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TEXT-BOOK

OF

COMPARATIVE ANATOMY

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COMPARATIVE ANATOMY

BY

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WITH

PREFACE TO THE ENGLISH TRANSLATION BY
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AND
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TRANSLATORS' PREFACE

THIS translation of the first volume of Professor Lang's *Lehrbuch der Vergleichende Anatomie* may be considered as a second edition of the original work. Professor Lang kindly placed at our disposal his notes, collected for the purposes of emendation and expansion, and they have been duly incorporated in the text.

We did not think it necessary to increase the size of the book by the addition of footnotes, either for the addition of new material where it seemed to us that the account might with advantage be fuller, or for calling attention to the opinions of other writers when these did not happen to agree with that expressed in the text. In one case a recent discovery (that of Jawarovski of antennæ in the embryo of Trochosa) lent such sudden and unexpected support to the morphology of the Arachnoidea set forth in the text that attention was called to it in a footnote.

In carrying out our work as translators we have kept as close to the original as the requirements of our own language would allow. How far we have succeeded must be decided by those who know by experience the difficulty of breaking down the long and weighty German sentences, and of rearranging their contents into readable English. We have endeavoured to steer a middle course between the too free use of periphrases which suits the German style, and the use of single technical terms which better suits the more concise English sentence. The former style has, we think, some advantages over the latter, so long as the multiplicity of words does not obscure the meaning. There can be no doubt that it appeals more directly to the understanding. The object of such a text-book as this is to enable an ordinarily intelligent reader to obtain a clear grasp of the facts and of their relation to one another; a knowledge of the technical terms is of secondary importance, and is easily acquired.

We trust that this translation of the work of our friend and (in the case of one of us) former teacher, Professor Lang, will prove as useful to earnest students of biology in the English-speaking world as it has proved to ourselves.

H. & M. B.

JENA, 1891.

PREFACE BY PROFESSOR ERNST HAECKEL

The morphology of the animal body, which is the subject of the following excellent text-book, has been, during the last forty years, *i.e.* since the commencement of my academic career, the favourite object of my scientific labours. During these four decades no other science has undergone such profound and striking transformation.

In the years 1852-1856, when I attended in Berlin and Würzburg the masterly anatomical and zoological lectures of Johannes Müller, Albert Kölliker, and Franz Leydig, the study of comparative anatomy and of comparative histology had been brought into great prominence through Müller's classical researches in the former, and Leydig's in the latter field.

Oscar Schmidt's text-book of comparative anatomy which resulted from the transcription of Johannes Müller's summer lectures, and passed through eight editions, gives evidence of the stage then reached by that science. Upon this work the present text-book of Professor Arnold Lang is founded, as its ninth edition; the present state and needs of the science, however, compelled the new editor to rewrite the whole book on a much larger scale.

Johannes Müller, the great master in the domains of comparative anatomy and physiology, died in 1858, after having held sway as the leader in these sciences for more than quarter of a century. This very year 1858 saw the simultaneous publication by Charles Darwin and Alfred Wallace of their preliminary sketches of the *Theory of Selection*. The year after appeared the *Origin of Species*, which at one stroke ushered in, by means of this theory, a new epoch for the biological sciences.

The theory of the mutual action and reaction of inheritance and adaptation in the struggle for existence clearly explained the forces at work in the production of biological phenomena. The facts themselves had already been set out in their wonderful array, and comparative anatomy had even arranged them with profound philosophical judgment, but no mechanical explanation of them was forthcoming.

Thomas Huxley in England, and Carl Gegenbaur in Germany, by means of their well-known text-books of comparative anatomy, were the first to succeed in revealing in detail the important transformation which this mechanical explanation of morphological phenomena, by means of the new theory of descent, had brought about in the biological sciences.

It was my happiness during the first twelve years of my occupancy of a University chair in Jena, *i.e.* from 1861 to 1873, to have Gegenbaur for my colleague and friend. My own attempts to give the theory of descent its widest application in those sciences which are comprised under the term biology owe much to this stimulating intercourse, and are embodied in my works: *Die Generelle Morphologie* (1866), *Die Natürliche Schöpfungsgeschichte* (1868, 8th ed. 1889), and *Die Anthropogenie* (1874, 4th ed. 1891).

Oscar Schmidt's and Gegenbaur's text-books and my above-named works all issued from the University in the small Thuringian town of Jena, and from the same source has now appeared this text-book of Professor Arnold Lang, formerly my distinguished pupil, and afterwards and till quite recently my helpful colleague. Professor Lang has here successfully carried out the very difficult task of selecting the most important results from the bewildering mass of new material afforded by the extensive researches of the last decades, and of combining them with great judgment. Besides this he has, more than any former writer, utilised the comparative history of development in explaining the structure of the animal body, and has endeavoured always to give the phylogenetic significance of ontogenetic facts. Lastly, he has, by the clear systematic reviews of the various classes and orders which precede the anatomical account of each race, further facilitated the phylogenetic comprehension of complicated morphological problems, his wisely chosen and carefully executed illustrations assisting materially in this result.

It is therefore with great pleasure that I commend this book to the English student, in accordance with the wish expressed by my friend Professor Lang and his translators Mr. and Mrs. Bernard, and in the hope that the English translation will promote to as great an extent as the German original the wider study and better comprehension of animal morphology, and will attract new students to this noble science.

ERNST HAECKEL.

JENA, 1891.

AUTHOR'S PREFACE TO PART I[1]

When requested by the publishers to undertake a new edition of Dr. Oscar Schmidt's *Text-book of Comparative Anatomy*, I found that this could only be done in one of two ways. Either the revision must be limited to trivial alterations, and to a different choice and a greater number of illustrations, or the book must be entirely re-written. I chose the latter course, which the great advance made in zoological research seemed to render unavoidable. The result is the *Text-book of Comparative Anatomy*, the first part of which I now publish.

In compiling the book I have endeavoured to do full justice to the numerous important results of the research of the last decades. I have been less anxious to supply a complete and detailed compendium of Comparative Anatomy than to emphasise those points which it seems to me are deserving of special attention. The present work in many respects exceeds the limits till now usually assigned to text-books of Comparative Anatomy. It contains, separated as far as possible from the portion devoted to the main subject, the elements of Comparative Embryology, which will perhaps not be unwelcome to many students. Following Oscar Schmidt's example, I have prefaced the Comparative Anatomy of the different animal races by short systematic reviews, which may be of use to the student of systematic zoology. The book had also to contain what was necesary for the zoological education of the medical student.

All these parts, not necessarily belonging to the domain of Comparative Anatomy, and also many theoretical discussions, are distinguished from the rest by smaller print.

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[1] The first part consisted of the first four chapters of this volume.

I have taken my own course as regards the arrangement and method of treating the material. I must naturally leave it to my fellow-zoologists to decide how far I have succeeded.

I have given special care to the illustration of the book. It contains a large number of illustrations now for the first time accessible to the majority of students; these I have, for the most part, myself adapted to the requirements of the text. I have to thank the practised hand of my pupil, the young scientific artist, Mr. Sokolofsky of Hamburg, for some particularly good illustrations.

I owe my best thanks to my honoured publisher, Mr. Gustav Fischer, for his obliging courtesy.

JENA, 1888.

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CHAPTER I

THE CELL

Unicellular animals—The cell as the starting-point in the development of the higher animals (egg and sperm cells)—The cells which compose the bodies of those animals (tissue cells and cell tissue).

INTRODUCTION.

THE starting-point of all organic life and of all organic structure is the **cell.** The simplest organisms, the lowest animals, are **cells.** Every higher animal begins individual existence as a cell, and every higher organism appears to be composed of cells which have arisen by multiplication from one cell.

The cell is **an organic individual of the first order.**

In all cases except that of the lowest organisms the descendants of one cell unite to form communities or states, which then rank as **individuals of a higher order.**

Every higher organism, every bird, every fish, and so on, is such a cell community. In such a community, the closely united cells share in the common work. Some undertake one function, some another, for which they are specially adapted.

Every cell consists of two essential parts: (1) the **Protoplasm**, and (2) the **Nucleus.** The latter may be considered as a special differentiation (specially developed portion) of the protoplasm. Chemically considered protoplasm is a carbon compound as yet not fully understood: it is related to albumen, and is, in life, a stable combination, though subject to variation within very narrow limits. It is viscid and capable of swelling. The nucleus lies within the protoplasm as a chemically and physically differentiated part of it. It is an essential portion of the cell, in whose multiplication it plays an important part. According to some observers, if the nucleus is removed from a cell the latter perishes. If, on the other hand, a nucleus is introduced into an unnucleated piece of protoplasm, certain characteristic phenomena of life otherwise absent appear in it.

There are very simple creatures, small masses of protoplasm, in which no nucleus has been found. Should the absence of nuclei in these creatures be established they would rank lower in the scale than cells. To such organisms the name "**Cytods**" is applied, and Haeckel has united them, as the simplest of all organisms, under the group of *Monera*.

A frequent though not necessary portion of the cell is the **cell integument** or **cell membrane**, a product of secretion, serving for protection or support. Such a membrane can also arise by the hardening and modification of the peripheral layers of the protoplasm itself.

A single cell (a unicellular organism, an egg cell) is in itself from the first capable of all those activities and functions which are contained in the conception of **Life**. These phenomena of life, though they may not as yet be physically and chemically explained, are certainly not to be referred to the working of any special **vital force** peculiar to organisms. There is also no special fundamental substance, no **life substance**, which can be found in organisms, and with which a special vital force is connected. We have to do here with the same forces and the same substances that we meet with elsewhere in nature.

The life of the cell shows itself in the simplest cases in—

1. **Motion.**—Protoplasm is contractile. The finest visible portions can change their relative positions. The cell can change its form and its position in space.

2. **Irritability.**—The cell responds to external stimuli by such movements.

3. **Metabolism.**—By means of its life-activity some of the cell substance is used up, decomposed. What has become useless is excreted (**excretion**). By means of the ingestion of food foreign substances are introduced. These are digestible if, when assimilated by chemical action, they can be changed into ingredients of protoplasm (**digestion, assimilation**). If, owing to their chemical properties, such a conversion is impossible, they are indigestible, and are expelled out of the body.

4. **Growth.**—By nourishment more protoplasm can be produced than was formerly present. The cell in consequence increases in size—**it grows.**

5. **Reproduction.**—It may be assumed that the size of an individual cell is limited. If it exceeds these limits of individual size it divides into two cells (reproduction by means of **division**). Each of the two portions has the same physical and chemical properties as the mother cell (simplest form of **inheritance**). The daughter cell by growth attains the size of the mother cell.

As the cell is the starting point both in the animal and in the vegetable kingdoms, it can easily be understood that no sharp line of demarcation between the lower forms in these two kingdoms can be established. Haeckel has therefore set up an intermediate kingdom, that of the

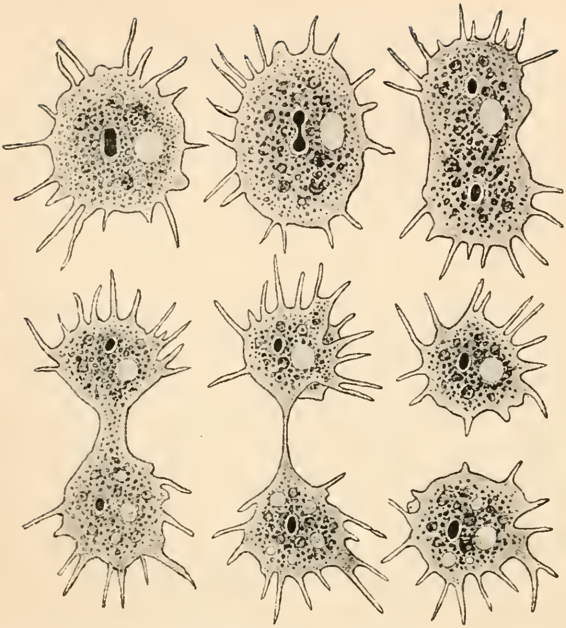

Fig. 1.—**Amœba polypodia** in the successive stages of division. The light spot is the contractile vacuole, the dark the nucleus (after **F. E. Schulze**).

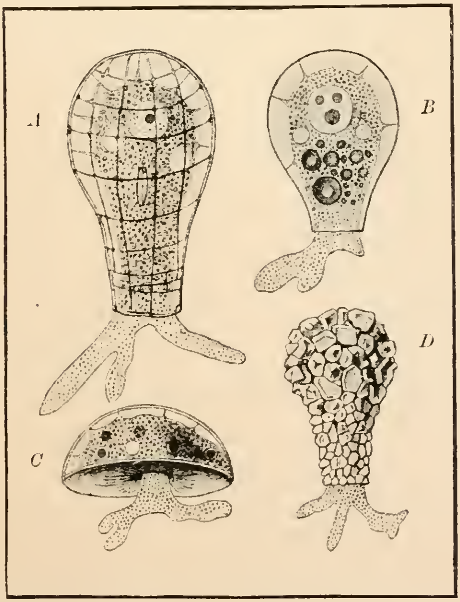

Fig. 2.—*A*, **Quadrula symmetrica**, after **F. E. Schulze**. *B*, **Hyalosphenia lata**, after **F. E. Schulze**. *C*, **Arcella vulgaris**, after **Hertwig** and **Lesser**. *D*, **Difflugia pyriformis** (after **Wallich**) completed.

Protista, consisting of the simplest organisms. But there is also no sharp line of demarcation between the *Protista* on the one side and animals and plants on the other. Some *Protista* are, chiefly by their method of nutrition, more nearly related to plants, others to animals. The latter are called **Protozoa**, in contradistinction to all other animals, which are classed as **Metazoa.**

THE FIRST RACE OR PHYLUM OF THE ANIMAL KINGDOM.

PROTOZOA.

Systematic Review.

Class I. Monera.

Simplest organisms. Small masses of protoplasm of varied changing form, in which till now **no nuclei** have been demonstrated. Locomotion and ingestion of food by means of blunt (amœboid) or long and fine processes (pseudopodia). Reproduction by fission and gemmation. All Monera live in water. *Protamœba, Myxodiction, Protomyxa.*

Class II. Sarcodina.

Unicellular organisms, with nucleus or nuclei. Locomotion and ingestion of food by means of filose non-vibrating processes of varying length (pseudopodia). Reproduction by fission or gemmation.

Sub-Class I. Amœbina.

Naked or shelled Sarcodina of changing shape. Locomotion and ingestion of food by means of streaming of the body and the formation of processes mostly short and lobate. Contractile vacuoles generally present. *Amœba* (Fig. 1), *Arcella* (Fig. 2, *C*), *Difflugia* (Fig. 2, *D*), *Quadrula* (Fig. 2, *A*), *Hyalosphenia* (Fig. 2, *B*).

Sub-Class II. Rhizopoda.

Sarcodina whose protoplasm secretes a very variously-shaped chitinous, generally calcareous, shell, which is at first uniaxial. Locomotion and ingestion of food by means of pseudopodia, which frequently fuse with one another, often in a reticular manner. Contractile vacuoles generally absent.

A. Imperforata.

Shells of one chamber or more, not perforated by fine pores, but having one or two larger apertures through which the protoplasm and the pseudopodia pass out. *Miliola* (Fig. 3, *C*), *Lituola*, *Gromia* (Fig. 3, *A*).

B. Perforata.

Shells of one chamber or more, perforated by fine pores for the passage of the pseudopodia. *Globigerina, Rotalia* (Fig. 3, *B*).

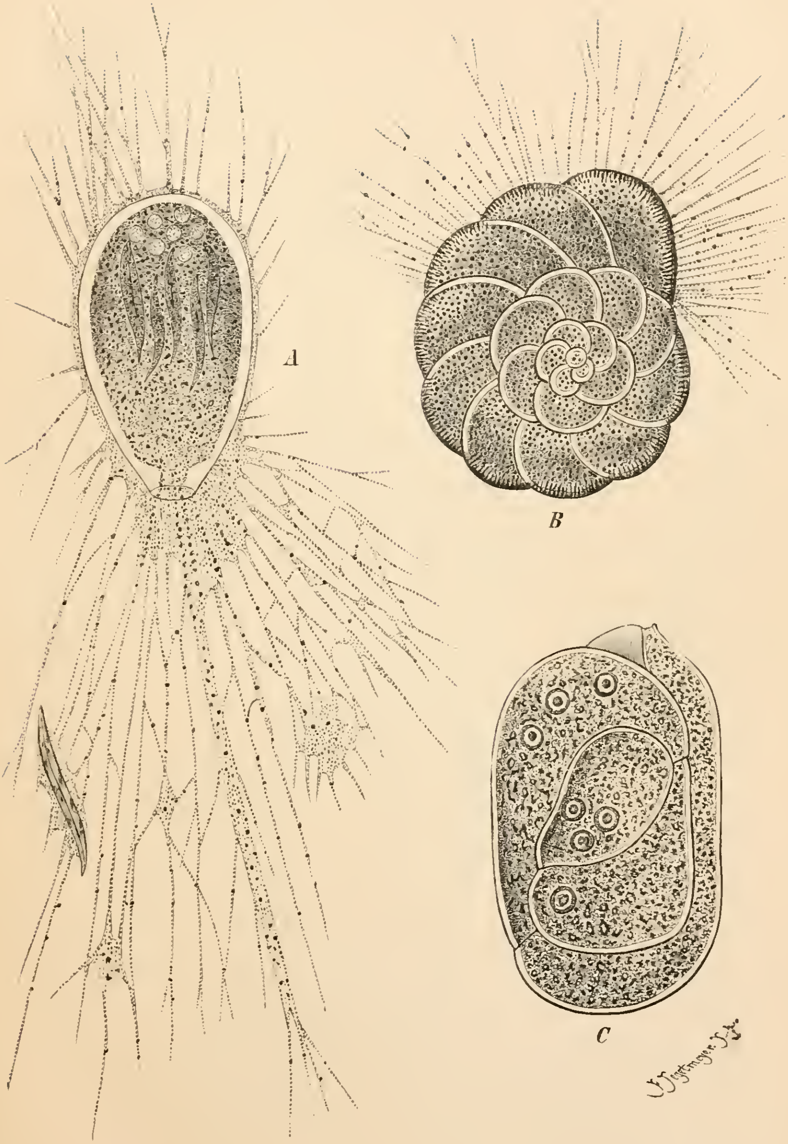

FIG. 3.—*A*, **Gromia oviformis** after **M. S. Schultze.** *B*, **Rotalia Freyeri,** after **M. S. Schultze.** *C*, **Miliola** (after **R. Hertwig**) the nuclei in the chambers.

Sub-Class III. **Heliozoa.**

Globular Sarcodina, naked or clothed with a siliceous skeleton, with fine more or less stiff pseudopodia radiating on all sides. Contractile vacuoles generally present in varying numbers. *Actinophrys* (Fig. 4), *Actinosphærium*, *Acanthocystis*, *Clathrulina.*

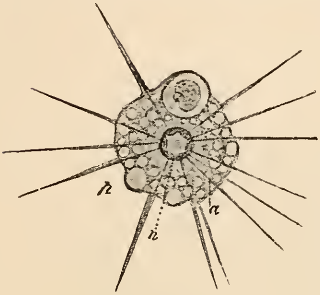

Fig. 4.—**Actinophrys sol**, after **Grenacher.** *p*, Pseudopodia; *n*, nucleus; *a*, axial filaments of the pseudopodia.

Sub-Class IV. **Radiolaria.**

Body divided by an originally spherical or egg-shaped capsular membrane into an outer, and an inner, nucleated portion (outer and inner capsules). The outer capsule consists of protoplasm (without nucleus) and of a gelatinous envelope (calymna). The protoplasm forms a layer round the inner capsule and a network round the calymna, these two being connected by means of protoplasmic threads. Fine flexible pseudopodia radiate in all directions from the surface of the calymna. Skeletons of extraordinarily various shapes, of silica or of chitin-like organic substance (acanthin), are seldom wanting. The extra- and intra-capsular protoplasm are connected through various openings in the cell-membrane. This division of the marine *Sarcodina* is wonderfully rich in forms and shapes. Without contractile vacuoles. Unicellular algæ (yellow cells) live symbiotically with the *Radiolaria*. The family of the *Polycyttaria* among the *Spumellaria* is distinguished by the formation of colonies.

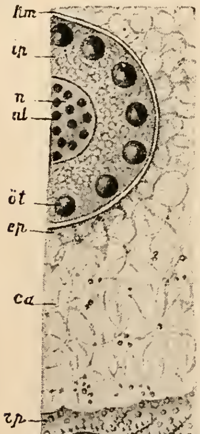

Fig. 5.—**Thalassoplancta brevispicula**, part of a section, after **Haeckel.** *km*, Capsular membrane; *ip*, intra-capsular; *ep*, extra-capsular protoplasm; *n*, nucleus; *nl*, nucleoli; *öt*, oil-drops; *ca*, alveolar calymna; *rp*, protoplasm on the surface of the calymna; *s*, spicules.

A. **Porulosa.**

Central capsule spherical, without a principal aperture, with innumerable fine pores.

I. **Spumellaria.**—Nucleus central, dividing late in the life of the individual. Skeleton siliceous or wanting, never penetrating into the intra-capsular protoplasm. *Thalassicolla*, *Collozoum*, *Sphærozoum*, *Thalassoplancta* (Fig. 5), *Collosphæra*, *Dictyastrum.*

II. **Acantharia.**—Nucleus eccentric, dividing early. Skeleton of acanthin, radiating from the centre of the central capsule. *Acanthometra*, *Phractaspis* (Fig. 6).

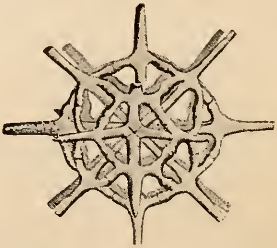

Fig. 6.—**Phractaspis prototypus** (after **Haeckel**), skeleton.

B. **Osculosa.**

Central capsule egg-shaped, with a principal aperture at the basal pole of the chief axis. Skeleton siliceous, always extracapsular. Nucleus dividing late.

III. **Nassellaria.**—Capsular membrane simple, a porous area at the oral pole of the chief axis. *Nassella, Cortina* (Fig. 7), *Cornutella.*

IV. **Phæodaria.**—Capsular membrane double; at the oral pole of the principal axis an osculum closed by a radially striped lid, with a central opening produced in the shape of a chimney. A collection of pigment bodies (phæodium) in the calymma. *Aulosphæra, Aulactinium* (Fig. 8), *Cannopilus, Challengeria.*

Class III. **Flagellata (Mastigophora).**

Organisms which are unicellular or united into simple cell colonies; properly standing on the boundary line between the animal and vegetable kingdoms, since some groups are directly connected morphologically and physiologically with the lowest plants, others, chiefly by their manner of taking nourishment (ingestion of solid food), with animals. Furnished during the principal part of life with one or more vibratile flagella,

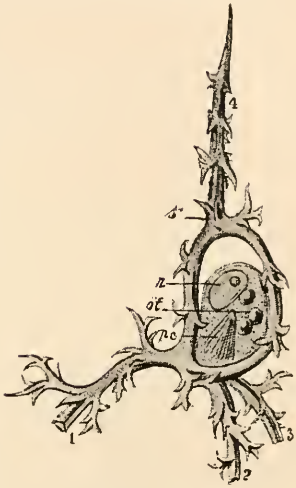

Fig. 7.—**Cortina typus** (after **Haeckel**) not quite fully drawn. *s*, Skeletal ring; 1, 2, 3, 4, principal rays; *n*, nucleus; *öt*, oil-drops; *pc*, podoconus.

