' A. N. H. (5), xvi; *Trichosphaerium* (= *Pachymyxa*), *Amoeba obtecta*, Id. ibid. xxxviii. 1883, pp. 46, 55, 330; cf. A. N. H. (5), xi; *Longicauda* s. *Ouramoeba*, *Pelomyxa*; Korotneff, A. Z. Expt. viii. 1879-80. *Amoeba cellarum*, Joseph, cf. Naples Zool. Jahresbericht, 1884, A. Protozoa, p. 131. *Lithamoeba*, E. Ray Lankester, Q. J. M. xix. 1879. *Endamoeba Blattae*, Leidy, A. N. H. (5), v. 1880; Bütschli, Z. W. Z. xxx. 1878, p. 273. *Amphisonella*, with *terricolous Amoebae*, Greeff, A. M. A. ii. 1866. *Zonomyxa*, Nüsslin, Z. W. Z. xl. 1884. *Nebelidae*, Taránek, Naples Zool. Jahresbericht, 1882, A. Protozoa, p. 88; cf. Id. ibid. 1881, p. 100. *Petalopus*, Claparède and Lachmann, Études sur les Infusoires, &c. i, 1858, p. 442. *Arcellina*, du Plessis, SB. Phys. Med. Ges. zu Erlangen, 1876. *Plectophrys*, Entz, Naturhist. Hefte des Nation. Museum zu Buda Pesth, i. 1877. *Pleurophrys* (= *Pseudodiffugia*) *Genuensis* (marine), Grüber, Nova Acta, xlv, 1884, p. 486.

<sup>1</sup> For the synonymy of the various genera, which is very difficult, and cannot be fully entered into in such a work as this, see the list of genera in Bütschli, op. cit. pp. 176-8, 183-8; also Leidy, op. cit. under the different genera and in his list of authors, pp. 297-319, in which he gives not only the titles of their works, but the names and synonymy of the species described.



*Amphistomatous genera.* *Diplophrys Archeri*, Hertwig and Lesser, A. M. A. x. 1874, Suppl. p. 139; Schulze, A. M. A. xi. 1875, p. 127; = *Cystophrys oculatea*, Archer, Q. J. M. x. 1870, p. 112; cf. Leidy, op. cit. *supra*, p. 256; *D. stercorea*, Cienkowski, A. M. A. xii. 1876, p. 44. *Ditrema*, Archer, Q. J. M. xvii. 1877, p. 336. *Amphitrema Wrightianum*, Archer, Q. J. M. x. 1870, p. 122; *A. stenostoma*, Nüsslin, Z. W. Z. xl. 1884, p. 717.

*Protoplasm, its layers:* Gruber, Biol. Centralblatt. vi. 1886-7; cf. Z. W. Z. xli. p. 196; *villous patch*, Gruber, Z. W. Z. xli. 1885, p. 199. *Formation of gas-bubbles*, Engelmann, Arch. Néerl. des. Sc. exactes. et Nat. iv. 1869; Id. Z. A. i. 1878; Entz, *ibid.*; du Plessis, Bull. Soc. Vaudoise Sc. Nat. xv; Bütschli, A. M. A. xi. 1875, p. 463; von Kennel, Arb. Zool. Zoot. Inst. Würzburg, vi. 1883, p. 271.

*Nucleus*, Gruber, 'Kerntheilung,' &c. Z. W. Z. xl. 1884, pp. 122-31; in *A. proteus* (= *quinta*), Id. Z. W. Z. xxxviii. 1883, p. 382; cf. Brandt, Biol. Centralblatt. iii. 1883-4, p. 389; Gruber, *ibid.* p. 542. *Multinucleate Amoebae*, = *A. prima*, &c. Gruber, Z. W. Z. xli. pp. 193-207; cf. Id. Biol. Centralblatt. iv. 1884-5, p. 710; *Diffugia proteiformis*, R. Hertwig, J. Z. xi. 1877, p. 346.

*Fission of Amoeba polypodia*, F. E. Schulze, A. M. A. xi. 1875, p. 592; of *Euglypha alveolata*, Gruber, Z. W. Z. xxxv. 1881<sup>1</sup>; cf. Leidy, op. cit. *supra*, p. 212; of *monothalamous Rhizopods*, Gruber, Z. W. Z. xxxvi. 1882. *Budding in Arcella*, Buck, Z. W. Z. xxx. 1878, p. 4; Bütschli, A. M. A. xi. 1875; Cattaneo, Atti Soc. Ital. Sc. Nat. xxi. 1879. *Conjugation: in Arcella*, Bütschli, A. M. A. xi; in *Diffugia globulosa*, Jickeli, A. N. H. (5), xiv. 1884; *fusion of marine Amoebae*, Kühne, Untersuch. über Protoplasma, Leipzig, 1864, p. 41; Maggi (quoted by Bütschli), Rendic. d. R. Istit. Lomb. ix. p. 436.

*Encystation. Amoeba*, Nüsslin, Z. W. Z. xl. 1884, p. 721; Fisch, Z. W. Z. xlii. 1885, p. 115; Wallich, A. N. H. (3), xii. 1863, p. 336; Carter, *ibid.* (3), xiii. 1864, p. 20; Lüders, Botan. Zeitung, xviii. 1860. *Plakopus*, F. E. Schulze, A. M. A. xi. 1875, p. 351. *Cochliopodium bilimbosum*, Auerbach, Z. W. Z. vii. 1855-6, p. 387. *Pseudochlamys* (= *Arcella*), Archer, Q. J. M. xvii. 1877, p. 108. *Phonergates* = *Pamphagus*, Buck, Z. W. Z. xxx. 1878, pp. 27, 31. *Platoum stercoreum*, Cienkowski, A. M. A. xii. 1876, p. 43. *Euglypha*, Hertwig and Lesser, A. M. A. x. 1874, Suppl. p. 127. *Diplophrys Archeri*, Cienkowski, op. cit. p. 45.

*Colony formation. Pamphagus*, = *Arcella hyalina*, Fresenius, Abhandl. Senck. Ges. ii. 1856-8, pp. 221-2; = *Gromia socialis*, Schulze, A. M. A. xi. 1875, p. 121; = *Phonergates* (?) Buck, Z. W. Z. xxx. 1878, p. 23. *Platoum stercoreum*, Cienkowski, A. M. A. xii. 1876, p. 42. *Plectophrys*, Entz, *supra*. *Diplophrys Archeri*, see Hertwig and Lesser, Schulze, *supra*.