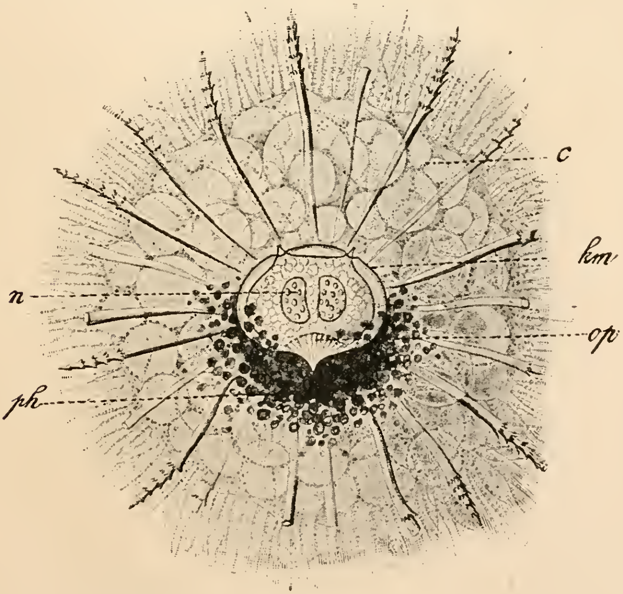

Fig. 8.—**Aulactinium actinastrum**, after **Haeckel**. *n*, Nucleus; *c*, calymma; *km*, capsular membrane; *op*, operculum; *ph*, phæodium.

serving for locomotion, and often also for capturing food. With contractile vacuoles. Multiplication by fission, or formation of spores, or gemmation, often after previous copulation of the reproducing individuals.

Order 1. **Flagellata** s. str.

During active life armed exclusively with flagella (without collar or cilia). *Monas*, *Euglena*, *Chilomonas* (Fig. 9), *Eudorina*, *Pandorina*, *Stephanosphæra*, *Volvox* (Fig. 21, p. 21).

Fig. 9.—**Chilomonas Paramæcium**, after **Bütschli**. *s*, Oral aperture; *cv*, contractile vacuole; *n*, nucleus.

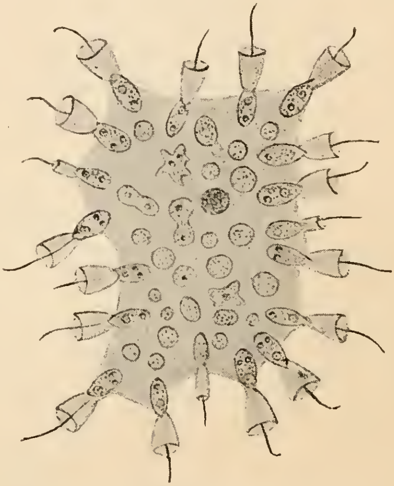

Fig. 10.—**Protospongia Haeckelii**, after **Kent**.

Order 2. **Choanaflagellata.**

Flagella at their basal portion surrounded by a funnel-shaped collar. *Phalansterium*, *Salpingœca*, *Protospongia* (Fig. 10).

Order 3. **Cystoflagellata.**

The protoplasm shows a reticulated structure similar to that of vegetable cells. *Noctiluca* (Fig. 11), *Leptodiscus*.

Order 4. **Dinoflagellata** (Cilioflagellata).

Shelled forms; besides the freely projecting flagellum there is a second, peculiarly placed, in a special groove running across the body, giving the appearance of vibrating cilia which deceived earlier observers. *Peridinium*, *Ceratium* (Fig. 12).

Class IV. **Gregarina.**

Parasitic Protozoa of elongated form. Invariably one nucleus. Without pseudopodia, without cilia, without contractile vacuoles, without special differentiation of the protoplasm, with outer cell integument. Multiplication by spore-formation, with previous copulation or conjugation.

Order 1. **Monocystidæ.**

Body simple. *Monocystis* (in the Earthworm), *Urospora* (Fig. 13, *B*).

Order 2. **Polycystidæ.**

Body divided by a partition wall into anterior (protomerit) and posterior (deutomerit) divisions. The protomerit often again divides, the anterior division (epimerit) being furnished with hooks, etc., for adhesion; this part is lost in time. Nucleus in deutomerit. *Actinocephalus*, *Stylorhynchus* (Fig. 13, *A*), *Clepsidrina*.

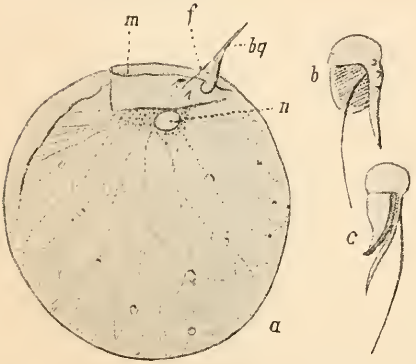

FIG. 11.—**Noctiluca Miliaris** (after **Bütschli**), somewhat altered. *bg*, Band-like flagellum; *f*, flagellum; *m*, oral aperture; *n*, nucleus; *b* and *c*, spores of **Noctiluca.**

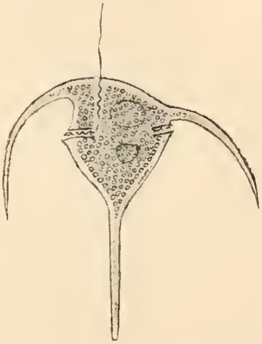

FIG. 12.—**Ceratium Tripus** (after **Bütschli**) somewhat modified.

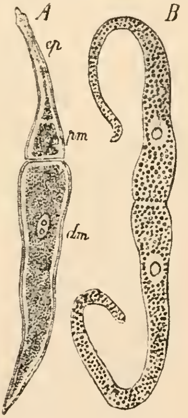

FIG. 13.—*A*, **Stylorhynchus longicollis**, after **Aimé Schneider.** *ep*, Epimerit; *pm*, protomerit; *dm*, deutomerit. *B*, **Urospora Sænuridis.** Conjugation of individuals, after **Kölliker.**

CLASS V. **Infusoria** (Ciliata).

Unicellular Protozoa, rarely united in simple colonies, with cilia or cilia-like processes for locomotion and alimentation. Generally with contractile vacuoles, oral and anal apertures. With double nucleus: a variously formed large *macronucleus* and a small *micronucleus* (erroneously called nucleolus). Reproduction by fission, conjugation frequent.

Order 1. **Holotricha.**

The whole surface is equally covered with fine cilia, often arranged in rows. *Paramœcium* (Fig. 20, p. 17), *Trachelius*.

Order 2. **Heterotricha.**

Possess, besides the clothing of cilia which spreads equally over the whole surface, a distinctly developed zone of bristle- or stylet-shaped cilia near the mouth. *Spirostomum*, *Stentor* (Fig. 15), *Freia*, *Balantidium*.

Order 3. **Hypotricha.**

Dorsal and ventral surfaces sharply distinguished. Ventral surface ciliated. *Chilodon*, *Euplotes*, *Stylonychia* (Fig. 14), *Oxytricha*, *Urostyla*.

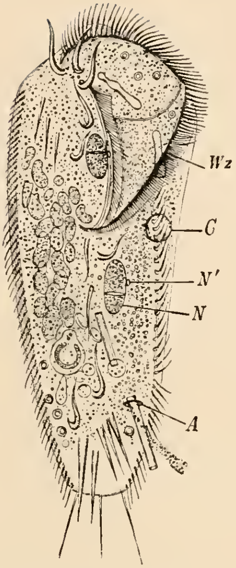

Fig. 14.—**Stylonychia mytilus**, after **Stein** (from Claus's *Zoology*), seen from the ventral surface. *Wz*, Adoral ciliated zone; *C*, contractile vacuole; *N*, nucleus; *N′*, micronucleus; *A*, anus.

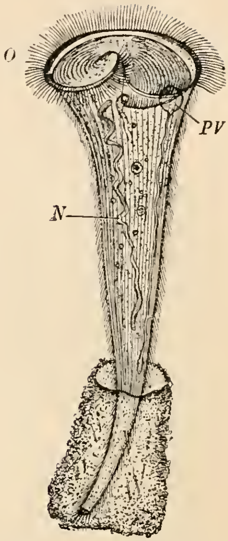

Fig. 15.—**Stentor Roeselii**, after **Stein** (Claus's *Zoology*). *O*, Oral opening with œsophagus; *PV*, contractile vacuole *N*, nucleus.

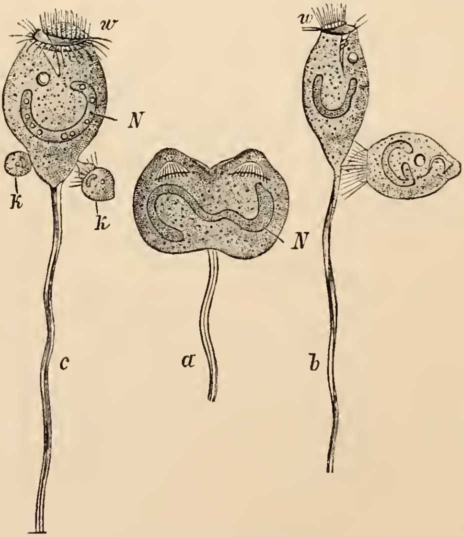

Fig. 16.—**Vorticella microstoma**, after **Stein** (from Claus's *Text-book of Zoology*). *a*, Dividing longitudinally; *N*, nucleus; *b*, after complete division one part severs itself after having formed a ring of cilia behind; *w*, oral ciliary organ; *c*, vorticellæ in conjugation; *k*, the adhering bud-like individuals.

Order 4. **Peritricha.**

Body globular or cylindrical, only partially ciliated, either near the mouth in a spiral, or in a belt. *Vorticella* (Fig. 16), *Carchesium*, *Epistylis*, *Trichodina*, *Strombidium*, *Tintinnus*, *Ophrydium*.

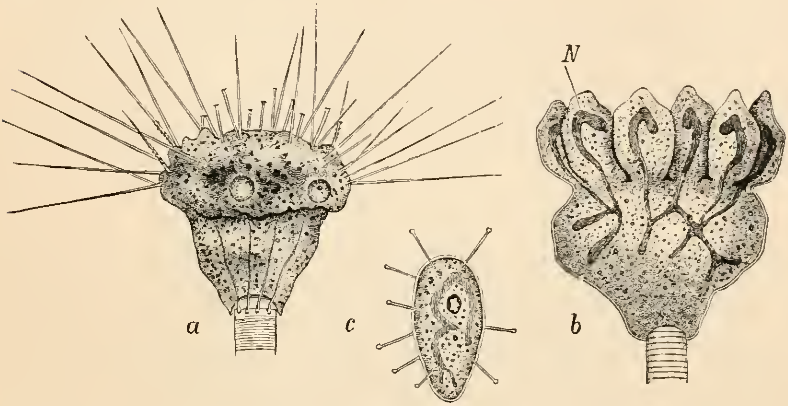

FIG. 17.—**Podophrya gemmipara**, after **R. Hertwig** (from Claus's *Zoology*); *a*, with protruded suctorial tentacles and capturing processes, with two contractile vacuoles; *b*, with buds into which processes of the branched nucleus *N* enter; *c*, one of the buds broken loose.

CLASS VI. **Suctoria** (Acineta).

Ciliated only in swarm-spore stage. With suctorial tentacles, by means of which they penetrate the bodies of *Infusoria* (principally) and suck in their protoplasm. Reproduction by gemmation. *Acineta*, *Podophrya* (Fig. 17), *Dendrocometes*.

CLASS VII. **Catallacta.**

Single genus and species: *Magosphæra planula* (Fig. 18), found swimming freely in the sea on the coast of Norway. A globular colony of pear-shaped cells, the stems of which meet at the centre of the sphere; the outer surface of the cells provided with cilia.

Reproduction: the colony dissolves into single cells, which sink to the bottom, become first amœboid, then encysted, and make a new colony within the capsule by means of successive division; this new colony frees itself later from the capsule.

FIG. 18.—**Magosphæra planula**, after **Haeckel**.

The Protozoa are **unicellular organisms**, or simple colonies of similar unicellular organisms. The typical character of a unicellular organism often appears disturbed by the presence of more than one nucleus, the original simple nucleus by successive division separating into several or even many nuclei. These divisions of the nucleus are in some cases connected with reproduction, as its first stage, in others the rest of the cell remains altogether unaffected.

Although the *Protista* are unicellular organisms they show a remarkable variety in form, and in some cases a great complexity of structure. Modifications may arise specially adapted to the most varied functions of life; these, however, unlike the modifications in the Metazoa, are always in one and the same cell. Nowhere in the organic world does the cell reach so high a degree of morphological differentiation as in certain Protozoa. In the lower Protozoa, on the other hand, the cell in its simplest form shows itself capable of all essential life processes. An *Amœba* (Fig. 19) may consist of a small mass of uniformly granulated protoplasm containing a nucleus. Locomotion is caused by the streaming forward of the protoplasm at some points and the consequent formation of processes of varying

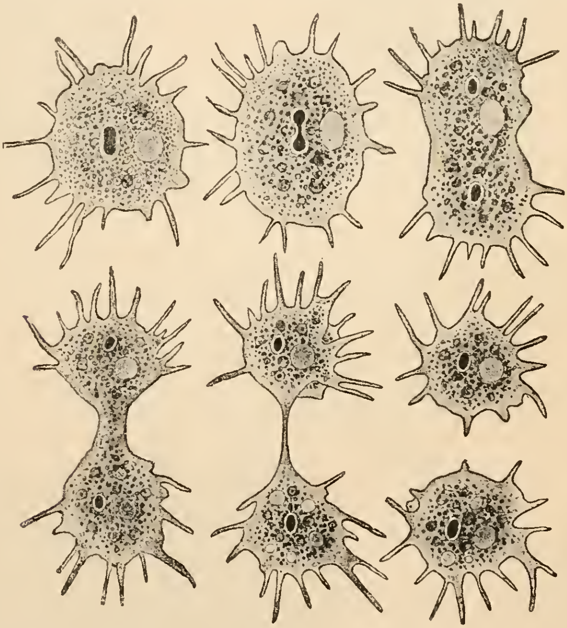

Fig. 19.—**Amœba polypodia.** In the successive stages of division. The light spot is the contractile vacuole, the dark spot the nucleus (after **F. E. Schulze**).

shape (amœboid). At other points processes already formed are withdrawn. The mass of the plasm flows towards the newly formed processes, and locomotion thus appears as an irregular streaming. In this way small foreign bodies are taken into the *Amœba* body; if they can be assimilated they are digested, if not they are left behind as the *Amœba* moves forward. The *Amœba* grows as its nourishment increases. It multiplies by the nucleus becoming constricted in the shape of a dumb-bell and finally dividing into two nuclei. After complete division of the nucleus the plasm of the body also becomes constricted and falls into two parts, each with its nucleus. In this way each daughter *Amœba* is, except in the matter of size, like the mother. **Reproduction by fission.**

I. Protoplasm.

The protoplasm of many Protozoa (of certain *Monera*, of the *Rhizopoda*, a few *Amœba*, and most *Flagellata*) is tolerably homogeneous, *i.e.* uniformly granular. In most cases, however, there is a differentiation into an outer and an inner layer; the former firmer, hyaline or more often finely granular, and generally more contractile **(cortical layer, ectoplasm, ectosarc)**; the latter more liquid and granular **(medulla, endoplasm, endosarc)**. In some *Heliozoa* the endosarc is the more homogeneous, the ectosarc granular. There is generally no sharply defined barrier between the two layers. In the *Radiolaria* the protoplasm is divided by a membrane (capsular membrane) into two parts, the extra- and intra-capsular protoplasm, which, however, communicate with one another by means of various perforations of the membrane, and thus do not correspond with the ecto- and endo-plasm above mentioned. In a similar way, in the *Rhizopoda* with calcareous shells, some of the protoplasm surrounds the shell.

The capsular membrane possesses either numerous fine pores (*Spumellaria*, *Acantharia*), or one single round aperture (osculum), with a porous cover or operculum (*Nasellaria*), or, in addition to two or more apertures, one principal aperture closed by a radially striated cover produced externally in the shape of a tube (*Phæodaria*).

Both ectoplasm and endoplasm are distinguished, in the case of most Protozoa, by special structural modifications and differentiations. The ectoplasm supplies the adaptations for locomotion and alimentation—pseudopodia, cilia, flagella, suctorial tentacles which also serve as feelers, oral and anal apertures. It frequently forms on its surface a **cell integument** (cuticle) which may form the substratum of a great variety of shell structures. The ectoplasm generally also supplies the material for the various skeletons met with in many forms. The contractile vacuoles and the stinging capsules (trichocysts), where such are found, almost always lie in it. In some cases it gives rise to special contractile portions (*Infusoria*, *Vorticella*).

The digestion of solid food takes place in the **endoplasm.** In it lie the nucleus or nuclei. It often contains non-contractile vacuoles, food vacuoles, products of excretion (crystals), fat drops, oil drops, etc., gas-bubbles, pigment granules. The endoplasm occasionally shows slow streamings (**circulation** in *Infusoria*).

In the *Heliozoa*, the protoplasm becomes, by means of the appearance of numerous non-contractile vacuoles, spongy, alveolar. In the *Cystoflagellata* we find a central plasmic portion from which the protoplasm radiates to the surface in a network forming numerous vacuoles. This arrangement of the plasm resembles that in the plant cells. Granular movement can be seen in the cords and strands of the protoplasm ; between them lies cell-sap.

In many true *Flagellata* which take in no solid food but feed in the manner of plants the protoplasm contains small pigment bodies (chlorophyl or similar pigment), organs of assimilation which form amylum. Chlorophyl (proper to the animal body and formed by it) is also to be found in *Infusoria* (in a *Vorticella*) in a dissolved form.

Besides these there are unicellular algæ, which live symbiotically with many forms of Protozoa in the same way as *Algæ* and *Fungi* live together to form lichens (yellow cells, and pigment bodies of the phæodium (?), of the *Radiolaria*, chlorophyl bodies of many *Infusoria*).

II. Adaptations for Locomotion.

The locomotion of the *Amœba* (and many *Monera*) by means of blunt processes of varying shape has been described above. In the *Rhizopoda*, *Heliozoa*, and *Radiolaria*, there are long filose processes of the exoplasm (where such a differentiation exists) which radiate from the body on all sides—the so-called **pseudopodia.** These processes serve, however, more for taking in food and as a hydrostatic apparatus than as organs of active locomotion. There are two principal sorts of pseudopodia—**myxopodia** and **axopodia.** The former are not stiff, they are protrusible and retractile, can fuse with neighbouring pseudopodia into a network, and, chiefly in *Rhizopoda*, can collect into small masses by flowing together outside the body at the points where they meet with food. Such myxopodia are characteristic of the *Rhizopoda* and most *Radiolaria.* The axopodia, which are found in the *Heliozoa* and in *Acantharia* among *Radiolaria*, are, on the contrary, more or less stiff, and not inclined to reticulate and fuse. In their axes there generally runs a stiff axial filament, a sort of elastic organ of support formed of organic substance. These axial filaments run towards the central point of the body—to the boundary of the endoplasm (*Actinosphærium*), or to the nucleus near the centre (*Actinophrys*), or they meet actually in the centre (*Acantharia*). All pseudopodia show more or less swift granular streamings.

In the *Rhizopoda* with calcareous shells, part of the protoplasm spreads itself in a layer over the latter, and from this layer the pseudopodia radiate. In the

Radiolaria, whose bodies are surrounded by a thick gelatinous envelope (calymna), filled with vacuoles and alveoles, the case is more complicated. The extra-capsular protoplasm forms a layer on the exterior of the capsular membrane (**sarcomatrix**) and, further, a network on the surface of the calymna (**sarcodyctium**). From the latter, which is connected with the former by intra-calymnary protoplasmic cords and strands, the extra-calymnary pseudopodia radiate.

Flagella cannot be sharply distinguished from pseudopodia. They are processes of the exoplasm (where such exists) which, in the *Flagellata* and in early stages of the life of many other *Protista*, appear at special points of the body in small numbers (one or two, rarely more).

Undulating membranes have also been observed in a few *Flagellata*. **Cilia** are characteristic of the *Infusoria* and the young stage of the *Suctoria*. These are fine vibratile processes of the ectoplasm, which vary in length, strength, and shape; they are arranged in different characteristic ways in each division, either spreading over the whole body or restricted to certain regions, and specially forming spirals about the mouth, or belts.

In the *Cystoflagellata* (*Noctiluca*), besides the ordinary flagellum at the base of the oral aperture, there is a large **band-like flagellum** which moves slowly; this is a protoplasmic outgrowth of complicated structure (Fig. 11, p. 9, *bg*).

In the *Gregarina* special organs of locomotion are wanting; the ectoplasm here appears peculiarly contractile, just as in the *Infusoria*, where it is often differentiated into parallel contractile and non-contractile strips (furrows and ribs). Another differentiation of the ectoplasm is the so-called **stalk muscle** of the *Vorticella* (Fig. 16, p. 10), which in contracting rolls itself up spirally. Here belong also the **myophrises** of the *Acanthometridæ*—filamentous processes which can contract suddenly, but not repeatedly, and which are arranged on the sarcodyctium in a circle round each skeletal spine. It is supposed that they perform hydrostatic functions.

In the *Suctoria* are found variable processes, mostly terminated by a knob, and used as suctorial tubes, which are closely connected with pseudopodia. The contents of the body of the penetrated *Infusorian* or *Alg* flows through the suctorial tube into the body of the *Acinetan*.

III. Membranes, Shells, Skeletal Formations.

These are extraordinarily numerous. Many *Protista*, *Amœba*, and *Flagellata* are naked. In simple cases the protoplasm secretes at the surface a chitinous **membrane** (*Gromia*), which may be composed of small plates (*Arcella*). Occasionally small foreign particles are united, by a binding medium supplied by the body, into a sort of case (*Difflugia*). A fine cuticle is found in most *Infusoria*; in some cases this may harden into shells or **carapaces**. A cuticle (cell-integument) is further found in *Gregarina* and many *Flagellata*, and can develop into a shell by becoming firmer and severing itself from the protoplasm. The structure of the shell of the *Dinoflagellata* is complicated; in this case alone the shell consists of **cellulose** (the substance of the membrane of plant cells). **Gelatinous envelopes** are also widely dispersed; they are found in *Heliozoa*, all *Radiolaria* (**Calymna**) and many *Infusoria*, especially in the attached forms. In the last case they are often plastered over with small foreign particles. In the marine *Rhizopoda* there arise, by secondary impregnation of an originally chitinous membrane with carbonate of lime, and by a further deposit of the same, variously shaped **calcareous shells**. These have either one chamber (*Monothalamia*) or become many-chambered (*Polythalamia*), with varied arrangement of the chambers. The shells either possess one large aperture for the emission of the protoplasm (*Imperforata*), or they are perforated by numerous fine pores (*Perforata*).

In *Heliozoa* pieces of skeleton come into existence by the impregnation of an organic substratum with **silica**; these generally lie loosely on the surface of the soft body. In *Clathrulina*, however, a globular, much fenestrated, siliceous skeleton is formed.

The skeletal formations of the *Radiolaria*, which are rarely absent, show a wonderful diversity of structure. They consist of fenestrated spheres, several of which, connected by means of rods, are often contained one within another, or of regularly arranged radial spicules, or of bivalve shells, etc. etc. We have to distinguish two altogether different skeletal forms. One consists of **silica** and never penetrates into the central capsule; the other consists of an organic substance akin to chitin (**acanthin**), and is always centrogen, *i.e.* it radiates from the middle of the central capsule (*Acantharia*).

In one principal division of the *Gregarina* (*Polycistidæ*) the extended body is divided by a partition into an anterior part (**protomerit**) and a posterior part (**deutomerit**). Another partition may cut off from the protomerit a front portion serving for adhesion and temporarily provided with hooks, etc. (**epimerit**). The partitions are, like the cell integument itself, products of the ectoplasm.

In contrast to the envelopes and skeletons above mentioned, we have the cysts or capsules. The formation of capsules and cysts (**encystation**) takes place in the most varied Protozoa for protection against dessication and putrefaction, after acquisition of food to admit of undisturbed digestion, in hibernation, etc.; very often reproduction (by fission, gemmation, or sporulation) takes place after the formation of, and under the protection of, a cyst.

IV. Adaptations for Ingestion of Food.

The organs of locomotion (amœboid processes, pseudopodia, suctorial tubules, flagella, cilia, etc.) generally also serve for the seizing and sucking in of food, and for the formation of currents which bring it within reach. There are no special points of the body for the taking in of food in the *Monera*, *Sarcodina*, *Gregarina*, *Suctoria*, and those *Flagellata* which feed after the manner of plants. In other *Flagellata* and in the *Infusoria*, there is at one special part of the body (in the *Flagellata* at the base of the chief flagellum) a depression of the ectoplasm (**mouth** and **œsophagus**), through which solid food is passed into the endoplasm. In the *Infusoria* there are, closely connected with the mouth, cilia specially arranged, in circles or spirals, which whirl into it the minute nutritive particles. A certain part of the body may also temporarily function as mouth. In this case the aperture is only visible at the moment of feeding. An **anal aperture** or **anal spot** can also be found for the evacuation of undigested remnants of food.

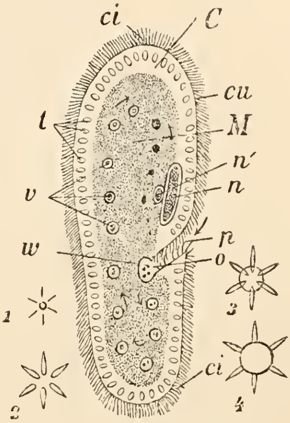

Fig. 20.—**Paramecium aurelia.** *M*, Medulla; *C*, cortical layer; *n*, macronucleus; *n′*, micronucleus; *cu*, cuticle; *ci*, cilia; *t*, trichocysts; *v*, food vacuoles; *p*, pharynx; *o*, cell mouth or cytostome; *w*, water. 1, 2, 3, 4, Formation of vacuole (after **Ray Lankester**).

V. Adaptations for Excretion.

The so-called **contractile vacuoles** may, with doubtful accuracy, be considered as adaptations for excretion, *i.e.* for removing from the body the useless products of metabolism. These vacuoles are found in most *Amœba*, *Heliozoa*, *Flagellata* (excepting *Cystoflagellata*), and *Infusoria*, but are wanting in the *Rhizopoda*, *Radiolaria*, *Gregarina*, and *Cystoflagellata*. They vary greatly in number. Where there is only one it generally has a fixed position. There is no sharp distinction between contractile and non-contractile vacuoles. The first are vacuoles without walls, filled with liquid, which in cases where a differentiation into ecto- and endo-plasm exists generally lie in the former. They gradually expand and then contract more quickly, often suddenly. Before and during contraction they move towards the surface and empty out their contents through an aperture only visible at the moment of evacuation. They again arise as a small drop, or as several drops which unite later. Perhaps they also serve the purpose of keeping up an exchange of water (evacuation of water taken in by the mouth), and thus of **respiration**.

VI. Trichocysts.

Small vesicles containing threads, which can be shot out rapidly like the nematocysts of the *Cœlenterata*, are sometimes found in the ectoplasm of the *Infusoria* and in one of the *Flagellata* (Fig. 20 *t*).

VII. Stigmata (red eye-spots).

Stigmata are found, generally singly, in many coloured *Flagellata*. It is highly doubtful if these are organs sensitive to light.

VIII. Nuclei.

These seem to be absent in the *Monera*. In all the other Protozoa they are found, either singly (many *Amœba*, some *Heliozoa*, all *Gregarina*, and most *Flagellata* and *Infusoria*) or in numbers. They lie in the endoplasm—in the *Radiolaria* in the central capsule, in the *Gregarina* in the deutomerit—and are either **vesicular**, with membrane, sap, and one or more nucleoli, occasionally with a sort of nuclear framework, or **homogeneous**. They vary greatly in shape. The nuclear processes in most *Infusoria* present complications. We here find a double nucleus, viz. a large **macronucleus**, and, lying more or less close to this, a small **micronucleus** (formerly erroneously called nucleolus). The micronucleus plays an important part in conjugation; the macronucleus, on the contrary, during this process falls to pieces and degenerates in a peculiar manner. When conjugation begins, the micronucleus divides twice, *i.e.* into four parts. Three of these four parts disappear, while the fourth again divides into two nuclei—the **migratory** nucleus and the **stationary** nucleus. The most important process during conjugation is the mutual exchange of the migratory nuclei of the two conjugating individuals **A** and **B**. The migratory nucleus of A passes over into B and fuses with the stationary nucleus of B, while the migratory nucleus of B passes over into A to fuse with the stationary nucleus of A. A new macronucleus and a new micronucleus arise, in the individuals which separate after conjugation, out of the nucleus which results from the fusing of the migratory and stationary nuclei.

The division of the nucleus is either a direct division (constriction, dumb-bell stage, separation into halves), or it resembles the indirect nuclear division found among Metazoa, which will be described later.

IX. Reproduction.

The phenomena of reproduction among the Protozoa deserve more detailed investigation, as we find included under this head a tolerably complete series of intermediate stages between the simplest reproduction by fission and sexual reproduction.

Reproduction by simple **binary fission** (cross, longitudinal, and diagonal fission) takes place in nearly all divisions of the Protozoa. It is especially characteristic of the *Monera*, many *Rhizopoda*, many *Flagellata*, and all *Infusoria*. It is, however, not observed in the *Gregarina*.

Reproduction by **budding** or **gemmation** is, in the simplest cases, distinguished from the above in that one part (**the bud**) is smaller than the other (**the mother**). The small size of the bud in most cases makes possible the production of numerous buds on the surface of the mother. This sort of reproduction is often found together with reproduction by fission in *Rhizopoda*, *Heliozoa*, *Radiolaria*, a few *Gregarina*, *Noctiluca*, and *Suctoria*.

In many forms reproduction by fission and gemmation are probably preceded by a **conjugation** (temporary connection or fusing) or **copulation** (permanent fusing) of two individuals.

In many Protozoa, belonging to the most varied forms, the individuals which are produced by fission or gemmation do not separate entirely from each other, but remain more or less closely connected, and so form colonies of unicellular organisms.

These colonies are of the greatest importance, as they represent a lower stage of the cell colonies of the Metazoa, and in many cases reproduce in a manner which strongly reminds us of the sexual reproduction of Metazoa and plants (see below).

As an example of reproduction by gemmation we choose the *Noctiluca*, where it occurs, probably after previous copulation of two individual *Noctiluca*, side by side with simple reproduction by fission. The typical process is briefly as follows. Gemmation occurs only in such individuals as have, when copulation has ended, lost their organs of locomotion and mouths, and are thus simple globular bodies, on the walls of which the chief mass of protoplasm (central plasm), with the nucleus, is still to be found in its original place. The central plasm at this spot bulges out somewhat, its nucleus divides by a kind of indirect fission, and the prominence at the same time separates into two by a furrow. The division of the protoplasm is, both here and in the following stages, merely superficial, since its deeper part remains undivided. By continuous fission, 4, 8, 16, 32, 64, and up to 512 nuclei arise, and the same number of superficial prominences of protoplasm. Then each prominence with its nucleus separates below the surface also from its neighbours and forms a separate bud, on which a flagellum and a peculiar process are developed; this bud leaves the mother animal as a **spore** (Fig. 11, *b*, *c*, p. 9). The further development of these spores into young *Noctiluca* has not yet been investigated. The whole process of the formation of buds is very similar to the discoidal furrowing of the meroblastic egg in the Metazoa, of which we shall speak later.

Reproduction by **continuous fission** and **spore-formation** is very common among the Protozoa. In the latter case the whole body falls to pieces, or else the greater part of it simultaneously dissolves into a usually very large number of nucleated portions, *i.e.* **spores**. Both these methods of reproduction are generally accomplished in resting encysted individuals, and often after previous copulation or conjugation; this is especially the case with *Gregarina* and *Flagellata*. They may occur together with ordinary reproduction by fission. The spores are generally capable of free movement, occasionally amœboid, or as swarm spores they are furnished with a flagellum or several flagella (*Flagellata*, *Radiolaria*, some *Heliozoa*, and *Rhizopoda*). Occasionally (*Gregarina*) the spores themselves redivide, and only the portions thus arising grow into adult animals.

Reproduction of Colony-forming Protozoa.

Freely swimming and stationary attached colonies alike come into existence by incomplete fission and gemmation. Among the colonial *Radiolaria* (the *Polycyttaria* among the *Spumellaria*) separate colonies can mingle with each other; colonies also can multiply by fission.

The ordinary method of reproduction of colonial *Flagellata* and *Radiolaria* is the production of swarm spores furnished with flagella, which takes place by simultaneous, or more often by successive, division of the body into numerous portions.

In the *Radiolaria* the contents of the central capsule alone take part in the formation of spores; and this process is preceded by the early or later division of the originally simple nucleus. In the case of *Radiolaria* which do not form colonies, every spore becomes a *Radiolarian.* In the colonial species, however, two sorts of spores are developed alternately—(1) **isospores**, representing the usual *Radiolarian* spores, and (2) **anisospores**, of which again there are two kinds, smaller **microspores** and larger **macrospores**. The isospores develop direct into young *Radiolaria*; the anisospores most probably do so only after the copulation of a micro- and a macro-spore. The young *Radiolarian*, by repeated fission and gemmation (formation of so called extracapsular bodies), produces a colony. The macro- and micro-spores are either formed in one and the same individual, or in different individuals of the colony. We have here in all probability a regular alternation of generations, one of which reproduces by means of isospores, the other by copulating anisospores.

The reproduction of the **colony-forming Flagellata** is particularly important and interesting. In the simplest cases every individual of the colony falls by successive fission into a certain number of portions which sever themselves from the mother-colony, forming daughter-colonies. In other cases (*Pandorina*), after a number of generations reproducing themselves as above, a generation arises whose individuals also divide; but the resulting portions (**gametes**) do not remain united, they separate. These gametes copulate in pairs, the individuals of each pair often differing in size. The product of copulation (**zygote**), after a resting stage of some duration, again produces a colony by continuous incomplete fission. The reproduction of the *Eudorina* is distinguished from that of the *Pandorina* by the formation of two sharply contrasted sorts of gametes, male and female. The **sexual** generation which produces gametes, and which follows a series of generations reproducing in the usual asexual manner, is either male or female. In the female colony there are certain individuals (**ovoid gametes**) distinguished by unusual size; in the male the individuals divide into groups (plates) of 32-64 **spermoid gametes**, each of which has two flagella. The plates sever themselves and swim about freely. If such a structure comes in contact with a female colony, it remains attached to it and breaks up into single male gametes. *Volvox* (which leads almost directly by its method of reproduction to the higher plants and animals) is closely connected with *Eudorina.*

In *Volvox* (Fig. 21) the colony appears on a higher scale of development, as a division of labour takes place among the different individuals. Only some individuals are capable of reproduction; in the asexual generation these individuals are the **parthenogonidia** (every parthenogonidium produces, by continuous incomplete fission, a colony which separates from the mother colony); in the sexual generation they are **gametes.** Unlike the *Endorina*, *Volvox* produces, in one and the same colony, male and female gametes. The female gametes are simple individuals of the colony, only distinguished by their greater growth. The male gametes, on the contrary, arise in masses, by the successive fission of certain individuals (cells) of the colony. From one such mother-cell as many as 128 male gametes may proceed. The male gametes separate, move about by means of their flagella, and copulate with the female gametes. By successive division (into 2, 4, 8, 16, and so on) of the stationary zygotes a colony, *i.e.* a young *Volvox*, arises.

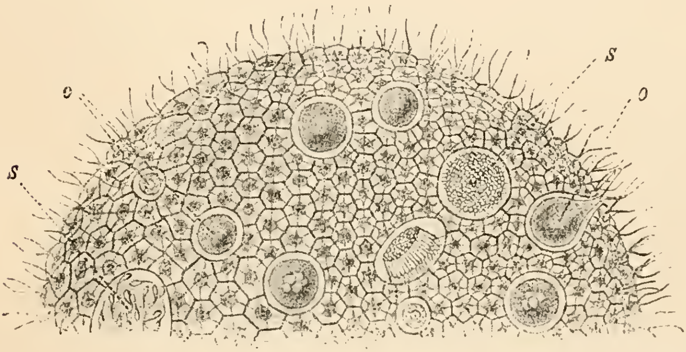

Fig. 21.—**Volvox globator.**—Sexual, hermaphrodite colony, after **Cienkovsky** and **Bütschli**, combined and somewhat diagrammatic. *S*, Male gametes (spermatozoa); *O*, female gametes (eggs).

We have here before us a true **alternation of generations,** asexually reproducing generations alternating with sexually reproducing generations. The sexual reproduction corresponds with the method of reproduction of the Metazoa and higher plants. The hermaphrodite *Volvox* (*Flagellate* colony) corresponds with a very simple hermaphrodite metazoon. The female gametes represent the eggs, the male gametes the spermatozoa; the copulation of the female and male gametes corresponds with a simple form of fertilisation of the egg by means of spermatozoa. The zygote represents the fertilised egg. The formation of a new Volvox colony by successive fission of the zygote answers to the repeated division of the egg-cell, described in the Metazoa as **furrowing** or **segmentation.**

In the colonial *Infusoria* also the copulation of larger with smaller individuals has been observed (Fig. 16, p. 10, *c*).

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Egg Cells, Sperm Cells, Fertilisation, Sexual Reproduction of the Metazoa.

Whereas Protozoa are either simple cells or colonies of similar cells, all other animals, or Metazoa, appear as complicated communities, the individual cells of which are no longer similar. **Division of labour** arises among the cells; every cell (or group of cells) in the community having to fulfil only one special function is constituted in correspondence with this function (polymorphism of the cells of a Metazoan colony). However wonderfully complicated such a cell community may be, it always develops (except in cases of asexual reproduction) by means of the continuous division of one single cell, the fertilised egg. This is the product of the fusing of a female reproductive cell with a male reproductive cell, *i.e.* it is the result of fertilisation. Reproduction by means of such sexually differentiated reproductive cells is called **sexual reproduction.** In all forms of Metazoa (with a few not quite certainly established exceptions) sexual reproduction occurs at least at times, and constitutes an essential characteristic by which Metazoa are distinguished from Protozoa. It is true that we found in the latter the beginnings of sexual reproduction. As among the Protozoa a series of phenomena lead up to the sexual reproduction of the **Volvox colony,** so the latter is directly connected with the simplest form of the sexual reproduction of the Metazoa.

In sexual reproduction we have to bear in mind two distinct points:

1. **The fusing of the cells, or more accurately of two cell nuclei, which here takes place**—a phenomenon which is analogous to the processes of copulation and conjugation in the Protozoa. The

origin and meaning of this phenomenon are not certainly ascertained. Many see in them a strengthening of the product of the fusion, *i.e.* the young new individual.

2. The different sizes, or the **the sexual dimorphism of the fusing reproductive cells.** This is to be explained by the principle of the division of labour. The reproductive cells have a double object to fulfil: (1) such a cell must mingle with another (**fertilisation**); and (2) must, after mingling, form a new organism like that of its parents. To secure the first object **free locomotion** is useful, so that the reproductive cells may seek each other and meet; and further, in certain circumstances a **power of resistance** to external influences is needed. To fulfil the second object the cell must be of a considerable size, and contain, if possible, **nutritive material** which can be used during development. Both these objects cannot be fulfilled by each of the reproductive cells without disadvantage. Here division of labour steps in. Some cells fulfil the first object; they move about with great ease; they are resistent, and moreover very small (the smallest cells of the organism). Their smallness has a further advantage; they are produced in greater numbers, and can easily penetrate the second sort of reproductive cell. These are called male reproductive cells, **sperm cells, sperm filaments,** or **spermatozoa.**

Other cells fulfil the second object. They are large and often filled with much reserve material (the largest cells of the organism). They substitute size and mass for free locomotion. These are called female reproductive cells, or **egg cells.**

Male and female reproductive cells are either formed in one and the same metazoan individual (**hermaphroditism**), or in two different individuals, male and female (**gonochorism, separation of the sexes**). The latter appears among the Metazoa generally as the rule, the former as the exception. The causes which determined the separation of the sexes are most probably quite similar to those which brought about fertilisation in the animal kingdom. If one remembers that even among hermaphrodite animals a copulation of two individuals often takes place, or adaptations are present which prevent the fertilisation of the eggs of an animal by the spermatozoa of the same individual (self-fertilisation), the recent opinion that all Metazoa were originally sexually separated, and that hermaphroditism has developed secondarily from the male or female condition gains in probability.

The utility of cross-fertilisation places in a new light the utility of a sexual differentiation of the reproductive cells into freely movable spermatozoa and massive eggs. So as still further to secure cross-fertilisation we find copulation in very many Metazoa. These animals possess special copulatory organs, by means of which the spermatozoa from the male body are carried into the sexual organ of the female, and thus into the neighbourhood of the egg.

The Animal Egg.

The mature egg, capable of fertilisation, is everywhere in the animal kingdom a simple cell, and shows the typical structure of such a cell. It consists of protoplasm, called **yolk**, and of a nucleus which is named the **germinal vesicle** in an unfertilised egg. The egg is either naked or surrounded by one or more **membranes** and **envelopes.** These are of very different nature according to their origin. They are either secreted by the egg cell itself, and then answer, as real primary **yolk** or **egg integuments,** to the membranes of ordinary cells, or they are in various ways supplied by the surrounding tissues of the mother body, and are laid round the egg externally. In this case they may be considered as secondary or **accessory egg envelopes.** The eggs arise in special organs of the Metazoan body, called **ovaria** or **germaria.** These, in the simplest cases, are masses of cells, some of which by stronger growth become egg cells.

The processes of the formation, growth, and ripening of the egg in the animal kingdom are as various as is the structure of the ovary itself. It is especially the necessity for the abundant **nourishment** of the eggs which determines the most manifold modifications. The eggs are developed either from a mass of protoplasm with nuclei scattered in it, or from an assemblage of similar little cells clearly defined one from the other. In the first case the nuclei, in the second the cells, multiply by fission. After this multiplication has lasted for some time the protoplasm round the nuclei in the first case separates off and gives rise here also to independent cells. All these young cells are young egg germs, and capable of growing and ripening into eggs; but only in the rarest cases do all the cells become eggs—a large number of germ cells have almost always another fate.

The nourishment of the egg, speaking generally, is secured in the following ways. In animals without a blood-vascular system and body cavity the ovaries lie on the wall of the intestine, or of a gastro-vascular system, which proceeds from the main intestine (*Cœlenterata*, *Platodes*). In many animals the eggs are developed on the wall of the body cavity and nourished by the body fluids, into which they sooner or later pass and mature while suspended in them (many higher worms). In the case of the greater number of the higher animals the nourishment of the egg is secured by a rich provision of blood-vessels in the ovaries. In those cases where only some of the egg germs are developed into eggs, the remainder often serve as nourishment for these or contribute to their nutrition. Amœboid moving egg cells can feed upon the neighbouring egg germs after the manner of *Amœbœ*; or the surrounding egg germs store up food, which they give over to the growing egg cell, either by emptying their contents into it (*Cephalopoda*) or by transfusion (follicle formations). In *Insects* the egg germs can develop in the ovaries alternately into nutritive cells and egg cells. In most *Platodes* the case is very complicated; the germ cells of an original germarium here fall into two more or less distinct groups. The germ cells of one group (**germarium**) become egg cells; those of the other group (**vitellarium**) become nutritive or yolk cells filled with nutritive yolk. In other *Platodes* only some of the originally numerous germaria retain their primitive function, while all the others are changed into vitellaria to supply nutritive yolk. The eggs either absorb the nutritive yolk of the yolk cells before fertilisation, or else many yolk cells are stored in an egg capsule together with a few fertilised egg cells, and are used up during development.

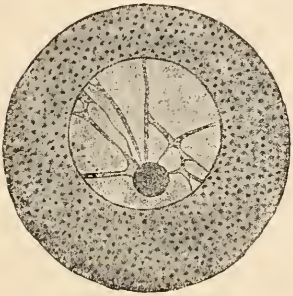


Fig. 22.—**Ovarian egg of an Echinoderm**, after **O. Hertwig.** In the middle the germinal vesicle with the nuclear framework and the germinal spot.

The **nucleus** or the **germinal vesicle** (**vesicula germinativa**) of the animal egg is remarkable for its relatively great size. It consists of an outer layer, in most cases differentiated into a distinct membrane, surrounding the light-coloured clear **nuclear fluid.** In this lie **one** or **more solid nucleoli** or **germinal spots** (**maculæ germinativæ**), which are often connected with each other and with the nuclear membrane by a **network of fine threads.** In many eggs the germinal vesicle lies, throughout, in the centre of the egg; in others it does so at least in the very early stages.

The Egg Yolk.

Investigations made by means of the improved optical appliances for research have lately shown that protoplasm itself (in Protozoa, egg cells, and tissue cells) exhibits a fine structure. It consists of very small firmer particles, arranged in the finest network of threads, which form the **spongioplasm**, and, lying between them, clear homogeneous more fluid portions, forming the **hyaloplasm.** Protoplasm thus constituted only in the rarest cases forms the whole of the yolk. In most cases reserve nourishment in the form of fat or oil drops, small plates and spheres, is found in the protoplasm, these being used as food by the developing egg. These constitute, in contradistinction to the **formative yolk**—*i.e.* the actual living active **protoplasm** of the egg—an inert lifeless constituent, only serving as nutriment, the **deutoplasm** or **nutritive yolk.** The quantity and arrangement of the deutoplasm in the egg is of great importance, since this determines the course of its first segmentation.

It rarely happens that there is no deutoplasm in an egg. Less rarely we find only a very small quantity equally distributed throughout the protoplasm (**holoblastic alecithal eggs**, Fig. 23, *C*). Such eggs are found among animals which can at a very early stage of development find their own food, or else among those whose embryos are developed within, and nourished by, the mother body.

In most cases the egg contains a considerable quantity of nutritive yolk. Two different types of eggs are distinguished, according to the arrangement and position of this yolk.

I. Types of Telolecithal Eggs.

A. In the simplest case the comparatively small quantity of nutritive yolk is imbedded in the formative yolk, principally in one hemisphere. This hemisphere is called the **vegetative**; the other, which contains the germinal vesicle, the **animal** hemisphere. Corresponding animal and vegetative poles are also distinguished.

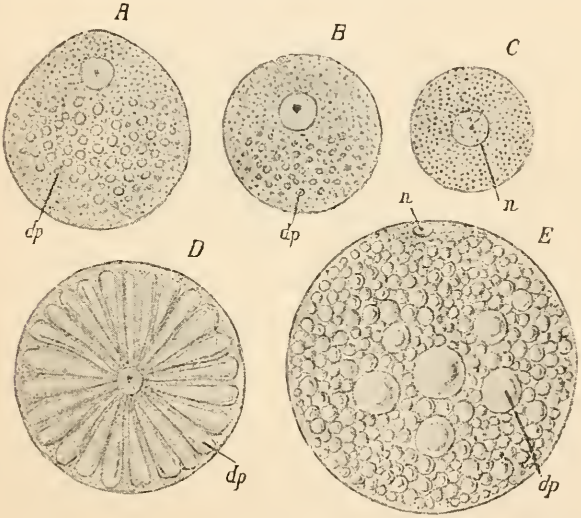


Fig. 23.—**Structure of different eggs.** *A* and *B*, **Holoblastic telolecithal eggs.** *C*, **Holoblastic alecithal egg.** *D*, **Centrolecithal egg** (of a spider). *E*, **Meroblastic telolecithal egg.** *dp*, Deutoplasm; *n*, nucleus, or germinal vesicle.

B. The quantity of the nutritive yolk increases so much that the formative yolk is reduced to a smaller or larger segment at the animal pole, in which lies the germinal vesicle. Besides this a thin layer of protoplasm spreads all round the egg as a rind. In the remaining portion of the egg the formative yolk is so much displaced by the development of the nutritive yolk, that it remains merely as a cementing substance in the interstices between the elements of the latter (**holoblastic telolecithal eggs**, Fig. 23, *A*).

C. The quantity of formative yolk is, in comparison with the enormously developed nutritive yolk, so small that it is only a small mass enclosing the germinal vesicle at the animal pole, and a very thin layer round the whole egg. In by far the greater part of the egg the formative yolk is quite supplanted by the nutritive yolk (**meroblastic telolecithal eggs**, Fig. 23, *E*).