*Parasitic Amoebae. A. parasitica*, von Lendenfeld, Proc. Lin. Soc. New South Wales, x. 1886. *A. coli*, Leuckart, 'Parasites of Man,' transl. by Hoyle, Edinburgh, i. 1886, p. 186. *Gigantic Amoeba in chronic enteritis of Egypt*, Kartulis, Virchow's Archiv für Pathol. Anat. und Physiol. 99. 1885; cf. also note 2, p. 903, *ante*. *Phonergates vorax* (= *Pamphagus*), Buck, Z. W. Z. xxx. 1878, p. 20 et seqq.

<sup>1</sup> In a paper published in the M. J. xiii, (1), as this sheet goes to press, Blochmann states as to *Euglypha alveolata*, (1) that the parent may towards the end of fission withdraw all protoplasm from the test of the new individual, leaving its nucleus dead; (2) that conjugation occurs, as a rule temporary, in one instance, however, two individuals giving origin to a third and unusually large individual, being themselves used up in the process.

## CLASS MYCETOZOA.

*Rhizopod Protozoa* (?) with coated spores s. *chlamydo-spores*, giving origin to *amoebulae*, which may or may not become temporarily *zoospores* or *flagellulae*. The *amoebulae* grow and multiply by binary fission; they then either collect together into a mass or aggregation-plasmodium, every *Amoeba* in which is converted into a *chlamydo-spore*; or they fuse together and form a multinucleate fusion-plasmodium, which continues to grow, but eventually encysts and is converted into *chlamydo-spores*. Inhabiting moist and decaying wood, vegetable debris or dung.

The spore of a Mycetozoan is a minute spherical or oval body, becoming concavo-convex if dried, inclosed in a membrane or episporium. This membrane may be smooth or ornamented in various ways, generally colourless, violet or violet-brown in the *Calcariaceae*, yellow or red in *Trichiaceae*, &c. The contained protoplasm is dense and variably granular; it lodges a single nucleus, or two if the spore is of unusual size. When the spore is suitably moistened and begins to germinate, two contractile vacuoles make their appearance, and the episporium bursts as the protoplasm swells. As soon as the latter is set free, it undergoes in *Ceratium* (i.e. *Exosporea*) binary fission repeated three times, the products of fission remaining together until the process is complete. But as a rule it commences life as an *amoebula*, which moves actively about and secretes a pellucid coat. Except in the *Sorophora* this *amoebula* develops a cilium and assumes a temporary zoospore condition, and alternate phases, amoeboid and flagellate, may recur. The *amoebula* or *Myxamoeba* multiplies by binary fission, but when it does so it becomes spherical and loses its contractile vacuoles. If food is wanting, or other conditions of life unfavourable, e.g. a lack of moisture, the *Myxamoeba* contracts into a sphere and develops a more or less firm membrane. This resting phase is known as the microcyst. When the conditions of life again become favourable, the encysted protoplasm perforates the membrane at some one spot and creeps out.

After a period of growth the *Myxamoebae* begin to gather together, and they either retain their individuality or fuse. The first of these two alternatives obtains in the *Sorophora*. The collected *Myxamoebae* constitute an aggregation- or pseudo-plasmodium. The heap they form assumes a determinate shape and is known as a sorus. The *Amoebae* which make it up either collect by degrees, and are transformed as they collect into *chlamydo-spores*, as in *Copromyxa*, or they collect quickly. Certain of them are then disposed in one or more linear series, enlarge, become vacuolate, acquire a cellulose membrane, and form a stalk or peduncle upon which the remaining cells are grouped. These cells are each converted into a *chlamydo-spore*.

Union of the *Myxamoebae* in a fusion-plasmodium is characteristic of the two other sub-groups of Mycetozoa, the *Exo-* and *Endo-sporea*. Two or three unite first of all; the large *Myxamoeba* thus formed serves as a focus of attraction, and by the repeated addition and fusion of other *Myxamoebae*, it eventually becomes a fusion-plasmodium, or simply a plasmodium. The plasmodia vary in size; the majority are either just visible or just invisible to the naked eye; those of the *Physareae*, however, cover surfaces of lin. to 1ft. They have as a rule the shape of a branched tree or network of moving protoplasm. *Lycogala epidendron* is an exception; it has the shape of cylindrical, varicose, slightly branched threads. Movement takes place by the extension of protoplasmic processes in one direction and their withdrawal in other quarters. If they should happen to be extended simultaneously and energetically in different directions, the result is a rending of the plasmodium into a number of separate portions. These portions, like the portions formed by artificial section of a plasmodium, behave in all ways as so many plasmodia. From a structural point of view, a plasmodium consists of a clear, dense superficial protoplasm, with a granular fluid central portion or medulla. The granules are of various kinds; some of them in the *Calcariaceae*, e.g. *Fuligo*, or the 'flowers of tan,' consist of Calcium carbonate. Yellow, red, violet, or brown pigment is met with in some instances. Vacuoles are present, and are sometimes contractile. The nuclei of the *Myxamoebae* persist. The surface is clothed by a soft, sticky, pellucid coat or hypothallus, to which earth and some other foreign bodies adhere, and which may be left behind as a trail in the onward movement of the plasmodium. If the conditions of life become unfavourable before maturity is attained, the plasmodium passes into a resting-phase known as the macrocyst, or thick-walled cyst. It breaks up into portions of unequal size, which become globular and develop in succession two membranes. The encysted protoplasm is only set free after a prolonged soaking of the macrocysts. But if the plasmodium is ripe for sporulation, its resting-phase, the sclerotium, has a different character. All processes are withdrawn by degrees, whilst foreign bodies are extruded and the granules of the protoplasm evenly distributed. The mass becomes rounded, and is resolved into minute globular or polyhedral cells; it becomes in consistence wax-like and finally brittle. Its cells have one or more vacuoles, and in two instances a cellulose membrane. They are bound together by an outer homogeneous layer covering the mass. If placed in water the sclerotium swells; its cells acquire one or more contractile vacuoles; their membrane, if present, is dissolved; the liberated portions of protoplasm become amoeboid and fuse to reconstitute the plasmodium.

As soon as a plasmodium has attained its definitive growth, it comes to the surface of the decaying wood, &c., whatever it inhabits, and proceeds

to form spores. This it does, either on the outer surface of a sporospore s. conidiophore, as in the *Exosporea*, or as in the *Endosporea*, within one or more sporocysts or sporangia, which are derived in most instances from a single plasmodium, but in a few, e.g. *Fuligo*, from a number of united plasmodia, or, as they are termed, an aethalium.

In *Ceratium*, the sole genus of *Exosporea*, the plasmodium first collects into a mass, and then grows up into a number of processes or conidiophores. Mass and processes alike are formed of a watery jelly supporting a network of granular protoplasm. This network traverses the whole substance of the mass; it passes into the processes as they develop and in them is confined to a superficial layer. It is finally resolved into polyhedral cells. Each cell grows out into a stalked sphere, protected by a delicate membrane. The protoplasm is concentrated by degrees in the sphere, which is converted into a spore by the development of a special membrane. The spores are detached with ready ease from their stalks, and the supporting jelly dissolves as soon as it is function-less.