II. Types of Centrolecithal Eggs.

The formative yolk is arranged in a regular layer round the whole egg, and besides this in a mass containing the germinal vesicle at the centre of the egg. The region between the centre and the circumference is occupied by nutritive yolk, either

A. In largely preponderating quantity (**holoblastic centrolecithal eggs** of many *Crustaceans*), or

B. Almost, or quite exclusively (**meroblastic centrolecithal eggs** of the *Tracheata* and many *Crustaceans*, Fig. 23, *D*).

The Egg Envelopes.

These are divided into (1) **primary** envelopes—yolk membranes, egg membranes; and (2) **secondary accessory** envelopes.

I. The **yolk membrane** is secreted by the yolk itself. It can be formed at different stages of the ripening of the egg, and shows great diversity of structure. Occasionally it is double. It is often penetrated by numerous pores (**zona radiata**). Not infrequently there is a special opening, the **micropyle.** Both the pores and the micropyle are connected with the nutrition of the egg, and serve in many cases for the passage of the spermatozoa.

II. The secondary envelopes are also very various. They are alike in one point—none of them are formed by the egg itself.

a. The **chorion** is a membrane which is very often secreted by the cells of the ovary which surround the egg (follicle cells). It lies between the egg and the follicle cells.

b. Other **accessory envelopes** are sometimes found, which are only added to the egg later by means of special glands on its way through the passages leading out of the ovaries. Such are the egg capsules, albuminous and gelatinous envelopes, calcareous shells, etc. Either only one of these egg envelopes is formed, or else two or more are simultaneously produced.

As an example of the development and ripening of an egg, we choose first the egg-formation of the mussel (Fig. 24, *A*, *B*, *C*). The eggs here arise out of definite cells of the germinal epithelium, which grow more strongly and soon project beyond the epithelium, with which, however, they remain for a time connected by a long stalk-like process. Through this stalk, in all probability, the nourishment of the egg by the epithelium takes place. Yolk granules, continually increasing in number, appear in the protoplasm of the egg. The nucleus becomes vesicular. The egg secretes on its surface a yolk integument, which is broken through at the point where the egg joins the germinal epithelium, so that when the egg severs itself an opening, the micropyle, is left.

The marine planaria offer a further example of a simple egg-formation (Fig. 24, *D*). These possess very numerous ovaries, whose nourishment is provided for by their position between the branches of the intestine and close to its walls. In each ovary there is a small germinal layer (*kl*) formed by a mass of small cells with nuclei and little protoplasm. Some of these cells grow and become eggs, numerous yolk granules forming in them, and their nuclei changing into the characteristic germinal vesicle. Other cells remain small; they take up a position between the strongly growing egg cells, and so form a framework in the ovary, which is continued into the oviduct.

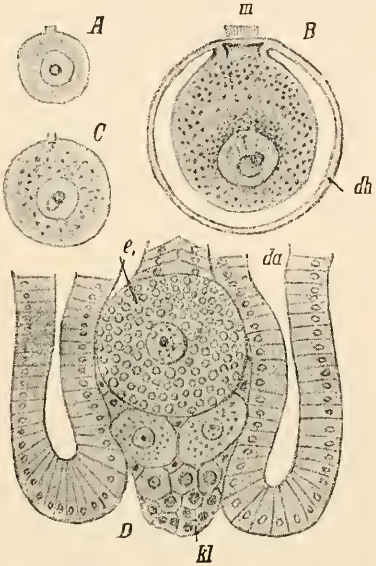


FIG. 24.—*A*, *B*, *C*, **Three ovarian eggs of a mussel in different stages of development**, after **Fleming.** *m*, Micropyle; *dh*, yolk membrane. *D*, **Ovary of a marine planarian** with eggs in different stages of development; *da*, branch of the intestine or gastro-canal; *kl*, germinal layer; *e*, advanced egg.

As a type of a perfect **meroblastic telolecithal egg** with complicated envelope-formation we have the **bird's egg** (Figs. 25 and 26). The egg is fertilised within the mother body, and has already begun to develop when it is laid. The different parts which can then be recognised have very different meanings and origins. In the interior of the egg we recognise the yellow yolk sphere, the well-known yellow of the egg (Fig. 25). This is formed in the ovary, and represents the real egg. In the ovary it is merely a simple meroblastic egg cell, consisting of the following parts:

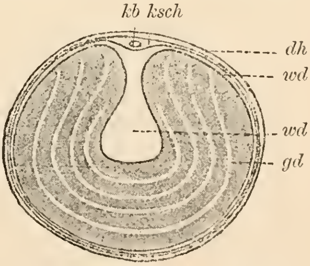


FIG. 25.—**Ovarian egg cell of a Fowl.** *ksch*, Formative yolk; *kb*, germinal vesicle; *wd*, white yolk; *gd*, yellow yolk; *dh*, yolk membrane. (After **O. Hertwig.**)

1. An outer yolk membrane, secreted by the yolk itself.
2. The formative yolk, a small whitish mass in which lies the germinal vesicle at one pole of the egg, viz. the animal pole.
3. The **yellow nutritive yolk**, which represents the principal mass of the egg, and which appears in concentric layers.
4. The **white nutritive yolk**, which forms a thin outer layer round the yellow yolk beneath the yolk integument and the formative yolk, and which also sinks into the middle of the yellow yolk from the animal pole in the form of a thick strand with a swollen rounded end.

When the egg thus formed passes out of the ovary into the oviduct, the walls of the latter secrete around it the last envelopes, which are:

1. The **albumen** with the **chalaza**, *i.e.* somewhat denser spirally twisted strands of albumen, which go from the yolk membrane out towards the two ends of the egg.

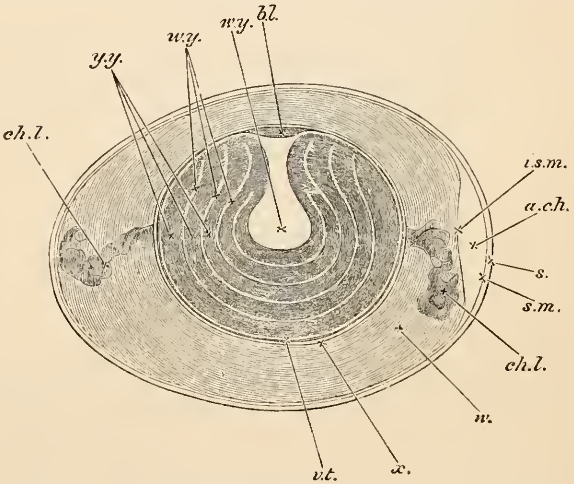


FIG. 26.—**Diagrammatic longitudinal section of a newly-laid Hen's egg, after Allen Thomson and O. Hertwig.** *b.l.* Formative yolk; *w.y.* white yolk; *y.y.* yellow yolk; *w.* albumen; *ch.l.* chalaza; *a.ch.* air-chamber; *i.s.m,* inner; *s.m.* outer layer of the shell membrane; *s.* shell. *v.t.* yolk membrane; *x.* a somewhat fluid layer of albumen surrounding the yolk.

2. The double **shell integument**, which surrounds the albumen on all sides. The two membranes which form this integument separate, and between them a cavity filled with air arises at the blunt end of the egg—the **air chamber.**
3. The porous **calcareous shell.** These three parts, therefore, represent the accessory integuments of the egg.

Male Reproductive Cells, or Spermatozoa (Fig. 27).

These belong to the smallest cells formed in the animal body. Each spermatozoon is a simple cell, as is shown by its development which is generally complicated, and is very difficult to observe. A very common form of the spermatozoon is the so-called **pin-shaped.** Such a spermatozoon consists of a small knot, **the head,** representing the remains of a cell nucleus, and a mobile filamentous appendage, the **tail**, which is of protoplasmic nature, and is much like the flagellum of the *Flagellata*. Besides the tail there may be accessory flagella. Between the head and the tail a special intermediate portion is sometimes interposed. Other forms of spermatozoa are occasionally found; round, pear-shaped, etc., either stationary or moving like *Amœbæ*. The spermatozoa arise in the testis from a germinal layer or epithelium, as do eggs. After repeated division of the original formative elements, cells are produced which are equivalent to egg germs, and which may be distinguished as **sperm germs**. Whereas, however, the egg germs become eggs direct by means of growth and maturation, the sperm germs are still further divided and produce spermatozoa. We have already seen a phenomenon similar, though not in all points parallel, in *Volvox*. An ordinary cell of the colony there becomes by growth a large egg, or by division a mass of small spermatozoa.

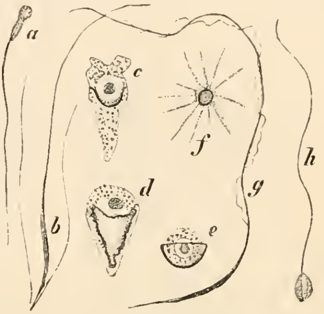


Fig. 27.—**Various forms of Spermatozoa.** *a*, Of a Mammal; *b*, of a Turbellarian, with two accessory flagella; *c*, *d*, and *e*, of *Nematoda*; *f*, of a *Crustacean*; *g*, of a *Salamander* (with undulating membrane); *h*, The commonest pin-shaped form.

Maturation of the Egg.

The **ejection of the directive or polar bodies** is the last stage in the maturation of the egg which precedes fertilisation. The germinal vesicle moves towards the surface of the egg (towards the animal pole in the case of eggs differentiated into poles), and here undergoes

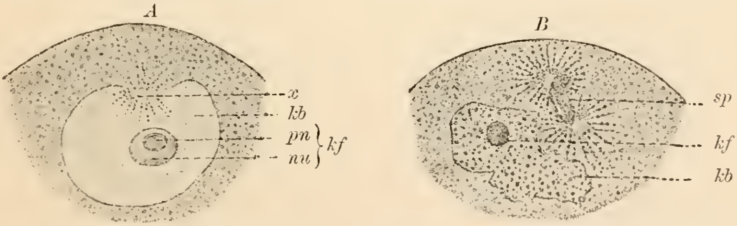


Fig. 28.—**Disorganisation of the germinal vesicle and formation of the nuclear spindle in eggs of Asterias glacialis, after O. Hertwig.** *x*, Prominence of protoplasm; *kf*, germinal spot which divides into two distinct substances, *pn* and *nu*; *kb*, germinal vesicle; *sp*, nuclear spindle.

considerable changes. It becomes partially disorganised (Fig. 28). Out of part of its contents is formed that spindle-shaped figure (Fig. 28, B) which is characteristic of indirect nuclear division (see below, pp. 35,36). The one half of the spindle enters a small mass of protoplasm which projects from the surface of the egg. This prominence then becomes completely constricted off from the egg (Fig. 29) as the first polar body. In a similar manner a second polar body is formed. The formation of a polar body thus appears like a process of gemmation, or a sort of cell division, in which one cell—the daughter cell—the polar body, is very much smaller than the other—the egg.

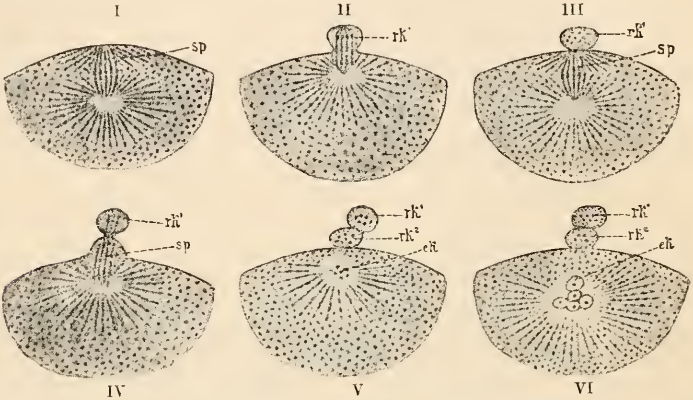


Fig. 29.—**Formation of the polar bodies in Asterias glacialis, after O. Hertwig.** *sp*, Nuclear spindle ; rk^1, first, rk^2, second polar body ; *ek*, female pronucleus.

The half of the nuclear spindle which remains in the egg after the formation of the second polar body changes into an egg nucleus very different from the original germinal vesicle, especially in its size, being much smaller. This germ is known as the **female pronucleus.**

In many divisions—*e.g.* many insects,—there are species in which, alternating with the sexual generations, which multiply by means of fertilised eggs, there occur other generations, which reproduce by means of **parthenogenetic eggs,** *i.e.* by means of such eggs as develop without fertilisation. In these eggs, according to some observers, only one polar body is formed. Many hypotheses have been brought forward as to the meaning of all these various phenomena of maturation. I can here only refer to the works of **Bütschli, Balfour, Minot, Sabatier, van Beneden, Weismann.**

Processes similar to those of the expulsion of the polar bodies from the egg have been observed in the formation and ripening of the spermatozoa. The nucleus of the ripe spermatozoon is called the **male pronucleus.**

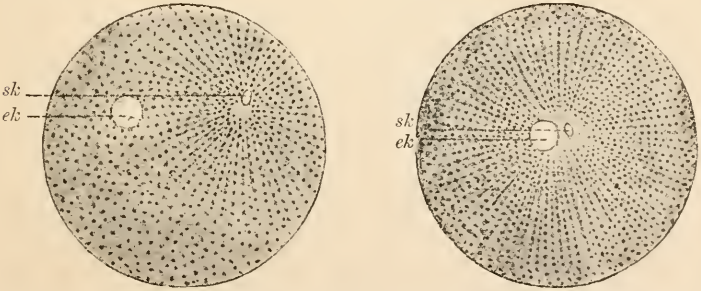
When the polar bodies have been expelled the egg is capable of fertilisation.

Fertilisation.

This process takes the following course; out of numerous spermatozoa pressing towards the egg there is only one, normally, which fertilises it. This is the one which first touches the egg at a definite point as it appears, viz. at the animal pole, in eggs differentiated into poles, near the polar bodies. Here, at the touch of the head of the spermatozoon, a prominence of the outer protoplasmic layer is formed—the **receptive prominence**—into which the spermatozoon penetrates. Gradually it presses further into the egg, its tail seeming to fuse with the protoplasm of the egg; the head (the remains of the original nucleus) increases somewhat in size. As male pronucleus, it moves forward to meet the female pronucleus. Finally they fuse and form one single nucleus, the so-called **segmentation nucleus.** The egg is fertilised.

Fig. 30.—**Fertilisation of eggs of Asterias glacialis**, after **Fol** (from **O. Hertwig**'s *Lehrbuch der Entwicklungsgeschichte*). One of the spermatozoa which have entered the mucilaginous envelope comes in contact with the receptive prominence. In *C* the yolk membrane is formed.

It seems tolerably certain that where the egg envelopes have a micropyle, the spermatozoon enters through it. When the first spermatozoon has penetrated the egg, the micropyle is closed by a fresh secretion from the yolk, so that no more spermatozoa can enter.



Figs. 31 and 32.—**Fertilised eggs of a Sea-urchin**, after **O. Hertwig**. Male (*sk*) and female (*ek*) pronuclei moving towards each other.

In other cases, at the moment when the first spermatozoon presses in, a membrane begins to rise from the yolk, which makes the entrance of other spermatozoa impossible. There are adaptations also with the object of preventing the entrance into the egg of more than one spermatozoon.

Abnormally, two or more spermatozoa may enter an egg. In such a case several male pronuclei may fuse with the female. Compare on this point the works of **Fol** and **Hertwig.** It is not improbable that twin- and triple-formations may be produced by such over-fertilisation. The development after over-fertilisation in all cases deviates characteristically from the normal course.

The most essential morphological characteristic of fertilisation is the fusing of two sexually differentiated cell nuclei, the male and the female pronuclei. In the conjugation of the Protozoa (*Paramœcium*) also we have to do (*cf.* p. 18) with a fusing of two nuclei (the stationary and the migratory nucleus). Fertilisation in this latter case, however, is mutual, and we cannot distinguish the conjugating cells as male and female.

Fertilisation is either internal, *i.e.* takes place within the mother body, or external, *i.e.* spermatozoa and eggs are expelled from the parental bodies and meet each other outside in water. In the first case at least the reproducing animals possess special organs of copulation.

Various theories about the nature of fertilisation have been recently brought forward, especially by Bütschli, Balfour, Sabatier, van Beneden, Hertwig, Weismann, Geddes and Thomson, and others.

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Tissue Cells and Cell Tissue.

We have till now considered (1) unicellular organisms, and (2) the egg- and sperm-cells, which fuse to form the starting point in the individual development of all the higher, *i.e.* multicellular, animals. We will now briefly deal with the manner in which the Metazoan body is composed of cells, and consider the various cells of which it consists. The observation of the cells of the animal body and of their complexes, the tissues, is the object of the **science of tissues** or **Histology.** How different cells and complicated tissues arise out of simple indifferent cells, is the subject of **Histogeny.**

As our first principle we can state that **all cells and tissues of the adult animal body arise by means of repeated division from the fertilised egg-cell.** These phenomena of division are the same as those with which we became acquainted among the unicellular Protozoa as widely spread asexual reproductive processes. Whereas, however, in most Protozoa the products of division separate, and, like the mother cell, lead an independent life, in the Metazoa the descendants produced by repeated fission of the fertilised egg-cell remain bound together in space. Similar cases were found among the Protozoa; we called them cases of colony formation. While, however, there, all the cells of the colony remained alike and each maintained itself quite like a Protozoan individual, the cell communities of the Metazoa by dividing among the individual cells the various duties of life, so that some cells are exclusively adapted for the performance of one function, some for the performance of another, raise themselves into stable and well-ordered states, the citizens of which (the cells) are dependent upon one another and can no longer exist alone.

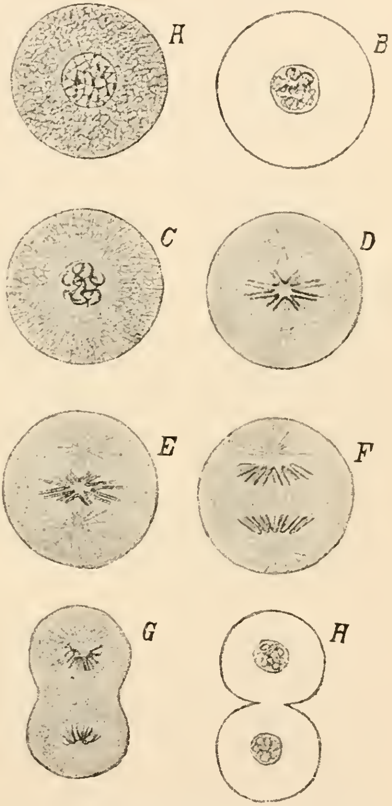

Fig. 33.—*A-H*, Consecutive stages of cell-division, with indirect division of the nucleus (diagrammatic).

The division of the egg-cell and its descendants occurs under peculiar inner conditions, which chiefly concern the nucleus. **Direct nuclear division** during cell division is distinguished from **indirect or karyokinetic nuclear division.** The first and, as it appears, the rarer agrees in essentials with that already figured in the *Amœba* (p. 12, Fig. 19). The second shows various modifications. The following course may be taken as typical (Fig. 33, *A-H*).

[Among the constituents of the cell nucleus are to be distinguished the **achromatin,**—that part which does not stain at all or only very slightly when treated with colouring solutions, viz. the nuclear fluid, and a part of the constituents of the fibrous net-work;—and **chromatin,** which freely imbibes colouring matter, viz. the nucleoli and other granules of the fibrous network.]

1. At the beginning of cell division, there appear near the nucleus two opposite attraction centres, round which the portions of protoplasm group themselves in a radiate manner (formation of the **amphiasters**). The chromatin of the nucleus arranges itself as a tangle of fibres (Fig. 33, *B*).

2. The nuclear membrane becomes indistinct; the tangled chromatin falls into several loops (Fig. 33, *C*).

3. These loops arrange themselves in an equatorial plane between the two attraction centres, in such a way that their free ends are directed outwards and their angles inwards. Fine achromatine fibres run to the attraction centres (Fig. 33, *D*).

4. The chromatin loops split lengthwise, so that their number is doubled (Fig. 33, *E*).

5. The one half of the chromatin loop which has thus arisen moves towards one attraction centre, the other towards the opposite centre. The halves thus move away from each other; fibres of achromatin stretch between them (Fig. 33, *F*).

6. The chromatin loops of each side have moved quite near their attraction centres. Their order now becomes irregular, and they again unite into a single tangle, round which again a nuclear membrane can be recognised (resting stage, Fig. 33, *G* and *H*).

During the last stages, at the surface of the cell in a plane between the two attraction centres, a circular furrow appears, which becomes deeper and deeper, and finally, when the two new nuclei have reformed, divides the cell into two halves, each with a new nucleus.

The cells which arise in the animal body by repeated division of the egg develop in various ways, but always in such a way that the greater number of them remain bound together in a special manner, forming the so-called **tissues.** Four chief sorts of such tissues can be distinguished:

1. **Surface** or **epithelial tissue.**
2. **Connective tissue.**
3. **Nerve tissue.**
4. **Muscle tissue.**

I. Epithelial Tissue.

This is the simplest form of tissue, and, as Comparative Histology and Histogeny teach, the most primitive complex into which cells can combine. It may therefore be correctly described as primitive tissue, from which all other tissues are derived. Even among the Protozoa epithelium-like combinations of cells occur, as, *e.g.*, in *Volvox*, where the individuals (cells) of a colony are placed side by side in a layer which, like a spherical mantle, encloses a central cavity. Such a form is, in many Metazoa, the immediate result of the first division of the egg; it is here called the *Blastula*. The epithelial character consists in the regular juxtaposition of cells into superficially extended membranes. These cover the outer and inner surfaces of the animal. The cells of an epithelium lie either in a single layer side by side (**unilaminar epithelium**), or several layers lie one above another (**multilaminar epithelium**). Different sorts of epithelium are always distinguished according to the differences in the individual cells which form them. Thus we speak of **tesselated epithelium** when the cells are flat, of **columnar** epithelium when the cells are cylindrical, and so on. The epithelial cells generally secrete externally layers of varying thickness, which often harden and possess different chemical and physical properties; these form a **cuticle** over the epithelium.

In the simplest cases every epithelial cell possesses nearly all the qualities of a Protozoon. Division of labour, however, soon steps in, so that the epithelial cells belonging to different areas undertake different functions. In a simple condition, which we meet with in certain low Metazoa, *e.g.* the *Hydra*, and which is also passed through by many higher Metazoa in the course of their development, the wall of the pouch-like body consists of two contiguous epithelial layers, an outer (**ectodermal** epithelium) and an inner (**endodermal** epithelium), the latter lining the central cavity of the pouch (archenteron). The two layers pass into each other at the opening of the pouch (mouth). This stage is known as the *Gastrula*. A certain not very sharply defined division of labour occurs between the cells of the inner epithelium and those of the outer epithelium. The cells of the outer epithelium appear to be specially suited, in correspondence with their position, to carry on the relations between the animal body and the outer world, and further to promote locomotion and movement; those of the inner epithelium are adapted more for the ingestion and digestion of the food taken into the gastric cavity. In correspondence with these functions, differences in the structure and in the size of the cells of the two layers appear. The higher we rise in

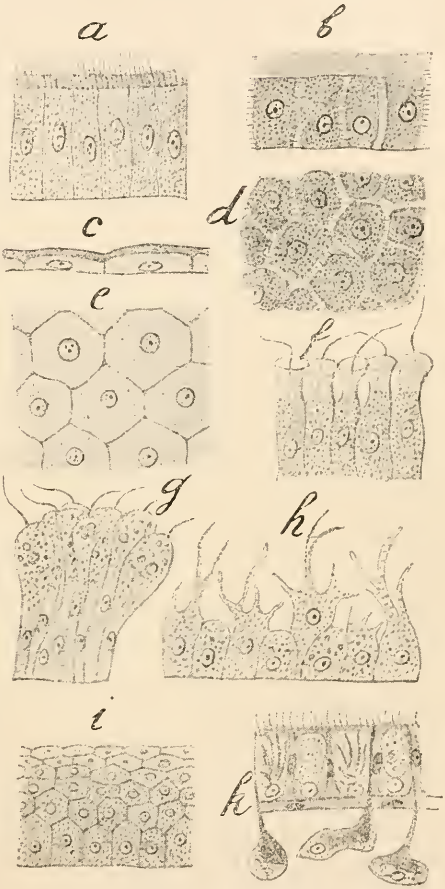

FIG. 34.—**Various forms of epithelium.** *a*, Ciliated epithelium; *b*, columnar epithelium in profile; *d*, surface view; *c*, tesselated epithelium; *e*, the same from the surface; *f*, epithelium of collar cells, with flagella (from the endoderm of a sponge); *g*, flagellate epithelium; *h*, epithelium of intestine with amœboid processes; *i*, multilaminar epithelium; *k*, body epithelium of a marine planarian, with pigment cells, rod cells, and sub-epithelial glands.

the animal kingdom the more sharply defined and the more thorough is the division of labour. The epithelial areas no longer consist of similar cells, but the cells of the same epithelium, having different functions to perform, are differently constructed.

The comparison of the adaptations by which different cells (especially epithelial cells) of the Metazoa seem to be suited for definite functions, with the adaptations we have described among the Protozoa, is very instructive. In the latter, in the most complicated cases, different portions of one and the same cell appear specially adapted for the performance of definite functions. Among the Metazoa, however, in a number of tissue cells one of the many adaptations of a complicated unicellular Protozoon becomes the principal adaptation suppressing all or most of the others, or totally obliterating them; in this way cells suited for the performance of one special function arise. We find among the Protozoa—as adaptations for movement, for taking in food, and for respiration—cilia, flagella, and so on. Epithelial cells of Metazoa very often assume such adaptations as the most prominent characteristic of the cells. Either all cells of an epithelium are covered with cilia—then we speak of **ciliated epithelium**—or only groups of cells or single cells are thus covered. The cilia of a cell may be replaced by a flagellum, *e.g.* in the endoderm of the sponges. Then the epithelial cells so provided are called flagellate cells, which often strongly remind one of the *Choanoflagellata.*

These cilia and flagella serve among the Metazoa, as among the Protozoa, for very various purposes.

1. They cause locomotion in Metazoa of small size which live in water (cilia of the body epithelium of a few *Rhabdocœlidæ*, ciliated plates of the *Ctenophora*, cilia of the wheel organ of some *Rotifera*), and especially in the free swimming larval stages of many Metazoa (general ciliation of many larvæ, ciliated rings and bands of the larvæ of *Platodes*, *Vermes*, *Molluscs*, and *Echinoderms*).

2. They serve for **whirling food within reach**, as they surround the oral aperture, *e.g. Rotatoria.*

3. They continually cause new digestible material to pass over the digesting epithelium; in many cases they at the same time cause in the enteric cavity a constant renovation of water and of the food suspended in it. **Intestinal respiration. Ciliated epithelium of the intestinal canal.**

4. They constantly bring fresh oxygenated water into contact with the epithelium. **Respiration. Ciliated epithelium of the gills.**

5. If they carry on these activities at certain parts of the epithelium where sensory nerves come to the surface, they subserve special functions of sensation. **Ciliated grooves. Olfactory pits.**

Very many Protozoa use pseudopodia and amœboid processes for locomotion and ingestion of food, and also perhaps for respiration. In many Metazoa the taking of nutritive particles into the intestinal epithelial cells by means of the protrusion of pseudopodia-like or amœboid processes is an important function of these cells, which serve exclusively for purposes of nutrition. In many lower Metazoa the amœboid character of one or of all the cells of the intestinal epithelium is so marked that they sever themselves from the complex of epithelial cells and float about independently in the intestinal cavity.

Formations similar to the **contractile vacuoles** of many Protozoa are found in the so-called excretory cells of the *Turbellaria.* In their protoplasm, and in that of their processes, small drops (products of metabolism) collect, and these may mingle to form one large drop (vacuole). The drop is emptied into the lumen of the cell (see Fig. 109, p. 152), and thence expelled by means of the excretory ducts.

In certain Protozoa the ectoplasm gives rise to stinging cells. In most *Cœlenterata* the production of such stinging capsules, the so-called **nematocysts,** is always the chief function of very many ectodermal cells (cnidoblasts) which do no other work for the organism.

In the Protozoa a membrane or shell for the protection of the unicellular organism is provided by the secretion of a resistent external envelope; so also in the Metazoa the epithelial cells, and naturally the cells of the outer body epithelium especially, provide a protection or covering for the body by the formation of outer **cuticular membranes.** Such cuticular formations arise by the mingling of the secretions of different cells, or the transformed products of the protoplasm, to form a layer. They may vary very much chemically and physically, and stand in just the same relation to the epithelial cells which produce them as do the glandular secretions to the gland cells. To these cuticular formations belong the chitinous integuments of the *Annulata* and *Arthropoda*, which sometimes by calcareous deposit become carapaces as hard as stone; these integuments are secreted by the epithelium (hypodermis) which underlies them.

The **Cuticle** is often penetrated by fine perpendicular pores, which probably owe their origin to the fact that, as the cuticle increases in thickness, the cell protoplasm remains connected with the cuticular surface by fine processes. A fine cuticle is also to be found in ciliated epithelium, in which case the cilia pass through the pores to the exterior.

There are, however, among the Metazoa a series of cells with special adaptations and functions which are wanting in the Protozoa. The aggregation of a large number of cells which can adapt themselves to the most various activities, presents much more favourable conditions for a far-reaching division of labour than are offered in the case of unicellular organisms. In the first place, we have in the epithelium the most various **glandular cells**—cells which are distinguished by peculiarities of form and structure, and possess a protoplasm capable of transforming the nutritive substances provided by the body into different sorts of secretions, or of assimilating from the body superfluous or waste material, which they then remove out of the body. Dermal glands secrete mucus or other substances.

When glandular cells remain single they form **unicellular glands**; if many combine for the same purpose they are called **multicellular glands.**

In the simplest cases, these glands are epithelial cells, chiefly distinguished by their size, and often pear-shaped. The nucleus lies at the basal end of the cell, *i.e.* the end away from the free surface of the epithelium. The secretion collects in the cell and is pushed forward towards its surface. Where a cuticle is developed it is often broken through above the gland cell, forming a pore for the discharge of the secretion (Fig. 35, *A*).

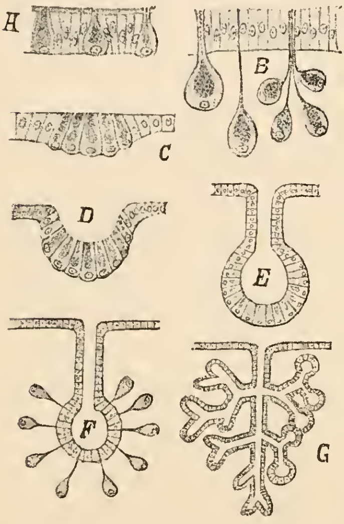

Fig. 35.—*A-G*, Various forms of glands.

Unicellular glands often partially leave the epithelium, the greater part of the gland projecting into the underlying tissue. They then only penetrate between the epithelial cells by means of thin processes, the efferent ducts (Fig. 35, *B*).

A greater or smaller area of epithelium often consists entirely or principally of glandular cells (Fig. 35, *C*). Such areas generally sink into the epithelium, so that a **glandular epithelial sac** arises, into whose cavity the secretion is emptied (Fig. 35, *D*, *E*). Such sacs again may form many branches (Fig. 35, *G*). The glandular portion is then frequently limited to the blind and often lobate ends of the sacs, while the rest serves as an efferent duct. Glandular cells again can sink under the epithelium of these glandular sacs, and only remain connected with it by their efferent ducts (Fig. 35, *F*).

It is only natural that certain cells of the epithelium which envelopes the body should undertake the function of carrying on the relations between the body and the outer world, *i.e.* of receiving impressions and imparting them to the body. Such epithelial cells are called **sensory cells.** They can either occur singly or form, in combination, a **sensory epithelium.** Originally these cells are very slightly differentiated, very slightly qualified for the reception of varied impressions. But here also, as the organism grows more perfect, division of labour steps in. Certain sensory cells appear qualified for the perception of definite sorts of impressions only. They enter into combination with certain tissue elements and form specific **sensory organs,** which give rise to perceptions of either touch or sound, sight, smell, or taste. The sensory cells will engage our attention again later.

Epithelial cells may become **pigment cells** by the deposition in their protoplasm of pigment material; these pigment cells are an important element in the external colouring of the animal. Deposited in certain sensory cells, pigment serves for the absorption of light and heat rays, and so contributes to the sensations of light, colour, and warmth.

Certain epithelial cells often perform the function of supporting their companions. They form, by mingling with each other, a tissue with meshes, the **interstitial tissue,** which is related to the other epithelial cells as the mortar in a wall is related to the bricks.

Since the protoplasm of neighbouring epithelial tissue mingles, and since in epithelial cells it is the nuclei only and not their protoplasm that divide, masses of protoplasm with nuclei scattered throughout them may arise. In such masses no cell boundaries can be recognised. They are called **syncytia.**

The epithelial cells do not always lie close to each other; they are sometimes separated by clear intercellular spaces for transmission of fluid, or by intercellular substances; but in such cases they remain connected by means of very fine protoplasmic processes which stretch across these intercellular spaces.

II. Connective Tissue.

Under this name is comprised a long series of tissue forms, which may have very different origins, structures, and functions. They originate either directly or indirectly from the epithelium. Their essential office is to bind together different portions of the body and different organs, or to serve as support for these by their possession of a certain degree of firmness. We divide the connective tissues, according to an important difference in their origin, into two principal groups.

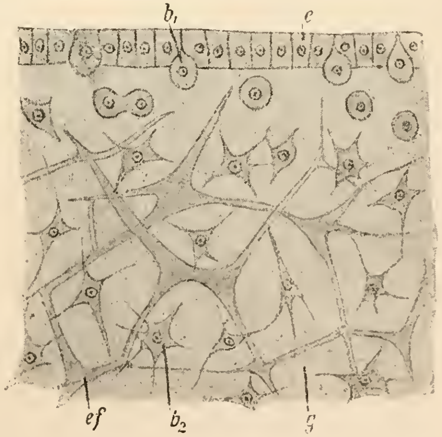

FIG. 36.—Gelatinous tissue of a *Scyphomedusa* (diagrammatic). *e*, Epithelium; *g*, Jelly; b_1, epithelial cell passing into the jelly; b_2, branched cells in the jelly; *ef*, elastic fibres.

I. **Gelatinous tissue** (Fig. 36) takes its origin direct from an epithelium. To this belong, *e.g.*, the **gelatinous tissue** of *Medusæ* and the *Ctenophora*. Between the inner epithelium which lines the intestine and the outer which covers the surface of the body a homogeneous jelly, containing a large proportion of water, is secreted by the epithelium. Cells leave the epithelium and enter the jelly, where they assume a different form. Sometimes they become spindle shaped, sometimes much branched cells connected together by their branches, sometimes elastic fibres. Occasionally such cells show amœboid movement. They can even become contractile muscle-cells.

II. The **Connective tissue proper** does not take its rise direct from the epithelium. In early stages of development of the animal variously sized groups of cells sink out of the epithelium below the surface, multiply by fission, and so produce the actual formative cells of the connective tissue. This fills the interstices between the organs and other tissues, or forms pillars, strands, plates, and variously shaped supporting masses. It often forms membranes round other organs and tissues, or lines cavities. Such a superficial extension may even assume the character of an epithelium.

Two chief types of connective tissue proper are to be distinguished.

A. The cells of the connective tissue lie close together and form no intercellular or connecting substance.

Vesicular connective tissue (Fig. 37). Vacuoles filled with fluid occur in the cells, which, growing in size, cause vesicular swelling.

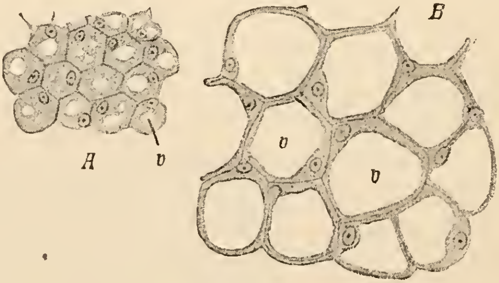

Fig. 37.—*A*, Younger, *B*, older vesicular connective tissue of a Platode. *v*, Vacuoles.

The protoplasm is then often limited to a thin layer surrounding the vacuole, and this can mingle with the neighbouring cells. Small aggregations of protoplasm may still be found massed round the nuclei.

Vesicular connective tissue passes into **reticular connective tissue,** when the fluid-filled spaces of neighbouring cells unite with one another. The connective tissue then takes the character of a spongy network containing imbedded nuclei, and the intracellular fluid which has flowed together becomes in a certain sense intercellular (reticular connective tissue of many *Platodes*). In **fatty tissue** (Fig. 38) smaller or larger fat drops appear in the protoplasm of the cells. In **pigment tissue** colouring matter is deposited.

B. The **formative cells of connective tissue** form externally a substance, the **intercellular substance,** in which they come to lie embedded. This substance is either secreted by the protoplasm of the cells, or it is produced by the metamorphosis of the outer protoplasmic layers.

However much developed the intercellular substance is, according to recent research it is probably nearly always penetrated by very fine processes of the connective tissue cells, which are thus maintained in organic union. Various hollow spaces are also frequently found in it.

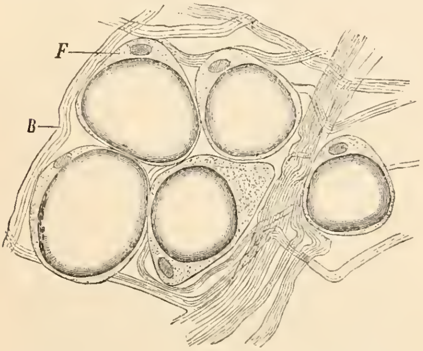

Fig. 38.—Fatty tissue, after Ranvier (from Claus's *Text-book of Zoology*). *F*, Fat-cells ; *B*, connective tissue fibrils.

Fig. 39.—Chorda tissue, after Leydig.

Cellular vesicular connective tissue arises from the vesicular connective tissue above described by the cells secreting an external membrane or cuticle which connects them together, *e.g.* **Chorda dorsalis** (Fig. 39).

There are kinds of cellular connective tissue in which the cells do not take the vesicular form, but remain compact and mostly round. The intercellular substance is inconsiderable in comparison with the cells. If it increases in mass, the tissue passes into the next form.

In **fibrous connective tissue** the intercellular substance is considerable. When boiled it yields glue. It is differentiated into fibres, which often unite in bundles, showing the most varied arrangements. They often run parallel, often cross each other, or branch and anastomose with each other. The cells of the connective tissue seldom

Fig. 40.—Reticular connective tissue, after Gegenbauer.

remain round; they generally assume a long spindle shape or a branched form. In the last case there again arises a **sort of reticular connective tissue.** The processes of the cells themselves are often differentiated into fibres, which associate themselves with those formed from the intercellular substance. Fibrous connective tissue may have a loose texture or a firm texture, as in tendinous tissue (Fig. 41). The fibres swell on treatment with acids and alkalis. If they are elastic and reticular, and if they do not swell under the influence of acids and alkalis, we have **elastic connective tissue.**

Fig. 41.—**Tendinous tissue**, from the longitudinal section of a sinew, after **Gegenbauer.**

Fig. 42.—**Hyaline cartilage.** To the right above are depicted the protoplasmic threads which connect the cartilage cells.

Cells of connective tissue may become pigment cells by the deposition of colouring material.

Cartilaginous tissue is a very good instance of the structure and rise of real connective tissue. The cells generally remain round. They secrete membranes, which continually become thicker and stronger by their own growth, and which finally mingle with those of the neighbouring cells and form a tolerably firm intercellular substance, the cartilaginous substance, which in boiling yields chondrine. The cartilage cells continue to divide; the daughter cells again surround themselves with membranes. Sometimes the membranes of various generations can still be distinguished—the less easily, of course, the older they are (Fig. 42).

If the cartilaginous substance is homogeneous and structureless we have **hyaline cartilage**; if it is fibrous we speak of **fibrous cartilage.** In cartilaginous tissue also the intercellular substance seems penetrated by exceedingly fine processes of the cartilage cells, which apparently were already present when the first membrane was secreted. **Calcified cartilage** is formed by the appearance of calcareous deposits in the intercellular substance.

Cartilaginous tissue, on account of its firmness, serves as supporting tissue in vertebrate and in some invertebrate animals.

FIG. 43.—**Fibrous cartilage**, after **Claus**.

Bone tissue forms, *par excellence*, the supporting tissue of vertebrates. The intercellular or bone substance becomes as hard as stone by a combination of lime-salts with some ground substance, which yields glue on being boiled, and does not dissolve under treatment with acids. In it are scattered the cell elements (bone cells); they are much branched, and connected by their processes; they are arranged in parallel layers, often concentrically round the cavity (Fig. 44). Bone tissue arises out of indifferent connective tissue cells, which are arranged in strands or flat expanses, and which function as formative cells of the bone tissue, **osteoblasts** (Fig. 45, *a*). They produce on one side bone substance, often in the direction of cartilaginous masses, which they supplant, at the same time forming processes which remain imbedded in the bone substance. New masses of bone substance being constantly formed from the osteoblasts, some of the latter come to lie in the bone substance, and become bone cells.

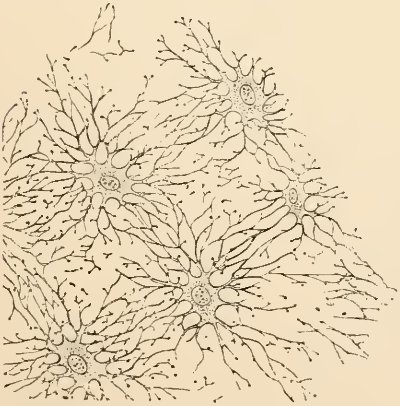

FIG. 44.—**Bone cells**, after **Gegenbauer**.

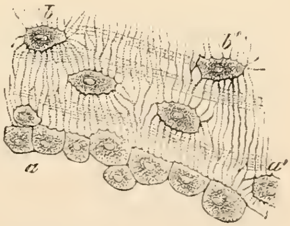

FIG. 45.—**Bone tissue.** *a*, Osteoblasts; *b*, bone cells (after **Gegenbauer**).

Dentine is nearly related to bone tissue. Here the formative cells (**odontoblasts**) do not enter into the dentine which they have secreted; they all remain at its base, but send into it numerous finely branched processes (fibres), which run parallel to each other in as many little channels of the bone substance. The fibres are connected by fine anastomoses.

It is clear from the above that bone tissue shows much similarity in its origin with gelatinous tissue, and dentine with epithelial cuticular formations.

The **blood cells** and **lymph cells** which float in the blood, the lymph or the cœlomic fluid of animals, at first rise out of connective tissue cells. The blood has even been described as fluid connective tissue, the blood fluid representing the intercellular substance, the blood corpuscles the connective tissue cells. Lymph corpuscles often show amœboid movement, and are capable of taking in solid materials (*e.g.* products of excretion, food material, products of suppuration, and foreign bodies).

III. Neuromuscular and Muscle Tissue.

The elements of both muscle and nerve tissue originally come from the epithelial cells. Both tissues appear simultaneously in the animal kingdom, and are connected in their origin. In its simplest form **neuro-muscular tissue** is met with among the lower *Cœlenterata* (*e.g. Hydra*). Here, in the outer epithelium, are found cells which form processes inward, and produce a layer of fibres close under the epithelium. These fibres are contractile, and represent muscle processes of the epithelial cells. The latter, which contain the nucleus, take part with their companions in limiting the surface of the body. These cells undertake the relations with the outer world, being suited to receive external impressions. The stimulus created by such impressions is carried through the protoplasm of the cell to the muscle processes, which contract in consequence. The cells, with their processes, are accordingly called **neuro-muscular cells.** In them the chief functions are of nerve and muscle tissue localised, in the most general undifferentiated manner, in different parts of one and the same cell. In consequence of the intimate connection of the neuro-muscular cells with one another, a locally created stimulus of one or more cells is communicated to the neighbouring cells, and thus to their muscle processes. The principle of the division of labour here again supplies the key for understanding the further differentiation of neuro-muscular tissue. One portion of the neuro-muscular cells undertakes principally the function of contractility, and the greater part of its protoplasm becomes differentiated into contractile substance; another portion of the neuro-muscular cells, while remaining in close organic connection with the first, performs the function of receiving external impressions,

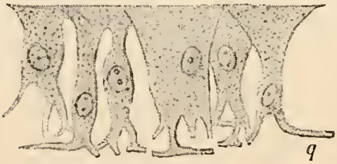

FIG. 46.—**Neuro-muscular cells of the Hydra, after Kleinenberg.** *q*, Muscle processes of the same.

changing them into sensations and carrying on the stimulus to the muscular elements.

In accordance with this, **muscle tissue** in its simplest form appears as a system of **epithelial muscle cells** (Fig. 47, *a*). They still lie in the epithelium, but no longer take part in **limiting** the body surface. They form inwards muscle processes which run under the epithelium. They are distinguished from neuro-muscular cells by the fact that their chief function is contractility, and that the body of the cell no longer acts as a neural portion. This cell body then appears merely a remainder of the original formative substance of the fibres; it lies below the upper epithelial cells, wedged in between them. In this way a neuromuscular cell becomes an epithelial muscle fibre, with a protoplasmic body containing a nucleus attached to it. From this to **sub-epithelial muscle fibres** (Fig. 47, *b*) is a short step. These no longer lie in, but under the epithelium. They consist of a contractile fibre, which carries along its whole length, on the side bordering on the epithelium, a thin layer of protoplasm.

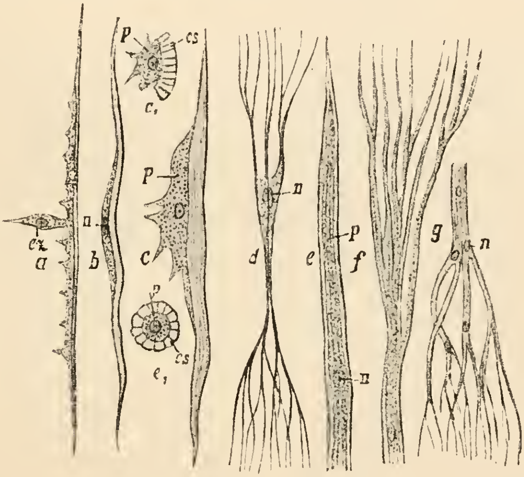

FIG. 47.—**Muscle fibres.** *a*, Epithelial muscle cell (*ez*), with fibre; *b*, sub-epithelial muscle fibre, with attached protoplasmic body, both of *Cnidaria*; *c*, longitudinal section of muscle fibre of a *Nematode*; c_1, transverse section of the same; *e*, of an *Hirudo*; e_1, the same in transverse section; *d*, dorso-ventral muscle fibre of a marine *Planarian*; *f*, the same of an *Hirudo*; *g*, branched muscle fibre from the jelly of a *Ctenophore*; *p*, protoplasm, or, in *e* and e_1, medulla; *cs*, contractile substance; *n*, nucleus.

In other cases, *e.g.* in the *Ctenophora*, epithelial cells can leave their complex and enter into the jelly secreted below the epithelium. Here they often grow into fibres branched at each end (Fig. 47, *g*), whose protoplasm changes into a contractile substance. Such fibres are known as **mesenchymatous muscle cells**, as opposed to epithelial muscle cells.

The above differentiations of muscle tissue are seen within the division of the *Cnidaria*. Various forms of muscle elements can here be found in one and the same animal.

Even if it is not impossible that muscle fibres respond to certain direct stimuli by contraction, it is generally characteristic of them that they respond only to stimuli communicated to them by the nerve elements.

A general division into two principal types of muscle fibres may be made: (1) smooth, and (2) transversely striated.