The plasmodium of the *Endosporea* gives origin to a single sporocyst, or by division to many. It gathers together, develops a superficial coat or membrane, and extrudes at the same time all foreign bodies, pigment and Calcium carbonate if present<sup>1</sup>. The resulting sporocyst has generally the shape of a sessile or stalked vesicle; in a few instances it is tubular, slightly branched, or even reticulate, and then frequently receives the name of plasmodiocarp. It is attached to whatever it rests upon by the dried mucoïd envelope or hypothallus, which forms either a thin flat expansion, a ridge, or peduncle. The protoplasm, freed from whatever is foreign to it, is colourless, and from it are derived the capillitium and the chlamydo-spores. The former consists of either stereonemata or coelonemata—stereonemata, that is to say cords cylindrical or flattened, solid, or at the utmost traversed by a fine canal; coelonemata, or tubes with thin walls and wide cavities. Both structures consist of a cuticularised membrane, and the stereonemata of the *Calcariaceae* include pigment and Calcium carbonate. As to the mode in which the capillitium is disposed, the stereonemata are either variously shaped thickenings of the walls of the sporocyst<sup>2</sup>, or they are branching strands crossing its cavity and attached by their ends to its walls; the coelonemata take one of three forms, tubes, or elaters, closed at their ends and lying free as in *Trichiaceae*, a narrow-meshed expansile reticulum with its ends attached to the walls of the sporocyst, as in most *Arcyriaceae* and the *Perichaenaceae*, or a branched structure with the cavity of its constituent tubes varying in width from point to point, as in the *Reticularaceae* and *Lycogala* among *Arcyriaceae*.

<sup>1</sup> In *Didymium* the Calcium carbonate dissolves, and reappears on the outer surface of the sporocyst as a crystalline deposit.

<sup>2</sup> De Bary does not apply the term capillitium to these thickenings.

The elaters are thickened spirally, the tubes of a reticulum by circular ridges, by spines, tubercles, or a network of lines. As soon as the capillitium is established, the nuclei of the protoplasm remaining multiply, the protoplasm itself segments, a portion to each nucleus, the nucleated portions become rounded, acquire a membrane, and so pass into chlamydo-spores.

The sporocyst is now fully formed. It has a membranous wall, single or double, of varying thickness, white, black, violet, red, yellow, brown, sometimes smooth, sometimes ornamented with ridges or tubercles. When it has a peduncle, that structure is also membranous, hollow, closed or open at its apex, empty, or filled with various descriptions of useless materials. A drying process sets in, and the sporocyst becomes brittle and breaks up in different ways. When the capillitium is a system of thickenings of the membrane of the sporocyst, it prevents the collapse of the latter; when it traverses its cavity, it not only affords strength, but there is reason to believe that it executes hygroscopic movements, aiding partly in the rupture of the walls, partly in the scattering of the spores. Such is the case to a very marked degree with the elaters, and the expansile tubular reticulum of the *Arcyriaceae*, &c. (*supra*).

The aethalium, or spore-forming mass, produced by the aggregation or coalescence of a number of plasmodia, is met with in thirteen genera only, belonging to different families of *Endosporea*. It takes various shapes, a disc, cake (*Fuligo*), ball, or a miniature bush. In *Fuligo* it may attain a great size, as much as 1 ft. long and 1 in. thick. Structurally it may consist of a number of prisms set side by side, of interwoven and anastomosing tubes (*Fuligo*), of branched stems, or finally the parts may so completely fuse as to show no trace of their complex structure. It is often naked, sometimes protected by a thin membrane, or in *Fuligo* and *Lycogala* by a cortex composed in the first-named of the dried hypothallus, and the collapsed superficial tubes filled with Calcium carbonate and yellow pigment, the protoplasm having withdrawn to the central tubes. The capillitium of an aethalium follows the type of the family to which it belongs.

As to the physiological relations of the Mycetozoa, it has been shown that they consume oxygen energetically, are repelled by light, attracted by a supply of food or by moisture, provided that the plasmodium is not ripe for sporulation, when it moves to drier spots. The *Sorophora* for the most part inhabit dung, one or two decaying vegetable matter; one of them, *Dictyostelium mucoroides*, has been grown in solutions of Hippuric acid and Potassium urate. The remaining Mycetozoa live in moist rotting wood, leaves, or other vegetable *débris*. It is stated that the spores, whether *amoebulae* or *flagellulae*, but especially the former, take up foreign bodies, e. g. Bacteria; so too the plasmodium ingulfs very various materials.

But it is not possible to say how far these foreign bodies are utilised as food. *Fuligo* is known to possess a peptic ferment, and all plasmodia one that dissolves cellulose or cuticularised membranes, e. g. those of macrocysts. It has been shown that they do not all react in the same way towards the same body, e. g. carmine, one taking it up and acting upon it, the other leaving it alone and not acting upon what few particles it does ingest.

By De Bary, the greatest authority on the class, the Mycetozoa have long been placed outside the limits of the vegetable kingdom. Whatever resemblances they may possess to various fungi is, he insists, superficial, certain *Chytrideae* excepted; but the latter, according to De Bary, have no plasmodia. On the other hand their peculiarities may be found in various undoubted Protozoa. Supposing them to be saprophytic, so e. g. are some *Flagellata* under certain conditions (p. 842); fusion to form plasmodia recurs in some Proteomyxan *Monadineae*, as to the animal nature of which there can be no doubt; so too in the same group the formation of sporocysts and chlamydospores (p. 915); if the nature of the membrane of the sporocyst be objected on the score that it sometimes stains blue with Iodine and Sulphuric acid, indicating the presence of cellulose, similar membranes are met with in some *Monadineae* (note 2, p. 919), not to mention other Protozoa and animals higher in the scale. There can be little reasonable doubt that the members of the class are Rhizopoda, adapted to a sub-aerial and perhaps saprophytic life.

The Mycetozoa, as defined above, are termed by Zopf, quoted *infra*, *Eumycetozoa*; the Mycetozoa, as he uses the term, include also the *Monadineae* (p. 917). The classification of the *Eumycetozoa* = *Mycetozoa*, as given by Zopf, is as follows:—

I. *Sorophora* (= *Acrasieae*, van Tieghem): no flagellula phase; pseudo- or aggregation-plasmodia; the sporocyst replaced by a sorus. *Copromyxa*, *Guttulina*, *Dictyostelium*, *Acrasis*, *Polyspondylium*<sup>1</sup>.

II. *Endosporea*: a flagellula phase; true or fusion-plasmodia; spores formed in sporocysts; a capillitium.

(i) *Peritricheae*: capillitium peripheral (see p. 910 and note 2), formed by stereonemata.