Smooth muscle fibres are almost always simple muscle cells. One single cell forms a fibre. The contractile substance is either formed by the cell on one side, so that the cell with the nucleus appear as an attached body (Fig. 47, c, c_1), or the contractile substance becomes differentiated on the whole surface of the formative cell, and then tubular muscle fibres arise (Fig. 47, e, e_1). In these we distinguish the outer contractile **corticle layer** from the central **medulla** which contains the nucleus; this medulla fills the axis of the muscle fibre, and represents the more or less unchanged remnant of the protoplasm of the formative cell. The contractile substance of the smooth muscle fibres often appears longitudinally striated, and under the influence of suitable reagents separates into the fine long fibrillæ which are the cause of this longitudinal striation. The smooth muscle fibres are often branched at one or both ends, especially in those cases in which they have an isolated course (Fig. 47, *d*, *f*). The above described muscle fibres of the *Cœlenterata* are of this sort.

Striated muscles.—These are considered as physiologically the most efficient muscle elements. Even among the *Cœlenterata*, the contractile fibres of the epithelial muscular cells appear transversely striated. The muscle processes of several cells unite to form a group of striated fibres. Striated fibres form the chief mass of the musculature in the *Arthropoda* and *Vertebrata*. They arise out of muscle-forming cells, the greater portion of one such cell becoming differentiated into transversely striated fibre. The remainder of the protoplasm, with the nucleus, often persists on the surface of the fibre. Perhaps it is this protoplasmic layer which produces the **Sarcolemma**, the membrane which envelops the muscle fibre. In nearly all cases, however, the number of nuclei increases as the muscle fibre grows and differentiates further; the fibre is thus to be considered as a many-celled structure proceeding from one cell by incomplete division. Often, however, several cells lying one behind the other share in the formation of a muscle fibre. Striated muscle fibre appears not only transversely but longitudinally striated. The transverse striation comes from a regular alternation of singly refractive with doubly refractive elements.

There are, at the present time, many different opinions about the finer structure of the striated muscle fibre. According to the last view of Van Gehuchten, supported by investigations of the transversely striated muscle fibres in the *Arthropoda*, the muscle fibre, like the protoplasm of the cells in general, consists of a network of close and very fine fibres, the spongioplasm, and of an intermediate homogeneous fluid substance, the hyaloplasm. The former is contractile and elastic, the latter is purely passive. In muscle fibres the spongioplasm is regularly arranged (Fig. 49, *A*). It consists of parallel filaments, which run longitudinally and are bound by transverse filaments at regular intervals in a plane at right angles to the longitudinal axis. A transverse section lying in such a plane would form a plate with reticularly arranged filaments and hyaloplasm between them (Fig. 49, *B*). There are no transverse connections between the longitudinal filaments, except at these regular intervals, so that on a transverse section of the fibre made at any other part of it only the transverse section of the longitudinal filaments would be seen. It is clear how, by such an arrangement of the finer portions, the transversely and longitudinally striated appearance of the fibre could be produced. There are weighty objections, however, to these views of Van Gehuchten.

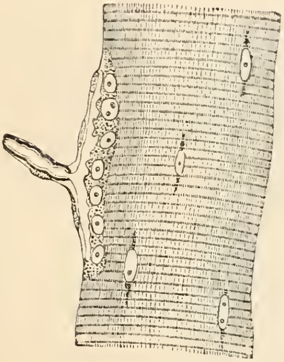

Fig. 48.—**Transversely striated muscle fibre**, after **Gegenbauer**.

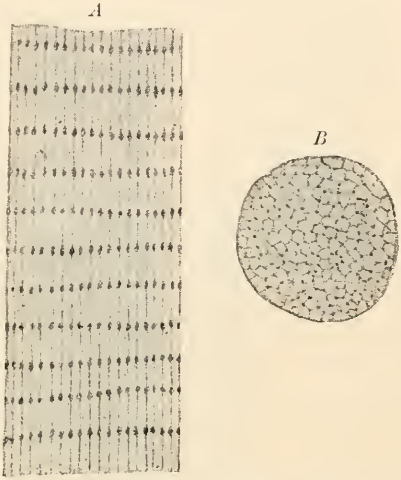

Fig. 49.—**Transversely striated muscle fibre** of an **Arthropod**, after **Van Gehuchten**. *A*, Lateral view. *B*, In transverse section.

The muscle fibres contract in response to stimuli transmitted to them by the motor nerve fibres. They therefore always stand in connection with the ends of such fibres in a manner which cannot here be further described.

Muscle fibres joined together by connective tissue unite to form bundles, bands, or tubes. These again can be united in layers or in thick muscle strands.

Muscle fibres, smooth as well as striated, arise, even in many higher Metazoa, out of epithelium; in many of these, however, the muscle-forming cells (**Myoblasts**) are descendants of cells which at an early stage of their development sank below the level of the epithelium to which they belonged. Both kinds of formation may occur in the same animal.

IV. Nerve Tissue.

As muscle elements pure and simple may be imagined to arise out of neuro-muscular cells by the gradual differentiation of most of the protoplasm of one part of the cell into contractile substance, the muscular function thus being brought to the front at the expense of the other possible functions, so nerve elements may be produced by the suppression of the contractile part of the cell and the further differentiation of the neural portion. We can perhaps imagine that the simple sensory cells of the body epithelium of the lower Metazoa arose in this way, always presupposing that they remained in connection with the neighbouring contractile elements, either by simple contact or by processes. In this way a stimulus received by the sensory cells could be transmitted to the muscle cells. The sensory cells are epithelial cells, which are generally distinguished by a delicate, usually immobile, **sensory hair**, projecting outwards. Division of labour could then go further. Single sensory or nerve cells of the most undifferentiated sort, found in contact with other sensory cells and muscle cells, could give up their connection with the surface of the body and sink into the lower part of the epithelium, thus playing the part of intermediaries between sensory and muscle cells (Fig. 50), and transmit the stimulus received by the former to the latter. Such cells are found in many *Cœlenterata*. They are here already known as **ganglion cells.** They possess processes by which they are connected with each other and with the sensory cells and muscle fibres. They represent the

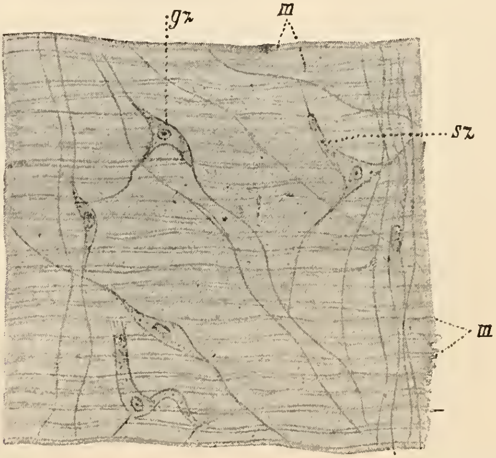

Fig. 50.—**Piece of a muscle lamella of the septum of an Actinian (Anthea cereus)**, with nerve plexus, after **O.** and **R. Hertwig.** *m*, Muscle fibres; *sz*, sensory cell, with sensory hair; *gz*, ganglion cell.

central elements of the nervous system; in them the impressions which have come from the sensory cells become sensations which can be transformed into will impulses; from them proceed the stimuli which cause the muscle fibres to contract.

The nervous system becomes complicated as low down as among the *Cœlenterata*, but more especially in animals of a higher grade. Between the central parts, *i.e.* the ganglion cells on the one side, and the sensory and muscle cells on the other, nerve cells are interposed, which, being stretched like fibres, become **nerve fibres.** These undertake exclusively the function of the transmission of sense impressions from the sensory cells to the ganglion cells, and the transmission of stimuli from the ganglion cells to the muscle fibres.

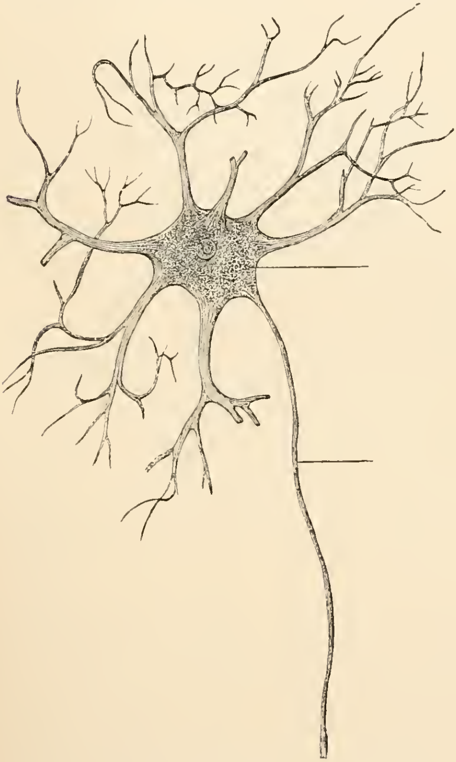

Fig. 51.—**Ganglion cell from the anterior cornu of the human spinal cord (after Gegenbauer).** *p.* Pigment; *n.* nerve.

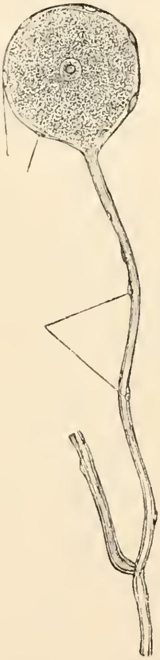

Fig. 52.—**Ganglion cell from a human spinal ganglion (after Gegenbauer).** *n*, Nuclei of the neurilemma.

Besides this, the glanglion cells no longer appear scattered, arranged in a plexus, but they unite into masses, which are defined as the **central organs** of the nervous system, *e.g.* the **brain.** The nerve fibres also unite into nerves. There are two sorts of nerve fibres: (1) **Sensory nerve fibres,** which transmit sensory impressions from the peripheral sensory cells to the central organ; (2) **Motor nerve fibres,** which transmit stimuli from the central organ to the muscles. The majority of sensory cells also do not remain in their undifferentiated condition. Division of labour steps in here also. Some cells seem specially suited for the reception of light and colour sensations, others for those of sound, others again for sensations of smell and taste. Tactile cells still remain in the most undifferentiated condition. Many sensory cells which are qualified to receive one and the same class of stimuli become, by the addition of accessory tissues, combined into complicated sensory apparati—the **specific sensory organs:** the **organs of sight, hearing, smell, taste,** and **touch.**

The ganglion cells possess one or more processes (unipolar, bi-polar, multi-polar ganglion cells), one or more of which pass over into the nerve fibres, while others only serve perhaps for the nourishment of the cells. The process of a unipolar ganglion cell sooner or later divides into at least two branches, one motor and the other sensory. The ganglion cells in peripheral ganglion centres are often enclosed in envelopes of connective tissue.

Nerve fibres may have many branches, and are often finely striated in a longitudinal direction. They are either **naked**—in some of the lowest Metazoa—or enveloped in a sheath, the **neurilemma,** which is supplied by the surrounding connective tissue. When many nerve fibres form one nerve, the single fibres of this nerve are, among all the higher animals, kept apart from one another by this sheath; the whole then in transverse section produces the effect of a spongy tissue, in whose larger or smaller meshes the transverse sections of the nerve fibres lie. The neurilemma is not generally continued on to the ganglion cells.

A further distinction between two sorts of nerves has been made, especially among the Vertebrata: (1) **nerves without medulla,** which remain simple; and (2) **nerves containing medulla,** in whose fibres two parts are found—an outer oleagenous tubular medullary sheath, and a fibre surrounded by this—the axis-cylinder. On entering a ganglion cell, the latter alone penetrates its process—it alone represents the path of transmission. Both these sorts of nerve fibre are enclosed in neurilemma sheaths.

In many of the lower animals the nervous system remains for the most part in its original place of formation, *i.e.* in the body epithelium. In the higher animals the nervous system remains in connection with the body epithelium through the sensory apparatus. This helps us to understand why, in the embryonic development of the highest animals, the nervous system is always produced by the outer epithelial layer.

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CHAPTER II

Introduction to the study of the Metazoa—Cœlenterata or Zoophyta as the lowest Metazoa constructed essentially of two cell layers—Yolk segmentation and formation of the two primitive germinal layers of the Metazoa (Gastræa theory).

INTRODUCTION.

IN contradistinction to **Protista** or **Protozoa** we have real **Animals** or **Metazoa**. The bodies of the former consist of one single cell or of several similar cells (with the exception of *Volvox*), each of which, however, is competent to perform all vital functions (cell colony); the bodies of Metazoa, on the contrary, always consist of a number of cells which are not all similar, but have divided among them the different forms of vital activity (cell community). The division of labour may be more or less complete, and according to it the degree of morphological complexity and of physiological perfection is determined. There are animals which are morphologically (according to structure) and physiologically (according to their vital activities) only a little raised above the Protozoan colony, *e.g.* the *Hydra*.

The bodies of these animals consist of only slightly different sorts of cells: digesting cells, neuro-muscular cells, stinging cells, and formative cells of eggs and spermatozoa. All these kinds of cells are, however, indispensable to the existence of the *Hydra* body; not one of them can be removed from the body without endangering its existence. The whole body is nevertheless physiologically an individual, but, as opposed to the cell, an **individual of a second**, *i.e.* **a higher order—a person.** Most animals remain at this stage of individuality. A Medusa, a Worm, a Crustacean, or a Mammal is such an individual of the second order. In many animal divisions, however, individuals of the second order multiply by fission or gemmation. The new individuals thus arising remain united, and together form **individuals of the third order—an animal stock.** The single individuals which collectively form such a stock may remain similar, and they then are related to the stock in just the same way as the cell-individuals of a Protozoan colony are related to the colony; or division of labour again steps in, resulting in variety of development in body form and structure of the persons forming the stock (**polymorphism**). Then such a stock is also physiologically again an **individual of the third order.** The single persons become equivalent to instruments of this complex individual, and bear the same relation to it as the various cell elements of a single individual, *e.g.* a *Hydra*, bear to it. As instances of animal stocks without division of labour among the persons we have most *Corals*; and of stocks with far-reaching division of labour and polymorphism the *Siphonophora*.

Even in the lowest Metazoa the cell elements are not found scattered in the body without any special arrangement. On the contrary, we find even among the simplest *Cœlenterata* that they are arranged in two epithelium-like layers, which are closely contiguous and form the wall of the body, which is pouch-shaped and provided with an opening. In keeping with the physiological activities of the various cells, the stinging cells and the neuro-muscular cells form the outer layer, while the digesting cells form the inner layer, which is turned towards the pouch cavity, *i.e.* the gastric cavity. The reproductive cells lie protected in the deeper portions of the outer layer. These two layers, which occur in the development of all Metazoa, are called the **Ectoderm** and the **Endoderm.**

Either similar or dissimilar cells or tissues, therefore, may combine to form cell or tissue complexes. Such complexes are called **organs** when the cells or tissues combining to form them perform in common one or more functions. The endoderm of the *Hydra* is a primitive organ, all the cells of which undertake the digestion. The tentacles of the *Hydra* are slightly more complicated organs; they serve as organs of touch, as weapons, and as organs for seizing food. For these purposes they contain neuro-muscular and stinging cells. For the nutrition of the tentacles canals lined with endoderm enter them from the gastric cavity. In this way the most various elements are drawn into the service of one or of several functions after which the organs are named. We therefore speak of the sensory organs and the organs of movement, respiration, etc.

Several organs of the same sort with similar functions may occur in the same body (this is especially the case among the higher animals); these are then portions of an **organic system**—muscular system, vascular system, nervous system, etc.

The observation of the construction of the animal body out of cells, tissues, organs, etc., is the object of **Anatomy, microscopic and macroscopic.** These become **Comparative Anatomy** when the structure of animal bodies is considered comparatively. Comparative anatomy, again, is the indispensable aid of zoology in one of its chief tasks—the discovery of the natural relations of affinity among animals and of the conjectural course of development of the animal world in the earth's history. Comparative anatomy seeks to define the relations of affinity between the different portions which combine to form the animal body.

It deals naturally, not only with the bodies of animals now living, but also with the bodies of animals of past geological periods in so far as these are attainable in a fossilised condition; not only with the bodies of adult animals, but with all the consecutive stages of development of such animals. For an animal form is characterised not only by its structure in a fully grown and sexually mature stage, but by its structure in all the previous consecutive stages of its development. Comparative anatomy only considers organs, as we have already said, according to their structure and their connections of affinity, not according to their physiological activities. The relationship of two organs rests upon their descent from the same organ of a common racial form. The proof of this relationship establishes the **Homology** of the organs in different animals. Thus the anterior or posterior extremities of the Amphibia, Reptiles, Birds, and Mammals are **homologous** to each other and to the pectoral or ventral fins of the Fish, because these organs have a common origin. The limbs of the *Vertebrata* and those of the *Arthropoda* are not homologous, but only **analogous**, because they cannot be referred to a definite organ in a common racial form. They were first formed independently within each of these groups, and the superficial similarity which they exhibit is only the result of their adaptation to the same function.

Zoological research has further proved that in the process of time organs can undertake functions quite different from those which they originally performed (**principle of the change of functions**). The air-bladder of fishes, for example, is principally a hydrostatic apparatus used by these animals for rising or sinking in the water. At the same time, in certain fishes the air-bladder may also undertake the secondary function of a respiratory apparatus. This secondary function becomes in the higher Vertebrata the chief function; the lung rises out of the air bladder, and the original function is quite lost. The so-called **rudimentary organs** are of great importance in comparative anatomy; these are degenerated organs which are not in the condition to perform any useful function for the organism. They are remains of originally well-developed and functionally important organs, retained by inheritance, but in the act of disappearing. Thus the human processus vermiformis is a small remainder of an intestinal cæcum which is greatly developed in certain Mammalia of a lower order and energetically takes part in the work of digestion.

How is the rise of the lowest, simplest Metazoa to be imagined? This question is answered by various theories; one of these, the **Gastræa theory**, has been very generally accepted. This theory rests upon two series of facts:

1. In the development of very many Metazoa there arises, by repeated division of the egg cell, a hollow group of similar cells, which in its structure shows a general correspondence with a Protozoan colony (*Volvox*, *Magosphæra*). The cells of this group

(**blastula**) arrange themselves in all Metazoa in a double layer, and in many cases they do this in the simplest manner, *i.e.* by the wall of the hollow sphere sinking in at one spot. The sunken portion lines the non-invaginated portion of the hollow sphere, and so we have a pouch with a double wall (ectoderm and endoderm). The inner layer, the **endoderm**, surrounds a cavity, the **arch-enteron**, which opens outward by an aperture, the **primitive mouth** or **blastopore**. The outer layer, or **ectoderm**, everywhere supplies the outer integument and the nervous system of the animal; the inner, the enteric epithelium and the glands which proceed from it. This germinal form is called *Gastrula*.

2. The body of one of the lowest Metazoa, *e.g.* one of the simplest *Cœlenterata*, throughout life consists of two layers, which in all essentials correspond with the two germinal layers of the *Gastrula*. The outer layer, the ectoderm, represents the **outer integument**; the inner, the endoderm, the epithelial wall of the **intestinal cavity**. The latter surrounds the intestinal cavity, which opens at one point, the **mouth**.

From these two series of facts the following conclusions may be drawn :—

1. All Metazoa are descended from one common ancestral form, which possessed essentially the structure of one of the lower *Cœlenterata*. This hypothetical ancestor, the *Gastræa*, is met with in all Metazoa as a transitionary stage in their development—as a **Gastrula**.

2. The *Gastræa* itself arose in a similar way from a Protozoan colony in the shape of a hollow sphere by the formation and the gradual deepening of a depression, just as in the individual development of many animals the gastrula arises by invagination out of a hollow group of cells, the product of the segmentation of the egg.

The three chief Divisions of the Metazoa.

A. The body consists essentially of two layers—the ectoderm and the endoderm. There is no middle layer as a rule, and where such does occur, its close relation to either the ectoderm or the endoderm, or to both, is clear. Intestine with one external aperture—the mouth. A body cavity between the intestine and the integument is wanting; so also are blood-vessels and excretory organs. A nervous system is either wanting, or, where it occurs, is little centralised.

Comprises: **The Second Race or Phylum of the Animal Kingdom**—*Zoophyta* or *Cœlenterata*.

B. With well-developed mesoderm sharply distinguished from the ectoderm and endoderm. Gastric cavity with a single aperture opening externally (mouth). Body cavity and blood-vascular system wanting. Excretory organs (water-vascular system) present. Nervous system centralised.

Comprises: **The Third Race or Phylum of the Animal Kingdom**—*Platodes*.

C. With well developed mesoderm, sharply distinguished from the ectoderm and the endoderm. Intestine with two external apertures (oral and anal). Generally with a body cavity in mesoderm. Blood-vascular and excretory systems usually present. Nervous system centralised.

Comprises all the remaining races of the animal kingdom,—viz. **the fourth**, *Vermes*; **the fifth**, *Arthropoda*; **the sixth**, *Mollusca*; **the seventh**, *Echinodermata*; **the eighth**, *Tunicata*; and **the ninth**, *Vertebrata*.

THE SECOND RACE OR PHYLUM OF THE ANIMAL KINGDOM.

ZOOPHYTA OR CŒLENTERATA.

Systematic Review.

Class I. **Gastræadæ.** Without pores in the body wall and without tentacles.

,, II. **Porifera or Sponges.** With pores in the body wall, without tentacles.

,, III. **Cnidaria or Stinging Animals.** Without pores in the body wall, with tentacles.

Of the three chief classes of the *Cœlenterata*, the *Gastræadæ* show essentially the structure of a Gastrula, while the other two groups contain animals more highly differentiated, which, developing in entirely different directions, cannot be comprehended in one description.

Class I.

The Gastræadæ.

Systematic Review.

A. **The Physemaria, Haliphysema, Gastrophysema.**
B. **The Dicyemidæ.** *Dicyema* (Fig. 53).
C. **The Orthonectidæ.** *Rhopalura* (Fig. 54).
Appendage: *Trichoplax adhærens* (Fig. 55).

The *Gastræadæ* are animals whose structure essentially corresponds with that of the *Gastrula*. In some forms the organisation is complicated; in others, no doubt in adaptation to the parasitic manner of life, somewhat simplified. The *Physemaria* are bi-laminar tubes attached to the sea bottom by that portion of their bodies which is opposite to the aperture. The ectoderm consists of fused cells (syncytium); the endoderm of collar cells, each with a flagellum. The sexual products are developed in the endoderm. Foreign bodies are contained in the ectoderm. Were the body wall of the *Physemaria* perforated by pores they would have to be considered as the simplest sponges.

The bodies of the *Dicyemidæ* (Fig. 53) and *Orthonectidæ* (Fig. 54) which are parasitic in *Cephalopoda*, *Echinodermata*, and *Turbellaria*, also consist of two principal layers; the ciliated ectoderm forms an unbroken layer of not very numerous cells round the inner solid layer, which is generally considered to be endoderm, and this layer consists either (*Orthonectidæ*) of a mass of cells, or of one single multinuclear axial cell (*Dicyemidæ*). The oral opening and gastral cavity have here disappeared in the same way as in the *Cestoda*. The body of the *Orthonectidæ* is outwardly ringed, and between ectoderm and endoderm has a layer of ectodermal muscular fibres. In the *Orthonectidæ* spermatozoa and eggs are produced in the endoderm, but in different dissimilar individuals. In the *Dicyemidæ* no spermatozoa have yet been discovered, but many egg-like germs, which apparently without fertilisation develop as eggs within the axial cell.

The course of development is as follows. The egg or the unicellular germ divides into two unequal portions. The larger segmentation cell which is thus produced (macromere) remains at first undivided, while the smaller (micromere) divides repeatedly. The descendants of the latter grow round the larger cell, finally completely surrounding it, and form the ectoderm, and, in the *Orthonectidæ*, the muscular fibres as well. The large cell remains undivided in the *Dicyemidæ* and becomes the axial cell, while in the *Orthonectidæ* it yields by division the group of endodermal cells.