(ii) *Endotricheae*: capillitium traversing the cavity of the sporocyst.

(a) *Stereonemea*: capillitium formed by stereonemata, e. g. *Calcariaceae*.

(b) *Coelonemea*: capillitium formed by coelonemata, e. g. *Trichiaceae*.

III. *Exosporea*: a flagellula phase; true or fusion-plasmodia; spores borne upon sporophores s. conidiophores (p. 910): *Ceratium*.

De Bary, Comparative Morphology, &c. of the Fungi, Mycetozoa and Bacteria, translated by Garnsey, Oxford, 1887, pp. 421-53; Zopf, Die Pilzthiere oder Schleimpilze, Encyclopaedie der Naturwissenschaften, Breslau, Handbuch des Botanik, iii. pt. 2, 1884.

<sup>1</sup> The *Protomyxomyces coprinarius* of D. D. Cunningham, Q. J. M. xxi. 1881, which inhabits the intestinal canal and dung of various animals, is a Sorophoran.

## CLASS LABYRINTHULIDEA.

*Rhizopod Protozoa* (?) with filamentary tracks and travelling spindles.

A group *Labyrinthuleae* was established, in 1867, by Cienkowski for the reception of *Labyrinthula*, an organism discovered by him growing upon piles in the harbour of Odessa. A somewhat similar organism, *Chlamydomyxa*, has been found by Archer in Westmeath and Connemara, infesting the leaves, &c. of *Sphagnum* and other freshwater plants; it has also been recently observed by Ray Lankester at Pontresina in the Engadine.

There are two species of *Labyrinthula*, *L. vitellina* and *L. macrocystis*. The former lives at the level of the watermark, and in the resting condition appears as reddish-yellow masses about the size of a pin's head. If such a mass is placed in water for twenty-four hours, it passes into a motile condition; and when examined under the microscope, is seen to consist of a central mass whence there extends towards the periphery of the drop of water an open network of filamentary tracks. Moving along these tracks at a rate of about  $\frac{1}{40}$  -  $\frac{1}{80}$  mm. per minute are yellow spindles which collect here and there into outlying groups. The central mass consists of a finely granular matrix imbedding numbers of yellow or brick-red globular cells .012 mm. in diameter, with a nucleolated nucleus and an envelope which stains brown with Iodine. When fresh they are stained blue by the same reagent. These cells assume a spindle-shape and wander from the central mass, which undergoes meanwhile no visible change along the filamentary tracks, as above stated, until in a few hours' time they have all, or at any rate the majority of them, quitted it. They multiply by binary fission. The filamentary tracks are glassy in appearance, homogeneous or fibrillate, rigid and unchanging; whether tubular or composed of fibrils lying at some distance apart, Cienkowski could not determine. Whatever their nature, they appear to consist of the same substance as the matrix of the central mass, not protoplasmic, but rather a secretion. Cienkowski states that after the wandering of the spindles is completed, the tracks become invisible in some places, in others, where there are isolated spindles or masses of spindles, gelatinous; that individual spindles or naked spindle-masses are capable of forming tracks, and that when the organism grows under water the amount of matrix is greatly increased. The motile condition of the organism was found naturally existing among the colonies of Campanularians and on the eggs of *Tergipes*.

*L. macrocystis* lives at some distance above the watermark. It differs from the foregoing species in the following particulars. Its resting-phase has the form of yellowish or white vermiform masses. Its cells are larger, .018-0.025 mm. in size, their nuclei more sharply defined, their contents more granular, colourless or feebly yellow, and not stained blue by Iodine. It

passes readily into a quiescent encysted stage. The cells then enlarge, turn more granular, and display a more pronounced tint; finally they become ovate and  $\cdot 035$  mm. long. Each of them secretes a smooth thick membrane, whilst the matrix becomes firm and superficially granular. If such an encysted mass is placed in water each cell in about six weeks' time divides into four parts, which are set free as motionless globular cells by the gradual absorption of the cyst-membrane. The cells appear to change into spindles which, whether single or in masses, produce filamentary tracks along which they move<sup>1</sup>.

*Chlamydomyxa* like *Labyrinthula* has a resting and a motile phase. It has, however, in the former condition the power of growing. The smallest encysted examples have the form of minute spherical bodies of a green colour, with or without a red granule, inclosed by a delicate cellulose membrane. Such bodies occur free when they grow for some time without losing their spherical shape, or else lodged within the cells of, e. g. a *Sphagnum* leaf. In this case they elongate, but at last force their way outwards to the surface of the leaf where they protrude. The protrusion increases in size by degrees, and finally the protoplasm may be withdrawn entirely from the portion of the cyst which remains within the leaf. During growth fresh laminae of cellulose are continually laid down within the membrane first formed. Encysted examples with the structures described are most variable in shape. The contents of a cyst may divide into equal or unequal parts, everyone of which surrounds itself with a cellulose membrane. The number of red granules increases, and it not infrequently happens that some of them become inclosed within layers of cellulose producing internal wart-like growths. In some instances the cysts acquire a ruddy hue. The motile condition has been seen only by Archer. The envelopes of the cyst burst at some one point, its contents push forth a stem which branches and spreads, the branches in turn giving origin to delicate, widely-extended, and ramified filamentary tracks. The last-named, though flexible, do not change their shape or do so but slowly. The contents of the ruptured cyst are, according to Archer, a hyaline protoplasm with an amorphous greenish substance, yellow-green granules, red granules, and great number of pale-blue globules. There is no nucleus but the stem and its branches possess a number of contractile vacuoles. The pale-blue and non-nucleated globules transform themselves into spindles which wander along the tracks; they change their shape when they reach a point where a track bifurcates. Their motion may cease or become retrograde, and they may, as in *Labyrinthula*, collect in outlying masses. The whole structure, tracks, spindles, branches, and stem may be withdrawn into the cyst; and it may happen that outlying

<sup>1</sup> Brandt has suggested that the yellow cells of the Radiolarian *Acanthometra tetracopa* are identical with the spindles of *L. vitellina*; Mitth. Zool. Stat. Naples, iv. 1883, p. 239.



masses are cut off and left behind. From Archer's statement it appears certain that *Chlamydomyxa* has the power of digesting such organisms as *Cosmarium* which may be carried with the protoplasm into the cyst.

Though there are undeniable resemblances between *Labyrinthula* and *Chlamydomyxa*, yet there are certain differences which make it possible that the two ought not to be classed together. In one the spindles are nucleated cells, the matrix and tracks apparently a secretion. In the other the spindles are non-nucleated, the tracks, the branches, and stem from which they spring protoplasmic; there are contractile vacuoles and other organisms may serve as food<sup>1</sup>.