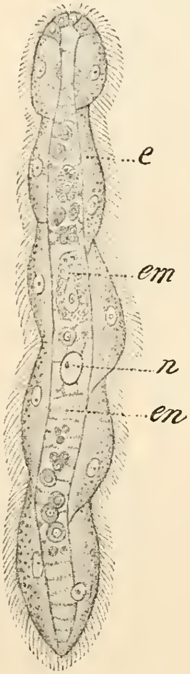

Fig. 53.—Young **Dicyema**, after **Whitman**. *e*, Ectoderm; *en*, endoderm cell, with nucleus (*n*); *em*, embryo.

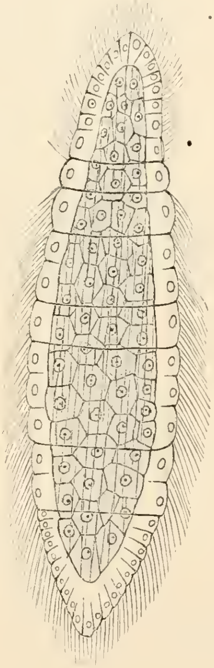

Fig. 54.—**Rhopalura Giardii**, ♀, after **Julin**.

Appendage: Trichoplax adhærens (Fig. 55).—This is a remarkable animal discovered in the Graz marine aquarium, which presents the appearance of a thin flat ciliated body like an *Amœba*, irregular and varying in shape. It is composed of three layers—the lowest, which adheres to the surface on which the animal rests, consists of cylindrical cells, the uppermost of tesselated epithelium. The layer between these consists of branched and partly anastomosing cells, which lie in a hyaline ground substance. The cells of the lowest layer possess processes, which pass into the processes of the cells of the middle layer without sharp distinction. As long as we have no knowledge of the reproduction and development of this animal, judgment as to its morphology must be suspended.

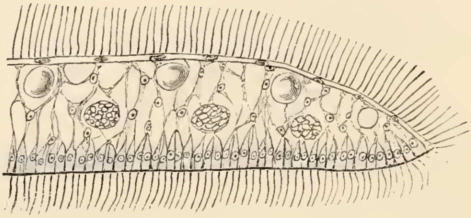

Fig. 55.—**Part of a vertical section through the body of Trichoplax adhærens, after F. E. Schulze.**

[**Note.**—*Cf.* p. 175. Where the author suggests that the *Dicyemidæ* and *Orthonectidæ*, on account of their similarity to the sporocysts, are degenerated *Trematoda*. —Tr.]

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Class II. **Porifera or Sponges.**

Systematic Review.

Sub-Class I. **Calcaria.**—Skeleton composed of spicules of carbonate of lime, always present. According to the structure of the soft body, Ascones, Sycones, and Leucones. *Olynthus, Ascandra, Sycandra, Leucandra.*

Order 1. **Calcispongiæ.**

Sub-Class II. **Non-Calcarea.**—Skeleton seldom wanting, but never of calcareous spicules, rather of siliceous spicules or spongin fibres. According to the structure of the soft body, *Leucones.*

Order 2. **Hexactinellidæ.**

Siliceous needles, isolated or bound together by masses of silica into a continuous firm framework, tri-axial. Flagellate chambers cylindrical, placed radially, similar to the radial tubes of *Sycandra*. Most forms fossil. Living: *Euplectella*, *Hyalonema*.

FIG. 56.—Skeleton of a horn sponge attached to a stone. *o*, Oscula.

Order 3. **Spiculispongiæ.**

Skeleton consisting of independent siliceous spicules of various kinds, rarely wanting. The spicules are often bound together into bundles by an organic substance, or form firmly connected skeletons interlocking by means of knotty outgrowths; they are, however, never cemented together by siliceous masses. *Geodia*, *Plakina*, *Chondrosia*, *Oscarella*, and *Halisarca* (without skeleton), *Tethya*, *Tuberella*, *Suberites*.

Order 4. **Halichondrina.**

Skeleton composed of siliceous spicules, chiefly uniaxial, cemented together by a more or less horny substance (spongin). *Halichondria*, *Reniera*, *Spongilla* (in fresh water) *Myxilla*, *Clathria*.

Order 5. **Ceraspongiæ** (Fig. 56).

Skeleton consists of horn fibres (spongin). Proper spicules wanting. Fragments of foreign spicules, sand, etc., are often used for strengthening. *Spongelia*, *Euspongia officinalis* (bath sponge), *Aplysina.*

The form of the body in the *Porifera* is so wonderfully varied that no general description of it is possible, on account of their great variety in shape. Sponges or sponge stocks can be knob-like, pear-shaped, crust-like, funnel-shaped, cylindrical, or spherical. Many are irregularly branched. Some have a radiate structure. All are attached, or have part of their bodies buried in mud.

With the exception of the *Spongillidæ*, all sponges live in the sea.

In many sponges the external forms to be met with, even in one and the same species, varies to an extraordinary degree. The same individual even, in different parts of its body, may show differences of texture and structure, and variations in the composition of the skeleton.

The inner structure of sponges is not less varied. As an example let us take **Olynthus** (Fig. 57). This sponge is vasiform and rather thin walled; it is attached by its blind end, while the opposite free end is broken through by an opening (**osculum**). The body wall is perforated by pores which can open and shut. The water streams through the pores into the body cavity, which may be compared with the gastric cavity of the gastrula, and flows out through the osculum. The wall, as far as is at present known, consists of two layers: (1) an outer layer formed of a tolerably homogeneous fundamental substance, in which are imbedded cells and calcareous needles; (2) an inner epithelium of collar cells. Perhaps here also, outside the layer which contains the skeleton, there is a thin tesselated epithelium, in which case the body would consist of three layers—an outer ectodermal layer, an inner endodermal epithelium, and an intermediate mesodermal layer of connective tissue. Those sponges, which are essentially of the same degree of organisation as the *Olynthus*, are called *Ascones.*

Fig. 57.—**Olynthus, after Haeckel.**

A higher degree of organisation is attained when the body wall becomes thicker and cylindrical tubes or pouches arranged close together penetrate into the thickened wall radially round the central cavity (Fig. 58). The outer surface of the sponge is then often raised in numerous cones over these radial tubes. The radial tubes are lined with collar epithelium, while the epithelium of the central or gastral cavity is changed into a pavement epithelium. The outer pores in this case lead first into the radial tubes, from these into the central cavity, and thence through the osculum to the exterior. *Sycones.*

In most sponges, however, the "canal system" is more complicated. The collar epithelium is limited to numerous so-called "ciliated chambers," which are sac-like, and generally lie scattered in the much thickened mesoderm of the body wall (Fig. 59, *gk*). The pores of the outer surfaces of the body lead into much-branched canals of varying width, which are lined with tesselated epithelium; these, as **afferent canals**, enter the ciliated chambers. Other canals of varying width, which often unite into larger canals, lead out of the chambers as **efferent canals** into the variously shaped central cavity, which again opens outward by means of an osculum. Such forms are known as *Leucones*.

The movement of the flagella of the collar epithelium maintains a constant stream of water through the canal system of the sponges. The water enters by the pores, passes through the canal system, and flows out again through the osculum.

The canal system may vary extraordinarily in details. Its structure and arrangement are of importance in classification.

The coalescence of the afferent canals often causes a system of large lacunæ and cavities lying quite near the surface, the sub-dermal spaces; into these the pores open either directly or through canals, the water passing on from the sub-dermal spaces by special canals into the ciliated chambers.

The canal system of the sponges may be greatly developed in comparison with the solid matter of the middle layer (mesoderm), or the solid tissue may preponderate. In the first case the sponge has a loose, in the second a firm, texture.

FIG. 58.—**Sycandra ciliata, Haeckel, after Vosmaer.** Longitudinal section through the body wall in the upper part of the body. The left half of the section is omitted.

The mesoderm of the sponges is represented by a middle layer of connective tissue, chiefly gelatinous, with cells imbedded in it. The latter are either spindle-shaped or star-shaped, occasionally vacuolated. Some of them often contain colouring matter (pigment cells); others can move like *Amœbæ* (migratory cells). Long spindle-shaped and finely-branched cells occasionally lie concentrically at the commencement of the afferent canals, and no doubt serve as contractile cells for closing the pores.

The mesodermal connective tissue is, in sponges, the place of formation of the very varied skeletal structures. These consist either of carbonate of lime, or of silica, or of horn known as spongin.

Skeletons of silica and of horn fibres are found combined. The siliceous or calcareous skeletons consist of small bodies of extraordinarily different shapes, the so-called spicules, most probably formed in the cells. There are uniradiate, triradiate, quadriradiate, sexiradiate, multiradiate forms, stars, spheres, etc. The skeleton of a sponge may consist of only one sort of spicule, or two or more sorts may occur together.

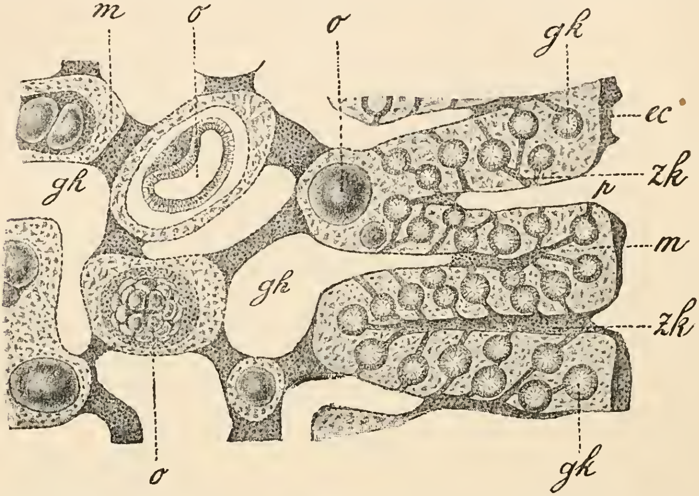

FIG. 59.—**Part of a section through Halisarca lobularis,** after **F. E. Schulze.** *ec*, Ectodermal pavement epithelium; *gh*, gastral cavity; *m*, mesoderm; *p*, pores; *gk*, ciliated chambers; *zk*, afferent canals; *o*, eggs in different stages of segmentation.

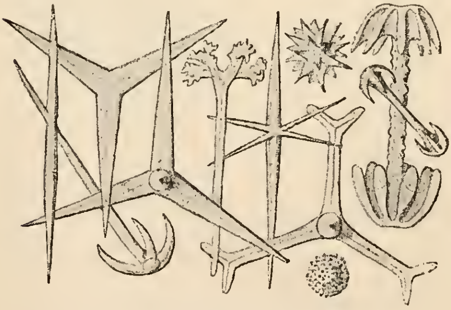

FIG. 60.—**Various forms of skeletal spiculæ from Sponges.**

The single spicules lie either loosely near each other, or are cemented together into coherent frameworks. The same is the case with horn fibres. The ordinary bath sponge is only a framework of such horn fibres; it is merely the **skeleton** of a marine animal (Fig. 56).

A **nervous system** is not yet with certainty proved to exist in the *Porifera*.

Reproduction is either asexual or sexual.

Asexual reproduction takes place by external or internal **budding** or **gemmation.**

External gemmation.—A sponge may put out buds at various points of the body surface. These, without detaching themselves, grow larger, and can in their turn form buds. Sponge colonies thus arise. As buds may at various points grow together, the colony itself may again have the appearance of a plexus or framework. The holes and interspaces of such a colony may then again assume the character of a canal system (pseudo-canals). These must, however, according to their origin, be sharply distinguished from the real canal system which runs through the walls of every sponge individual. Separate sponge individuals may also fuse and form colonies. The number of oscula generally corresponds with the number of individuals which form the colony (Fig. 56, *o*).

In the so-called **internal gemmation** groups of cells called **gemmulæ** detach themselves from the sponge body, and after a period of rest develop into complete sponges. Observers differ as to the finer processes which take place during the development of these gemmulæ.

Sexual reproduction.—Sponges are either hermaphrodite or diæcious; in the former case the eggs and spermatozoa are not produced at the same time in the same individual or colony; they are **protandrously hermaphrodite.** The eggs and spermatozoa seem to develop from mesoderm cells.

Development.—The course of development of the sponge from the fertilised egg, which often begins within the mother body, seems, to judge from the as yet insufficient and often contradictory observations which have been made, to be so varied that it is hardly possible to form a generally applicable scheme. We select the newly investigated development of *Oscarella* (*Halisarca*) *lobularis* (Fig. 61).

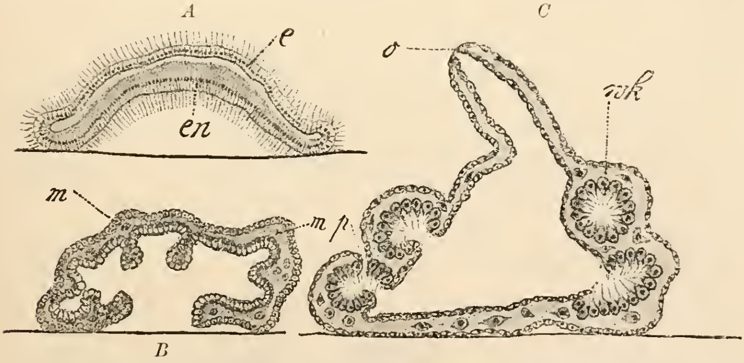

Fig. 61.—Sections of three stages of development of Oscarella lobularis, after K. Heider. *A*, Gastrula which has attached itself. *B*, Rudiments of mesoderm and canal system. *C*, Formation of the osculum and ciliated chambers. *e*, Ectoderm; *en*, endoderm; *m*, mesoderm; *o*, osculum; *p*, pores; *wk*, ciliated chambers.

By means of repeated egg division a freely swimming larva arises, the **Blastula.** This is a hollow sphere, whose wall consists of one single layer of flagellate cells. The blastula by invagination becomes a **gastrula.** This attaches itself by the gastrula mouth or blastopore, and the aperture gradually narrows and finally closes.

Gelatinous substance is secreted between the ectoderm and endoderm, and into this cells migrate most probably from the endoderm. Thus the connective tissue mesoderm arises. At the same time radial invaginations of the endoderm which lines the arch-enteron are formed in the mesoderm, and grow towards the ectoderm. These invaginations are rounded off and become the ciliated chambers (*wk*). Their communication with the gastric cavity becomes narrowed. The ciliated chambers become connected with the surface, either by the formation of pores through the external membrane (in the case of chambers lying superficially), or by the formation of short invaginations of the ectoderm, which finally reach the ciliated chambers. The **osculum** arises at the aboral pole, by the lengthening and breaking through of the body cavity. **Sycone stage.**

According to these observations, the epithelium of the ciliated chambers, the efferent canals, and the central cavity (gastric cavity) is of endodermal origin ; the tesselated epithelium on the surface of the body and the epithelium of the afferent canals (at least partly) of ectodermal origin.

According to other observers, in fresh water sponges the ectoderm is thrown off by the larva, and the whole adult sponge is derived from the endoderm.

The observations of several investigators agree in establishing the fact that the gastrula of the sponge attaches itself by the edges of the blastopore. The osculum of the sponge therefore represents neither the blastopore of the gastrula nor the mouth of the *Cœlenterata*. The *Porifera* thus appear as a laterally developed group of the lower Metazoa, which do not admit of direct comparison with other *Cœlenterata*, but are only distantly related to them.

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Compare also the older works and treatises of Grant, Lieberkühn, and Bowerbank, and newer investigations of Zittel, Barrois, Keller, Heider, Marshall, Lendenfeld, Götte, etc.

Class III.—**Cnidaria.**

Systematic Review.

Sub-Class 1. **Hydrozoa.**

Prototype : *Hydropolyp* or *Hydrula*. In all Hydrozoa an ectodermal œsophagus is wanting ; the mouth leads direct into the endodermal gastric cavity. Gastral filaments are wanting. The sexual products mostly arise from the ectoderm. The sexes are generally separate.

Order 1. **Hydridæ** (**Fresh-water polyps**).

Single individuals or small stocks without envelopes consisting of a few similar individuals. Reproduction asexual by gemmation, and sexual. Hydra develop direct from the egg. Hermaphrodite. *Hydra,* in fresh water.

Order 2. **Hydromedusæ.**

Hydroid colonies, which are at least *di*morphic, since, besides the sterile nutritive polyps, there arise by gemmation sexual persons, which either detach themselves as *Craspedote Medusæ* and swim about freely, or remain united with the colony as medusoid gonophores. In one series of *Hydromedusæ* the attached *Hydroid* form is suppressed, as the *Craspedote Medusa* develops direct from the fertilised egg into another *Medusa.* The systematic relationship of single forms is naturally determined both by the *Hydroid* and by the *Medusa* forms. As the whole life-history and development of only a minority of the many species is available, and in many species only the Hydroid form is known, in others only the Medusa form, a natural system of the *Hydromedusæ* is still a desideratum.

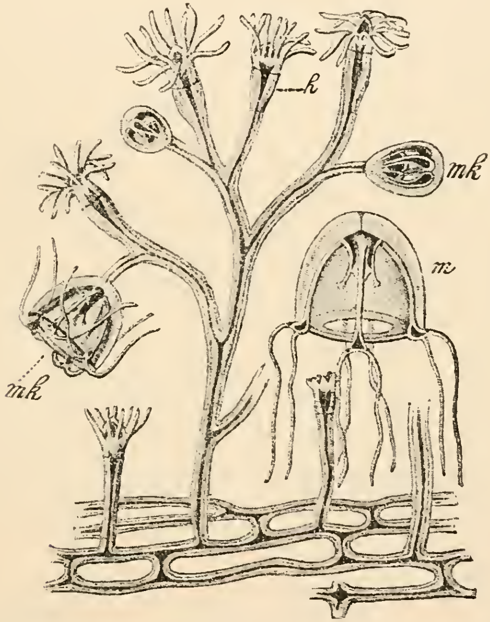

Fig. 62.—**Bougainvillea ramosa** (after **Allman**), with budding Medusæ. *h,* Nutritive polyps; *mk,* Medusa buds; *m,* detached young Medusa (*Margelis ramosa*).

Sub-Order 1. **Hydrocorallia.**

Hydroid form.	**Medusa form.**
Hydroid stocks, with calcified periderm skeleton. The sexual products are produced in gonophores. *Stylaster, Millepora.*	Wanting.

Sub-Order 2.

Hydroid form.	**Medusa form.**
Tubularia.	**Anthomedusæ.**
Small hydroid colonies, naked or covered with a chitinous envelope (periderm). The chitinous envelope never widens into a cup (*theca*) round the polyp head. In many forms the *Medusæ* are reduced to gonophores, which do not detach themselves.	*Craspedote Medusæ*, without marginal vesicles and otoliths, with ocelli at the bases of the tentacles. Gonades in the outer wall of the gastric peduncle; 4, seldom 6 or 8, radial canals.

Examples.

Syncoryne Sarsii.	*Sarsia tubulosa.*
Podocoryne carnea.	*Dysmorphosa carnea.*
Eudendrium ramosum.	*Lizusa octocilia.*
Bougainvillea ramosa (Fig. 62).	*Margelis ramosa* (Fig. 62, *m*).
Stauridium cladonema.	*Cladonema radiatum.*
Cordylophora lacustris (in fresh water).	Wanting.
Tubularia larynx.	Wanting.
Unknown.	*Ctenaria ctenophora.*

Sub-Order 3.

Campanaria.	**Leptomedusæ.**
Small hydroid stocks with chitinous periderm, which widens round the polyp-head into a theca, into which the head with the tentacles can be withdrawn. The *Medusa* buds or sessile gonophores generally arise united into groups in special modified polyps devoid of tentacles and mouth (gonangia).	"*Craspedote Medusæ*, some without, some with, marginal vesicles, the latter developed from the base of the velum with ectodermal otolith cells. Ocelli at the tentacle bases sometimes present, sometimes wanting. Gonades always in the course of the radial canals. Number of radial canals various, often very great" (Haeckel).

Examples.

Campanularia geniculata.	*Obelia geniculata.*
Unknown.	*Eucope campanulata.* (Fig. 65, p. 74.)
Campanulina tenuis.	*Phialidium variabile.*
Unknown.	*Gastroblasta Raffaelii.*
Unknown.	*Aequorea Forskalea.*
Laomedia Caliculata.	Wanting.

The *Plumularia* and the *Sertularia* are generally placed near the *Campanaria*. These are elegantly branched *Hydroid* stocks. In the first, the cups (thecæ) which contain the nutritive polyps are in a single row, in the second in two rows on opposite sides of the stem. The sexual products form bud-like outgrowths (gonophores), which generally arise in groups on special modified polyps devoid of

Hydroid form.	Medusa form.
mouth and tentacles, and they are surrounded by a chitinous periderm. It is as little known in this case as in that of the *Hydrocorallia*, whether these gonophores are degenerate *Medusæ* which remain sessile, or simple sexually differentiated *Hydropolyp* buds.	

Sub-Order 4.

Wanting.	**Trachomedusæ.** *Craspedote Medusæ* with auditory organs (tentaculocysts), with endodermal otolith cells, which sometimes stand freely on the margin of the umbrella, sometimes enclosed in auditory capsules. Ocelli generally wanting. Gonades always in the course of the radial canals. Number of radial canals 4, 6, or 8, never more; between them often blind centripetal canals. Direct development with metamorphosis. *Olindias Mülleri*, *Rhopalonema velatum*, *Aglantha digitalis*, *Geryonia proboscidalis*, *Carmarina hastata*.

Sub-Order 5.

Wanting.	**Narcomedusæ.** *Craspedote Medusæ* with auditory organs, always standing freely on the margin of the umbrella, with endodermal otolith cells. Ocelli mostly wanting. Tentacles at some distance from the margin of the umbrella, inserted on the exumbrella, bound to the umbrella margin by clasps (peronia), which divide it into a number of collar lobes. Gonades on the gastric peduncle, often spreading from it peripherally in radial gastric pouches. Radial canals sometimes wanting, sometimes spreading out in the shape of flat gastric pouches. Circumferential canal sometimes obliterated. Number of tentacles, lobes, and pouches variable; seldom 4, generally 8 or more, up to 32. Development usually direct, with metamorphosis. *Cunina*, *Pegantha*, *Ægineta*, *Æginopsis*, *Solmaris*.

Order 3. **Siphonophora.**

Polymorphic, freely swimming *Hydrozoa* stocks, whose individuals or persons, *Craspedote Medusæ*, are modified for special functions.

Sub-Order 1. **Siphonanthe.**

The heteromorphic persons bud on a variously formed stem, which may be compared with the gastric peduncle of a *Medusa.*

Family 1. **Calyconecta.**—Without pneumatophore and feeler (taster); with one or more swimming bells at the upper end of the stem. The remaining heteromorphic persons arranged in groups (cormidia), which can detach themselves from the stem as *Eudoxiæ* and *Ersææ. Praya* (Fig. 85, p. 111), *Diphyes, Abyla, Hippopodius.*

Family 2. **Physonecta.**—With pneumatophores, without aurophore, with several swimming bells, and with feelers. *Apolemia, Agalma, Anthemodes, Halistemma, Physophora, Forskalia.*

Family 3. **Auronecta.**—With one large pneumatophore, under which stands a circle of swimming bells, and in the dorsal middle line of the latter a large medusoid air bell (aurophore), which secretes gas, and may be considered as a modified swimming bell. Stem shortened and thickened. Without feeler (?). *Stephalia* (Fig. 84, p. 110), *Auralia, Rhodalia.*

Family 4. **Cystonecta.**—With large pneumatophore, without aurophore. Swimming bells and covering pieces wanting. *Rhyzophysa, Physalia.* Stem under the pneumatophore very much shortened, and flattened into a disc.

Sub-Order II. **Disconanthe.**

The heteromorphic individuals bud from the under side of a disc, which contains a many-chambered pneumatophore, and may be compared with a *Medusa* umbrella. The margin of the disc carries a ring of numerous tentacles. In the middle of the subumbrella stands the central gastric peduncle as chief siphon.

Family 5. **Disconecta.**—*Discalia, Porpita, Porpalia* (Fig. 87, p. 114), *Velella.*

Sub-Class II. **Scyphozoa.**

Prototype: The *Scyphopolyp* or the *Scyphula.* In the *Scyphozoa* we find an ectodermal œsophagus. Gastral or mesenterial filaments are present in all cases on the septa or gastric ridges. The sexual products arise out of the endoderm. The sexes are generally found in separate individuals.