*Labyrinthula*, Cienkowski, A. M. A. iii. 1867; cf. Q. J. M. xv. pp. 121-4. *Chlamydomyxa*, Archer, Q. J. M. xv. 1875; Geddes, *ibid.* xxii. 1882; at *Pontresina*, Ray Lankester, Nature, xxxiv. 1886, p. 408.

#### PROTEOMYXA.

The assemblage of forms, for the most part inhabitants of the freshwaters, gathered together under the designation Proteomyxa (Ray Lankester), are characterised mainly by the negative feature that they cannot be assigned with certainty to any of the foregoing classes; nor is it possible to frame any satisfactory and common definition of them as a whole. The discovery of new forms, and a better acquaintance with some of those already known, will in time lead, without doubt, to their dispersal.

A certain number of Proteomyxans have a Heliozoon-like aspect, which they may exchange for an irregular one; they may be colonial or capable of indefinite growth. Others have been grouped by Zopf as *Monadineae*. The typical feature of these forms is that they have two kinds of cysts, one (zoocyst) within which the organism breaks up into spores, the other (sporocyst) within which it contracts, encysts perhaps again, but eventually, assuming a spherical or oval shape and acquiring a membrane, passes into the state of a resting spore or chlamyospore, usually single. The spores originating from the zoocysts are either *flagellulae* s. *zoospores*, or *amoebulae*; hence a subdivision of the *Monadineae* into the *M. zoosporeae* and the *M. azoosporeae*. But in the *M. zoosporeae*, with the exception of *Colpodella*, the zoospore passes into an *amoebula* which grows in size and finally encysts. Fusion of Amoebae into plasmodia is known to occur in some instances; and, partly on the strength of this fact, and partly on account of the

<sup>1</sup> Ray Lankester is of an opinion that the spindles in the two genera above-described are really nuclei. Q. J. M. xix. 1879, p. 481.

character of the spores (*flagellulae* and *amoebulae*), the formation of sporocysts or free chlamydo-spores, Zopf relegates the *Monadineae* to the Mycetozoa as 'lower Mycetozoa.' But they are all distinctly animal in their nutrition, with two exceptions, *Haplococcus* which lives between the muscle-fibres of swine, &c., and *Bursulla* which flourishes in horse-dung. Another difference, as compared with the Mycetozoa, is the fact, pointed out by Zopf himself, that the higher Mycetozoa have nothing to correspond to the zoocyst phase. As will be seen from the account given below, our knowledge of some of the forms is very defective, and others do not follow completely the typical life-history.

There remain some Amoeboid organisms about which little is known, differentiated from one another by shape, character of the pseudopodia, mode of locomotion and of occurrence. Many of them, like some of the forms of Heliozoon-aspect, are non-nucleate, or are said to be non-nucleate. The latter were grouped together by Haeckel as *Monera*, but it is doubtful how far the distinction, even if found to hold good, justifies such an association<sup>1</sup>.

The following epitome of the Proteomyxa is given principally for the use of persons who may take an interest in these simple organisms.

*Heliozoon-like genera; Nuclearia, Myxastrum, Archerina, Monobia, Myxodictium.* The first-named is freshwater, globular when in a state of rest, elongate and somewhat lobed when in motion. Its pseudopodia are long, pointed and branched at an acute angle, radiating or confined to a portion of the body when in motion. It is frequently surrounded by a hyaline gelatinous layer beset with minute rods. It has one or many nuclei, and a number of slowly contractile vacuoles. It lives on *Alga*-cells, the contents of which it sucks out. A double cyst has been observed in one of the two species. *Myxastrum* is marine; it is globular with radiant pseudopodia, long, pointed, in one species sometimes branched at an acute angle, and anastomosing. *M. Liguricum* is multinucleate, *M. radians* is said by Haeckel to be non-nucleate. The latter forms a structureless membraneless cyst, within which the protoplasm segments into a number of radially arranged oval spores. Each spore acquires a siliceous investment, and gives exit to a minute *Myxastrum*. *Archerina* is freshwater and non-nucleate. It is *Actinophrys*-like, and  $\frac{1}{2000}$  of an inch in diameter. It has motionless radiant pseudopodia, one or more non-contractile vacuoles, and a bifid or double chlorophyll body. The chlorophyll body divides into four and does so repeatedly; at the same time the protoplasm increases in amount,

<sup>1</sup> The evidence for the complete absence of a nucleus rests in some instances on the authority of observers, working with full command of the most modern histological methods, e. g. Ray Lankester on *Archerina*, Gruber on *Protamoeba vorax*. See also a paper by Brandt, 'Microchemische Untersuchungen,' S.B. Physiol. Ges. Berlin, 1879. Gruber has pointed out that non-nucleate parts of individuals may grow in size, heal a wound, carry on to complete development an organ which has begun to develop, but they are incapable of starting the development of an organ and of reproduction; see Biol. Centralblatt. iii. p. 580, and A. N. H. (5), xvii. p. 482. But non-nucleate organisms such as *Archerina* or *Monobia* are capable of reproduction. The cases are therefore not parallel.

and becomes irregular in shape; it gives off lobose processes while the radiant pseudopodia are confined to a few spots. Ingestion of *Bacteria* was observed. The colonies thus produced appear to grow till food is scarce, and then to break up. Each chlorophyl body carries away with it a portion of protoplasm. Large encysted individuals occur; the cyst membrane is resistant. The chlorophyl may be disseminated through the encysted mass. The two remaining Heliozoon-like genera are also both non-nucleate, but are characterised by the fact that they form colonies. *Monobia confluens* lives in freshwater, and perhaps damp earth; its pseudopodia are radiant with minute varicosities. It multiplies by fission, and the two individuals thus formed may remain united by a bridge of protoplasm. Union may take place also by the pseudopodia. *Myxodictum sociale* is marine; the colony is formed by the union of the branching and anastomosing pseudopodia.

*Monadineae*. Forms typically characterised by having two kinds of cysts, a zoocyst in which the organism undergoes division into spores either *flagellulae* or *amoebulae*, a sporocyst in which it becomes a resting-spore or chlamydospore. Zopf makes two subdivisions, *M. zoosporeae* and *M. azosporeae*<sup>1</sup>.

*M. zoosporeae*. The zoocyst gives origin to *flagellulae* s. *zoospores*. There are three families.

The first, *Pseudosporeae*, is characterised by the fact that the chlamydospore is formed in a sporocyst. There are four genera. *Colpodella pugnax* is sickle-shaped, with a single cilium, nucleus and contractile vacuole. It perforates the membrane of the green Flagellate *Chlamydomonas pulvisculus* and sucks out its contents. Next it comes to rest, becomes globular, forms a double membrane, an outer thick, and an inner thin; then segments into a number of zoospores which are set free by the bursting of the thick membrane, the protrusion and gelatinisation of the thin. When it passes into a chlamydospore it becomes globular, secretes a membrane and then contracts into a small globular or ellipsoidal body. The genus *Pseudospora* differs from *Colpodella* in that the zoospore passes into an *Actinophrys*-like *Amoeba*. *Ps. aculeata* is parasitic in the cells of the algal *Oedogonium*; *Ps. parasitica* in those of *Spirogyra*; *Ps. Bacillariacearum* in Diatoms; *Ps. maligna* in the protonemata of the Moss *Hypnum*. The resting-spore is known in the two first named. *Protozonas* is distinguished from the foregoing by forming fusion-plasmodia. *P. amyli* is an inhabitant of stagnant waters, and lives upon starch grains. The zoospore is biciliate, the two cilia being at one or at opposite ends of the body. It passes into an *Actinophrys*-like *Amoeba*, which as it grows loses the power of emitting pseudopodia; it then forms a cyst and segments into zoospores. Or several spores may fuse into a plasmodium round a starch grain. The plasmodium does not emit pseudopodia, and finally secretes a membrane. It then segments into zoospores, or before it does so, it may escape from the cyst and creep about by means of long pseudopodia. The resting-spore is ellipsoidal or globular with a thick cyst which has minute internal tubercles. *P. Spirogyrae* is parasitic in *Spirogyra* and *Zygnema*. The zoospore is uni-ciliate; it forms amoebae or plasmodia with blunt pseudopodia. The resting-spore behaves like that of *Pseudospora*. *P. Huxleyi* is marine, and lives upon Diatoms. The genus *Diplophysalis* is characterised by the fact that the resting-

<sup>1</sup> The following epitome is made from Zopf's article in the 'Encyclopaedie der Wissenschaften,' quoted *infra*.

spore has a double cyst. *D. Stagnalis* and *D. Nitellarum* live in the cells of *Chara* and *Nitella*. The inner cyst-membrane to the resting-spore is spinose in the former, smooth in the latter. *D. Volvocis* feeds on the zooids of *Volvocis*.

The second family of *M. zoosporeae* is the *Gymnococcaceae*. The resting-spore has as usual a membrane but no cyst, and the ingesta are expelled before its formation. *Gymnococcus* forms its zoospores in a cyst; *G. Fockei* is parasitic in Diatoms; *G. perniciosus* in the cells of *Cladophora*, *G. spermophilus* in the spores of the blue-green Alga *Cylindrospermum*. *Aphilidium deformans* inhabits the cells of the Alga *Coleochaete*; its zoospores have no cysts. *Pseudosporidium* lives in cultures of Algae. The zoospore gives origin to a slug-like Amoeba, which may form a resting or hypno-cyst and become free again. It ends by becoming globular, secreting a membrane, perforated and furnished with an operculum at one spot where the zoospores, to which it gives rise, escape. *Protomyxa aurantiaca* is marine, and was found by Haeckel on the shell of a *Spirula* in the Canary Islands. It forms a laminated globular cyst .12–.2 mm. in diameter, the orange-coloured contents of which segment into some hundreds of uni-ciliate pyriform zoospores. The latter become amoeboid; some of the Amoebae fuse into an orange-coloured plasmodium with reticulate pseudopodia which feeds on Diatoms and *Peridinidae*, and eventually encysts again. Haeckel found no nucleus.

The third family of *M. zoosporeae* is the *Plasmodiophoreae*. Its members are parasitic in the cells of the roots of plants. The amoeba breaks up within the cells into minute zoospores and there is no cyst. *Plasmodiophora Brassicae* infests *Cruciferae*, especially species of *Brassica*; *Tetramyxa parasitica* various water plants. The latter is peculiar in that the Amoeba first divides into cells, and the latter in turn each into four spores which remain united. It is possible that the Amoeba is a plasmodium.

*M. azoosporeae*. The zoocyst gives origin to *amoebulae*. There are three families.

The first is the *Vampyrellaceae*, all aquatic and feeding on living or dead Algae, Fungi, Protozoa, &c. *Vampyrellidium vagans* is aberrant. It infests *Oscillatoriae*, *Saprolegniae*, &c., and when full fed becomes globular or oval and develops a thin or thick membrane, in either case escaping as a single Amoeba. Zopf places here with some doubt *Spirophora (Amoeba) radiosa* which feeds on *Scytonemeae*. When floating it is globular, when creeping flattened. Its pseudopodia are long, with a tendency to twist terminally into spirals; they vibrate to and fro (see Bütschli, Z. W. Z. xxx. p. 271). It passes into a globular resting-spore, after ejecting all foreign bodies. The spore gives rise to a single Amoeba. *Haplococcus reticulatus* lives between the muscle-fibres of animals, especially swine. Its zoocyst is globular with three or several round papilliform spots from which the *amoebulae* (6–15) escape. The resting-spore is round or tetrahedral, but has no cyst. The genus *Vampyrella* has seven or eight species, one of which, *V. Gomphonematis*, is marine, and feeds on the branched Diatom *Gomphonema*. The other species feed principally on various freshwater Algae either engulfing Diatoms, Desmids, or sucking out the cell-contents of filamentous Algae by pseudopodia emitted from a stout process which perforates the cell membrane. The chlorophyl of the Algae is partly dissolved and changed, colouring the protoplasm red, rosy, orange, yellow, or brown. *V. polyblastae* feeds on *Euglenae*. The Amoeba is large, more or less *Actinophrys*-like, but of irregular shape, with pointed pseudopodia except in *V.*

*pedata*<sup>1</sup>, which moves by a one-sided hyaline border. It is uni-nucleate. Binary fission has been observed as well as the fusion of 2-4 Amoebae into plasmodia in *V. variabilis* and *V. polyblasta*. The plasmodia may divide, and in *V. polyblasta* pass into a resting or hypnotic phase. The cysts may have one, two, or several membranes. The zoocyst, which is very irregular in shape in *V. variabilis*, in *V. pendula* attached to its host by a peduncle, and in *V. pedata* by a plug or process projecting into the cell it has just plundered, gives origin to 2-4 *amoebulae* which escape simultaneously at as many different spots, leaving faecal residues behind as brown balls. The sporocyst contains a single resting-spore except in *V. variabilis* where there are two or more. The resting-spore contracts successively several times, forming a cyst membrane at each contraction<sup>2</sup>. The *Monodopsis Vampyrelloides* of Klein is probably a *Vampyrella*. One or more of its Amoebae surround a *Tetraspora*, fuse and encyst. The contents of the cyst divide into 2-3 *amoebulae*. *Leptophrys (Vampyrella) vorax* is large, sometimes colourless, sometimes reddened by digested chlorophyl, multi-nucleate, filled with paramylum bodies, often mistaken for vacuoles. In locomotion it pushes out irregular lobes and its pseudopodia, which spring from the lobes, are fine and pointed. It undergoes fission, and forms fusion-plasmodia. The zoocyst is of irregular shape and gives origin to 2-6 *amoebulae*. The sporocyst is globular or elongate with a thin membrane, and all ingesta are expelled before its formation. Its contents contract, and may form a second membrane and contract again; they are enveloped in a tough spore-membrane. *Endyomena polymorpha* is a uni- or multi-nucleate amoeba of variable size and irregular shape, living within the sheaths of *Scytonemeae*. The cyst (? zoocyst) is globular or irregular in shape; its contents form a second cyst-membrane.

The second family of *M. azosporeae* is the *Bursullineae*. It contains only *Bursulla crystallina* which lives on horse-dung. The Amoeba has long pointed pseudopodia. Two or more Amoebae fuse into a rose-red plasmodium. The latter gives origin to one, or if large to 2-3 zoocysts, which are globular or oval and pedunculate. The contents divide into eight Amoebae; the apex of the cyst then gelatinises and suffers them to escape. The resting-spore (? phase) is globular with a thick membrane; the latter bursts and its contents give rise to a zoocyst.

The third family is the *Monocystaceae*, which contains aquatic genera of voracious habit and giving rise only to a sporocyst<sup>3</sup>. Zopf places here *Myxastrum* (p. 916, *ante*). The other member is *Enteromyxa paludosa* which feeds on *Oscillatoriae* and Diatoms, the former tinging the protoplasm blue-green. The Amoeba is typically long ( $\frac{1}{2}$ -1 mm.) and worm-like; it may become branched or reticulate.

<sup>1</sup> ? = *Hyalodiscus = Plakopus*, p. 905 and note, *ante*.

<sup>2</sup> Leidy in his 'Freshwater Rhizopoda of N. America' speaks, p. 255, with reference to *Vampyrella lateritia (= Spirogyrae)* of the rapid emission and withdrawal of pin-like pseudopodia, consisting of a short stalk with a head. As he himself points out (p. 256), other observers (Cienkowski, Hertwig, and Lesser) have noticed rapid shooting out and as rapid withdrawal of granules in the pointed or lobose pseudopodia of this species. It may be noted here that Zopf states that the membrane of the zoocysts of *Vampyrella pedata*, *Monodopsis Vampyrelloides*, and *Leptophrys vorax*, yield with Iodine and Sulphuric acid the blue colour characteristic of cellulose.

<sup>3</sup> Zopf speaks in his article in the Encyclopaedie, &c., quoted *infra*, of plasmodia in *Myxastrum* and *Enteromyxa*. But in neither of these genera has the formation of a plasmodium been actually observed. Both organisms are of large size, *Myxastrum*  $\frac{1}{10}$  in., *Enteromyxa*  $\frac{1}{10}$ - $\frac{1}{8}$  in.

At first it emits numerous cylindrical hyaline pseudopodia, in later stages short broad processes, by which it gathers its food. When it encysts, it secretes a thin membrane, contracts, especially in breadth, and is by degrees segmented into a number of rounded portions. Each portion becomes multangular, secretes a tough membrane and breaks up into two or several, rarely many, resting-spores. The latter are ellipsoidal or bean-shaped with a membrane. The sporocyst is frequently violet in colour.

There remain a few amoeboid forms not included in the above described groups. *Boderia* is marine,  $\frac{1}{16}$ – $\frac{1}{4}$  inch in size, orange or brown in colour, of varying shape, with a membranous investment (?) from openings in which protrude 3–4, sometimes more, long and branched pseudopodia with granule streaming. It has one or more nuclei (?). *Gymnophrys cometa* is non-nucleate, marine and freshwater, naked, colourless, with a few branched and anastomosing pseudopodia displaying granule streaming. *Biomyxa vagans* is also marine and freshwater. It is amoeboid and passes through most varied changes of form, from a Heliozoon-like aspect to a network. It has minute contractile vacuoles, and many nuclei. *Protamoeba* is non-nucleate, with pseudopodia not branched nor anastomosing, varying in shape but constant in different species; of variable size, multiplying by fission. Its different species are found in either fresh or salt water. The freshwater *Gloidium* closely resembles a *Protamoeba*. It has lobose pseudopodia, a contractile vacuole, and divides simultaneously into four parts while in a mobile condition. It surrounds itself sometimes with a laminated cyst. *Protogenes* is marine, non-nucleate, globular or irregular in shape, with fine branched and anastomosing pseudopodia. Binary fission has been observed. *Arachnula impatiens* is a fresh or brackish water form, rapid in motion, non-nucleate, with contractile vacuoles, the pseudopodia a little branched, sometimes anastomosing, generally originating from lobes which appear at any part of the body. The latter is usually drawn out into a narrow band. A transparent cyst has been observed. The *Monopodium* of Mereschkowski appears to be identical with the *Aletium* of Trinchese. It is marine, and found attached by a pseudopodium to the algal *Chaetomorpha* or *Leptothrix* (*Lingbya*) and is characterised by its mode of locomotion. It throws out a long pseudopodium which attaches itself to another algal filament and then draws the body onwards, releasing afterwards the original pseudopodium of attachment. Trinchese describes *Aletium* at rest as pyriform, 3 mm. long, yellow in colour, feeding on the *Chaetomorpha*, and giving off branched pseudopodia. He observed it resolved into a number of globular bodies held together by a colourless mass and in one instance showing amoeboid motions. Mereschkowski witnessed the fusion of two individuals, the resulting mass breaking up into three. *Protobathybius* is the name given by Bessels to large masses of free protoplasm dredged in Smith's Sound at a depth of 92 fathoms. The protoplasm has the form of a sticky network, which shows amoeboid motion, and takes up foreign bodies. A similar organism, known by the name of *Bathybius Haekelii*, was supposed by several authorities to cover the bottom of the deep sea with a living network of protoplasm. It has been recently determined to be a colloid precipitate of Calcium sulphate, thrown down from the seawater by the action of Alcohol on the specimens of sea-bottom in which it was found.

Two remarkable Protozoan parasites recently discovered may be mentioned here. One has been found in the sputum of whooping-cough. It has the form of

a nucleated cell rounded at one end, drawn out into a point at the other. The rounded end may emit fine pseudopodia. It appears to feed on the leucocytes of the sputum, and passes into a resting phase in which it is so curved that the two ends touch or nearly touch each other. The other parasite, *Schizogenes*, inhabits the coelome of certain *Ostracoda* and *Cladocera*. It is composed of a homogeneous protoplasm and is non-nucleated. In size and shape it is very variable. The smallest individuals are rounded discs. Its mode of reproduction is peculiar. A split occurs in the protoplasm which slowly cuts off a portion.

*Heliozoon-like genera.* *Nuclearia*, Cienkowski, A. M. A. i. 1865, p. 225-6, = *Heterophrys varians*, F. E. Schulze, *ibid.* x. 1874, p. 386, = *Heliophrys variabilis*, Greeff, *ibid.* xi. 1875, p. 28; cf. Leidy, 'Freshwater Rhizopoda of N. America,' U. S. Geological Survey of the Territories, Washington, 1879, p. 243. *Myxastrum radians*, Haeckel, J. Z. iv. 1868, p. 91; *M. Liguricum*, Gruber, *Nova Acta*, xlv. 1884, p. 505. *Archerina*, E. Ray Lankester, Q. J. M. xxv. 1885. *Monobia*, Schneider, A. Z. Expt. vii. 1878. *Myxodyctium*, Haeckel, *op. cit.* p. 99.

*Monadineae.* Zopf, *Encyclopaedie der Naturwissenschaften*, Breslau, 'Handbuch der Botanik,' iii. pt. 2, 1884<sup>1</sup>.

*M. zoosporeae:* Zopf, *op. cit.* pp. 115-31. *Pseudospora maligna*, *Protomonas amyli*, *Diplophysalis stagnalis*, *D. Nitellarum*, *Gymnococcus Fockei*, *Aphelidium deformans*. Zopf, 'Zur Morphologie und Biologie der niederen Pilzthiere,' Leipzig, 1885. *Colpodella pugnax*, Cienkowski, A. M. A. i. 1865, p. 214. *Protomonas amyli*, Cienkowski, *op. cit.* p. 213; *P. Huxleyi*, Haeckel, J. Z. vi. 1871, p. 29; *P. Spirogyrae*, Fisch, Z. W. Z. xlii. 1885, p. 119. *Diplophysalis* (= *Pseudospora*) *Nitellarum*, Cienkowski, *op. cit.* p. 213; *D.* (= *P.*) *Volvocis*, *Id. ibid.* p. 214. *Pseudosporidium*, Brass, *Biol. Studien*, i. 1883-4, p. 70. *Protomyxa*, Haeckel, J. Z. iv. 1868, p. 71. *Plasmodiophora*, Woronin, Pringsheim's *Jahrbücher*, xi. p. 548. *Tetramyxa*, Goebel, *Flora*, No. 23, 1884.

\* *M. azoosporeae.* Zopf, *op. cit.* pp. 99-115. *Vampyrella Spirogyrae*, *V. variabilis*, *V. pendula*, *Leptophrys vorax*, Zopf, 'Zur Morphologie,' &c., *supra*. *Spirophora* (= *Amoeba*) *radiosa*, Auerbach, Z. W. Z. vii. 1855-6, p. 400; Bütschli, Z. W. Z. xxx. 1878, p. 271; = *Dactylosphaerium vitreum* (?), Hertwig and Lesser, A. M. A. x. 1874, *Suppl.* p. 55. *Haplococcus*, Zopf, *Biol. Centralblatt.* iii. 1883-4, p. 673. *Vampyrella Spirogyrae*, Cienkowski, A. M. A. i. 1865, p. 218; Hertwig and Lesser, *op. cit.* p. 61; Leidy, *op. cit. supra*, p. 253; *V. pendula*, Cienkowski, *op. cit.* p. 221; *V. variabilis*, *V. pedata*, Klein, *Botan. Centralblatt.* xi. pp. 189, 204-8, 257-9; *V. polyblasta*, Sorokin, *Grundzüge der Mycologie*, p. 495; *V. Gomphonematis*, Haeckel, J. Z. vi. 1871, p. 23. *Leptophrys* = *Vampyrella vorax*, Cienkowski, *op. cit.* p. 223; *Id. ibid.* xii. 1876, p. 24; *L. cinerea*, *L. elegans*, Hertwig and Lesser, *op. cit.* p. 57; cf. Archer, Q. J. M. xvii. 1877, p. 345. *Bursulla*, Sorokin, A. Sc. N. *Botan.* (6), iii. 1876, p. 40.

*Amoeboid genera.* *Boderia*, Strethill Wright, *Journal of Anat. and Physiol.* i. 1867, p. 335. *Gymnophrys*, Cienkowski, A. M. A. xii. 1876, p. 31; cf. Archer,

<sup>1</sup> All or nearly all the genera and species are described in this work, some indeed only in it. To certain genera and species references are given which may prove useful to those to whom Zopf's work is inaccessible.

Q. J. M. xvii. 1877, p. 348. *Biomyxa*, Leidy, op. cit. *supra*, p. 281; Gruber, Nova Acta, xlv. p. 503. *Protamoeba*, Haeckel, J. Z. iv. 1868, p. 104; vi. 1871, p. 32; Gruber, op. cit. p. 483; Korotneff, A. Z. Expt. viii. 1879-80, p. 467; Mereschkowski, A. M. A. xvi. 1879, p. 214 (? does his species = *Polymastix sol* of Gruber, op. cit. p. 508; it is much smaller); Trinchese, Mem. Accad. Bologna (4), v. 1884. *Gloidium*, Sorokin, M. J. iv. 1878. *Protogenes*, Haeckel, Z. W. Z. xv. 1865, p. 360; Trinchese, op. cit. *Arachnula*, Cienkowski, A. M. A. xii. 1876, p. 27; cf. Archer, Q. J. M. xvii. p. 347. *Monopodium*, Mereschkowski, Z. A. iii. 1880, p. 139. *Aletium*, Trinchese, op. cit. and Rendic. Accad. Sc. Ist. Bologna, 1880-1, p. 134. *Protobathybius*, Bessels, J. Z. ix. 1875, p. 277, note 1. *Bathybius*, Huxley, Q. J. M. viii. 1868; Haeckel, J. Z. v. 1870, p. 499; Gumbel, Neues Jahrbuch für Min. Geol. Palaeont. 1870, p. 753; Murray, P. R. S. xxiv. 1876, p. 530; Buchanan, *ibid.* p. 605; cf. Wyville Thomson, 'Depths of the Sea,' 1873, p. 411; Haeckel, Kosmos, i.

*Parasite of whooping-cough*, Deichler, Z. W. Z. xliii. 1886. *Schizogenes*, Moniez, Journal de l'Anat. et Physiol. (Robin), xxii. 1886.



# INDEX.

v. = *vide*; n. after numbers = note.

Generic names only are in italics.

In the accounts of the classes, the different points are treated as nearly as possible in the same order:—external form; integument and exoskeleton; endoskeleton if present, and musculature; nervous system and organs of special sense; digestive, circulatory, respiratory, renal and sexual organs; development and larval forms if any; distribution in time and space; classification; literature.

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