Order 1. **Anthozoa (Corals).**

Attached individuals or colonies. The body remains essentially on the same grade as the *Scyphula.* The ectodermal œsophagus sinks in the form of a tube into the spacious gastric cavity, and round it the latter is divided by septa into a variable number of separate pouches. The free internal edges of these septa run through the gastric cavity to the aboral end of the body.

A. **Octocorallia.**

Sub-Order 1. **Alcyonaria.**—Generally with 8 septa and 8 pinnate tentacles. Polyp colonies of very various shapes. Skeletal forms very varied. *Alcyonium, Pennatula, Kophobelemnon* (Fig. 63), *Gorgonia, Isis, Tubipora.*

B. **Tetracorallia.**

Sub-Order 2. **Rugosa.**—Number of septa great, a multiple of 4. With calcareous skeleton. Fossil Paleozoic forms.

C. Hexacorallia.

Sub-Order 3. **Antipatharia** (horn corals).—With 6 or 24 simple tentacles. Colonies with horny axial skeleton. *Antipathes* (6 tentacles, only 2 developed septa), *Gerardia* (24 tentacles and septa).

Sub-order 4. **Madreporaria** (stone corals).—Mostly colonies, more rarely individuals with strongly developed calcareous skeleton. 6*n* simple tentacles, and septa present in great numbers and variously arranged. *Madrepora, Astroides, Fungia, Astræa, Mæandrina, Cladocora, Caryophyllia, Flabellum.*

Sub-Order 5. **Actinaria** (flesh corals).—Mostly individuals with 6*n* tentacles, and septa generally in considerable numbers and varied arrangement. Without skeleton. *Cerianthus, Zoanthus, Actinia, Anemonia, Adamsia, Edwardsia.*

Order 2. Scyphomedusæ (Acraspeda).

Mostly free-swimming individuals of bell- or disc-shape, in which the mesodermal supporting lamella is developed into a large gelatinous mass. The ectodermal œsophagus lies within a gastric peduncle which hangs down from the middle of the subumbrella. The 4 radial pouches of the *Scyphula* degenerate in the higher forms. The exumbrellar and subumbrellar walls of the peripheral portion of the gastric cavity grow together in such a way that only a variously developed system of radial gastro-canals remains. With tufts of gastral filaments. A true velum is wanting; in its place, marginal lobes, containing processes of the gastro-canal system are present.

A. *Medusæ* with deeply vaulted umbrella.—The 4 radial gastric pouches and the septa which separate them more or less clearly retained.

Sub-Order 1. **Stauromedusæ.**—4 septa retained (*Lucernaria*) or reduced to 4 pillars (*Tessera*), 4 or 8 gonades in the subumbrellar wall of the 4 gastric pouches, without sensory bodies (rhopalia). *Lucernaria* (attached, with 8 marginal lobes, each carrying a tuft of stinging batteries). *Tessera* (free, without distinct marginal lobes, with 8 tentacles).

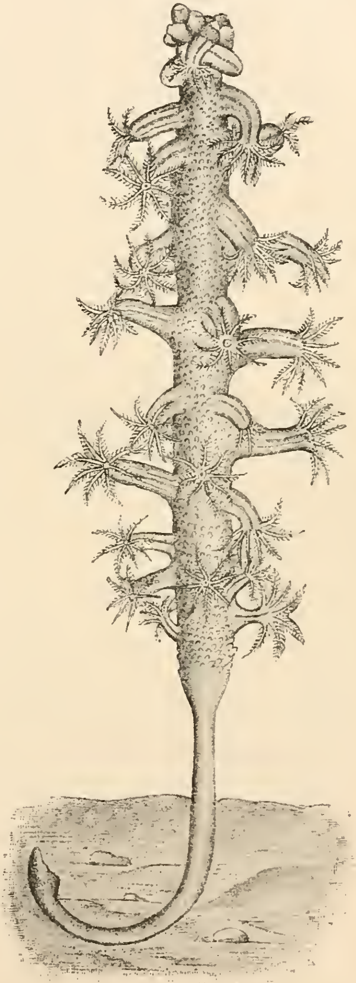

FIG. 63.—Kophobelemnon Leuckartii.

Sub-Order 2. **Peromedusæ.**—The 4 septa reduced to 4 pillars, in consequence of which the 4 gastric pouches are united into a circumferential sinus. With 4 inter-radial rhopalia. 8 or 16 marginal lobes, 4 or 12 tentacles. *Pericolpa*, *Periphylla*.

Sub-Order 3. **Cubomedusæ (Charybdeidæ).** 4 septa retained. 4 pair of gonades on the septa, freely protruding into the gastric pouches. With 4 perradial rhopalia, which contain tentaculocysts with endodermal otolith sacs, and are provided with one or more eyes. 4 interradial tentacles or tufts of tentacles. Mostly with velarium. *Charybdea*, *Chirodropus*.

B. *Medusæ* with flat, disc-like umbrella.—The 4 primary gastric pouches of Scyphula degenerated by disappearance of the septa, instead of which there are 8, 16, 32, or more radial canals of varying width, and often branched or anastomosing, as survivals of the gastric cavity on the growing together of the subumbrellar and exumbrellar intestinal walls. The 4 interradial gastric ridges or tænioles are retained as remains of the septa, and these carry the phacelli, or tufts of gastral filaments. Development either direct with metamorphosis, or with alternation of generations. In the last case an attached *Scyphula* arises out of the gastrula and develops into a young attached *Medusa* (*Scyphistoma*). This multiplies in most cases by a sort of repeated fission or gemmation (strobilation). The constricted *Medusa* (*Ephyra*) changes through metamorphosis into the adult form.

Sub-Order 4. **Discomedusæ.**

Family 1. **Cannostomæ.**—With simple mouth tube, without oral arms, with square mouth, and short solid tentacles. *Nausithoë* (Fig. 67, p. 77).

Family 2. **Semostomæ.**—With 4 long flag-like oral arms and cross-shaped mouth. With long hollow tentacles. *Pelagia noctiluca*, *Cyanea*, *Aurelia aurita*.

Family 3. **Rhizostomæ.**—Mouth grown together. With numerous small suckers on the 8 long root-like oral arms; without tentacles. *Cassiopæa*, *Pilema* (*Rhizostoma*), *Cotylorhiza*, *Crambessa*, *Cannorhiza* (Fig. 70, p. 85).

Sub-Class III. **Ctenophora.**

Cnidaria with sensory bodies at the aboral pole; with 8 meridional rows of ciliary or ctenophoral plates, with ectodermal œsophagus. Without gastral filaments. Development direct, without alternation of generations. Mesodermal jelly strongly developed, with muscle, nerve, and connective tissue elements. Hermaphrodite.

Order 1. **Tentaculatæ.**—With 2 capturing filaments with one row of simple branches; the filaments can be withdrawn into sacs situated in the lateral perradii. Gastro-canals ending blindly.

Family 1. **Cydippidæ.**—Body globular or egg-shaped. *Hormiphora* (Fig. 68, p. 79).

Family 2. **Lobatæ.**—Body compressed in the lateral plane, with 2 oral lobes in the median plane. *Eucharis*.

Family 3. **Cestidæ.**—Body band-like, compressed in the lateral plane, without oral lobes. *Cestus*.

Order 2. **Nuda.**—Without capturing filaments. Mouth wide, œsophagus very spacious. Gastro-canals much branched and anastomosing.

Family 4. **Beroidæ.**—*Beroë*.

The *Hydrozoa* and *Scyphozoa* probably descend from attached forms, which are only distinguished from gastrula attached by the aboral pole, either, on the one hand (*Hydrozoa*), by their possession of circumoral tentacles, or, on the other (*Scyphozoa*), by the formation of an ectodermal œsophagus. Indications of this descent can still be seen in the freely swimming *Hydromedusæ* and *Scyphomedusæ* in their radial structure and in the absence of all organs at the aboral side of the body (exumbrella), *i.e.* at that part of the body by which the stationary forms are attached; and further in the fact that very many *Hydromedusæ* and many *Scyphomedusæ* actually pass through such a stage of attachment in the course of their development. As for the *Ctenophora*, their descent from attached forms, and, generally, their position among the *Cnidaria*, seems very doubtful. The presence of complicated sensory bodies at the aboral pole, and the constant occurrence of 8 rows of rowing plates with correspondingly arranged gastro-canals, and the marked departure from the strictly radial type, point to the fact that in their case the adoption of the swimming manner of life dates very far back.

I. General.

We shall better understand the varied organisation of the *Cnidaria* if we keep clearly in mind that they can in all cases be referred to one of the three following forms: (1) the *Hydropolyp* or *Hydrula*, (2) the *Scyphopolyp* or *Scyphula*, (3) the *Ctenophora*.

1. The simplest form (from which all others can be deduced) is that of the *Hydropolyp* or *Hydrula*.

A *Hydropolyp* (Fig. 64, *A*) (type: *Hydra*) is a pouch-shaped gastrula attached by its aboral pole, and possesses, round its mouth, hollow tentacles as evaginations of the body wall. The gastric cavity is continued into the tentacles. Between endoderm and ectoderm there is a structureless supporting membrane (*sl*).

A more highly developed form, the *Craspedote Medusa* (Fig. 64, *B*) may proceed from the *Hydropolyp* by adaptation to a free-swimming manner of life. The aboral portion of the *Hydropolyp* body (from the attached pole to the tentacles) spreads out like an umbrella or bell, and becomes the **exumbrella** of the *Medusa*. The oral portion of the body (from the tentacles to the mouth) also widens out, deepens, and becomes the subumbrella. We thus have a convexo-concave body, on whose circular margin the tentacles are radially arranged (Fig. 65, *A*). The mouth lies in the middle of the concave side, and generally on the summit of a projection (gastric peduncle, gastric tube).

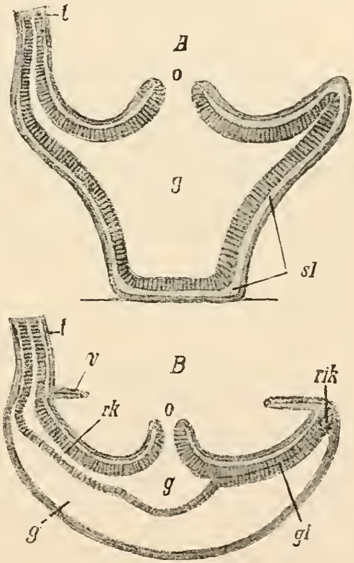

FIG. 64.—**A, Diagram of a Hydropolyp** (longitudinal section); **B, of a Craspedote Medusa.** *o*, Mouth; *g*, gastric cavity; *t*, tentacle; *sl*, supporting lamella; *g′*, jelly between ectoderm and endoderm; *rk*, radial canal; *gl*, vascular lamella or cathammal plate; *v*, velum; *rik*, circumferential canal.

The **supporting membrane** of the *Hydropolyp* thickens very much, and becomes the **gelatinous disc** of the *Medusa*, an elastic passive organ for locomotion and support. The partial fusing of the inner wall of the oral portion of the body with that of the aboral portion considerably reduces the gastric cavity lying between them, which originally spread throughout the whole extent of the disc. There remain only:

1. the cavity of the gastric peduncle into which the mouth leads.
2. A central stomach above the oral peduncle. These two parts form the **main intestine.**
3. A peripheral canal at the edge of the disc (the circumferential canal) which is continued into the tentacles.
4. Radially arranged connecting canals between the central stomach and the circumferential canal. These canals become nutritive gastro-canals, which also serve the purpose of blood-vessels (which are wanting) and convey food from the central stomach to the organs at the disc's edge. These two portions form the **peripheral intestine.**

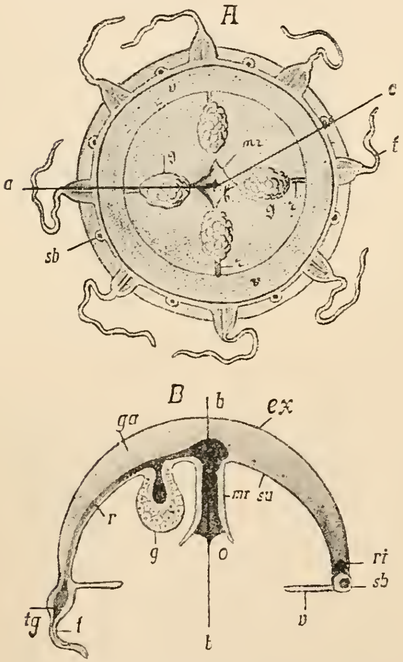

Fig. 65.—**Eucope campanulata,** partly after **Haeckel** *A*, From the surface. *B*, Section in the direction *a-b-c* in Fig. *A*. *a-b*, Perradius; *b-c*, adradius; *t*, tentacle; *sb*, marginal vesicle; *g*, gonades; *mr*, gastric peduncle; *r*, radial canals; *v*, velum; *ri*, circumferential canal; *ex*, exumbrella; *su*, subumbrella; *ga*, jelly; *tg*, tentacular vessel; *b-b*, main axis.

In some *Craspedote Medusæ*, besides the radial canals and the circumferential canal, the endoderm from the centre to the circumference persists, its two layers being pressed together by the strongly developed oral or subumbrellar and aboral or exumbrellar jelly, thus forming the so-called **vascular lamellæ** or **cathammal plates,** the layers of which, separating in radial strips, form the **radial canals.**

The **radial canals** in simple *Medusæ* are 4 in number, and are placed cross-wise. The radii in which they lie are called **perradii** (Fig. 65, *A*, *a-b*). In order to define the position of other tentacles, canals, and organs, the radii exactly half way between the perradii have been called **interradii.**

Half way between the 4 perradii and the 4 interradii lie the 8 **adradii** (*b-c*); half way between the 8 former and the 8 latter lie the 16 **subradii.**

From the margin of the disc a thin muscular membrane projects into the subumbrellar cavity like a diaphragm; it is known as the **Velum** (*v*), and is one of the principal locomotory organs of the *Craspedote Medusæ*.

There are many other organs at the margin of the disc, the principal being:

1. **A double nerve ring.**
2. **Marginal vesicles.**
3. **Eye spots.**
4. **A ring of nematocysts.**

We shall speak of these organs later on.

The derivation of the *Medusa* form from the *Hydropolyp* is the more probable as *Medusæ* belonging to many divisions, in their individual development, proceed from *Hydropolyps* by lateral budding. Such *Medusæ* are then specially developed buds which have the function of forming the sexual products and of scattering them abroad.

2d Form: the *Scyphopolyp* or the *Scyphula* (type: *Lucernaria* or a simple *Coral* individual) is the original form of the *Scyphozoa*, as the *Hydropolyp* is of the *Hydrozoa*. It is distinguished from the *Hydropolyps* in that at the oral pole the region about the mouth sinks in to form an œsophageal tube (Fig. 99, p. 130). The epithelium which lines it is thus ectodermal. Around this tube the gastric cavity falls into 4, 6, or 8 compartments separated by walls; these partition walls, whose free edges project into the gastric cavity as **septa** or **tænioles**, bearing either **mesenterial thickenings** or **gastral filaments**, are continued along the body wall even to the aboral end of the body. All *Corals* remain essentially at the stage of the *Scyphopolyps* (Fig. 66; Fig. 82, p. 107). Their typical form is that of the cylinder or reversed truncated cone. The two ends of the body are almost circular; by the **aboral pedal disc** the animal attaches itself, and hollow tentacles stand round the **oral disc** (especially at the edge). In the middle of the oral disc lies the generally elongated slit-like external mouth.

The **external mouth**, in keeping with the *Scyphopolyp* plan, leads, not directly into the gastric cavity, which is lined with endoderm, but into a tube which has arisen by an invagination from without, and is therefore lined with ectoderm. This tube (**œsophageal tube, stomodaeum**) is open at both ends. One opening, the external mouth, leads to the exterior; the other (the **enteric aperture**) leads into the spacious gastric cavity.

The body wall consists of ectoderm and endoderm, between which a solid middle layer is interposed, of which we shall speak later. The endoderm and the middle layer raise themselves from the body walls, forming vertical ridges which project into the gastric cavity throughout the whole length of the body; these ridges are the **septa**. In the neighbourhood of the œsophageal tube these septa project far enough to fuse with its walls, so that the gastric cavity here appears divided into chambers or compartments arranged radially round the œsophageal tube (Fig. 66, to the left).

In the remainder of the body (Fig. 66, to the right) the septa project their free inner edges into the gastric cavity, which thus appears divided into a central portion and into radial niches separated by the septa (analogous to the gastro-canals of the other *Cnidaria*). These niches, in the neighbourhood of the œsophageal tube, are continued direct into the radial compartments between the tube and the body wall, and these compartments again are continued into the axial cavities of the tentacles, which are lined with endoderm (*cf.* Fig. 82, p. 107). The axial cavities of the tentacles occasionally open externally at the tip by a pore.

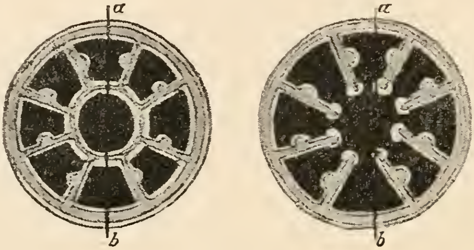

FIG. 66.—**Diagrammatic transverse section of a Coral individual**; to the left on the level of œsophagus, to the right on the level of the gastric cavity. *a-b*, Direction of the plane of symmetry.

The number of tentacles represents, generally, the number of the septa. The *Octocorallia* have 8 septa, and 8 tentacles placed so as to alternate with them. The *Tetracorallia* generally have a large number of septa which are always a multiple of 4. The *Hexacorallia* possess 6 or 6*n* partition walls and tentacles, arranged in a definite order which cannot here be described. We can only say, quite generally, that the oldest septa project farthest, and the youngest septa least far, towards the axis.

Most *Corals* have not a strictly radial structure; on the contrary we often find, anatomically and ontogenetically, a bilateral symmetry in the arrangement of the parts of the body. The slit-like shape of the mouth even is a departure from radial structure. A plane through the chief axis of the body in the longitudinal direction of the mouth (Fig. 66, *a-b*) is, in fact, a median plane—the only plane which divides the body into two exactly similar halves.

More exact ontogenetic investigation has shown that (*e.g.* in the *Hexacorallia*) two septa lying opposite each other to the right and left of this plane are first formed; these septa incompletely divide the gastric cavity into two portions of unequal size. Two new septa are then formed symmetrically in the larger—say the anterior—division;

then two symmetrical septa in the posterior division. The rise of the other septa does not by any means occur in all *Anthozoa* after one and the same simple plan. (In most *Actinaria* the other septa arise in pairs, each pair in the space between two older septa.) We repeat what we said above, that the septa project the farther towards the chief axis of the *Corals* the older they are. The tentacles also arise symmetrically with reference to the median plane over the interseptal spaces of the gastric cavity.

The **mesenterial thickenings**, or **mesenterial filaments**, are inserted in all *Corals* at the free inner edges of the septa.

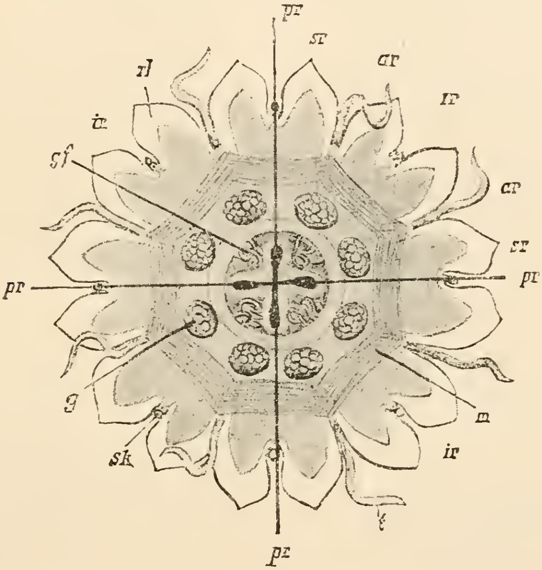

FIG. 67.—**Nausithoë.** *pr*, Perradii; *ir*, interradii; *ar*, adradii; *sr*, subradii; *rl*, marginal lobes; *t*, tentacle; *gf*, gastral filaments; *m*, circular muscle of the subumbrella; *sk*, sensory bodies (rhopalia); *g*, sexual glands (gonades); in the middle the cross-shaped mouth.

As the free-swimming *Craspedote Medusa* can be referred back to the *Hydropolyps* or *Hydrula*, so the free-swimming *Acraspede* or *Scyphomedusa* (Figs. 67 and 70, p. 85) can be referred back to the *Scyphopolyp* or *Scyphula.* The lower *Acraspeda*, with deeply vaulted, often cup-shaped body, are only slightly distinguished from the *Scyphula*, and we find among them forms still attached (*e.g.* the *Lucernaria*).

The 4 radial gastric pouches separated by septa are still present, or they flow together to form a great circumferential sinus, the septa dwindling into 4 small points of connection between the subumbrellar and exumbrellar gastric walls, between which the circumferential sinus remains in wide-open communication with the central stomach. The 4 septa which carry **phacelli** or **tufts of gastral filaments** are continued as **gastric ridges** or **taenioles** on the exumbrellar gastric wall to the aboral pole of the body. In the higher *Acraspeda*, the *Discomedusæ*, the exumbrellar and subumbrellar walls of the peripheral intestine (circumferential sinus) coalesce, so that here again there arises a **cathammal plate,** in which variously-shaped radial canals and radial pouches remain as survivals of the circumferential sinus; at such points the lamellæ of the cathammal plate separate, leaving between them spaces, the lumens of these canals. The derivation of the *Discomedusæ* from a *Scyphula* form is further justified by the fact that in many of them the *Scyphula* appears as an attached early stage (Fig. 99, p. 130).

The **third form** of the *Cnidaria* is the *Ctenophora* (Fig. 68). Its body is ovate, with 2 dissimilar poles; its principal axis, which connects the two poles, coincides with the long axis of the oval. At one pole of the chief axis (the oral) lies the mouth. The opposite pole here, as in other *Cnidaria*, is called the aboral pole.

The oral aperture leads into a spacious cavity lying in the chief axis, which has its rise, ontogenetically, through an invagination from the exterior, and is lined, like the œsophageal tube of the *Scyphozoa*, with ectoderm. We call this cavity the **œsophageal cavity** ("stomach" of authors) (*s*).

In form the œsophageal cavity is neither round nor radial, but very much flattened; in a transverse section its lumen appears like a slit. In this we find the first departure from the radial body structure of the *Medusa*. A plane running in the direction of the flattened œsophageal tube, and in which the chief axis lies, is called the **median** plane (*c-d*).

The œsophageal tube leads through another opening into a smaller cavity lying above it and lined with endoderm—the stomach (*m*). The stomach is elongated at right angles to the chief axis and the median plane, and thus, when the animal is viewed from either the oral or the aboral pole, forms a cross with the œsophagus. A plane running through the chief axis in the direction of the stomach stands at right angles to the median plane, and is called the **lateral plane** (*e-f*).

The median and lateral planes thus cross each other at right angles in the chief axis, just like the cross axes of the *Medusa*, each axis consisting of two opposite perradii. While, however, in the radially constructed *Medusa* the cross axes are quite similar, and the planes which run through them in the chief axis divide the body into four entirely similar quarters, the two cross axes in the *Ctenophora* are not alike, and the lateral and median planes divide the body into four quarters, of which only the two which are diametrically opposite are similar. Either of the two planes by itself, however, cuts the body into two similar halves.

At the aboral pole of the *Ctenophora*, as opposed to all other *Cœlen-*

terata, there is a complicated sensory organ, the **sensory body**, which, according to its structure, is best described as an auditory organ, but perhaps serves for regulating the position of the body in the water.

From near the aboral to near the oral pole, there run along the surface of the body in 8 meridians 8 rows of swimming plates, the so-called **ribs** (*r*). If we use the terms applied to the *Medusa*, these ribs are **adradial**.

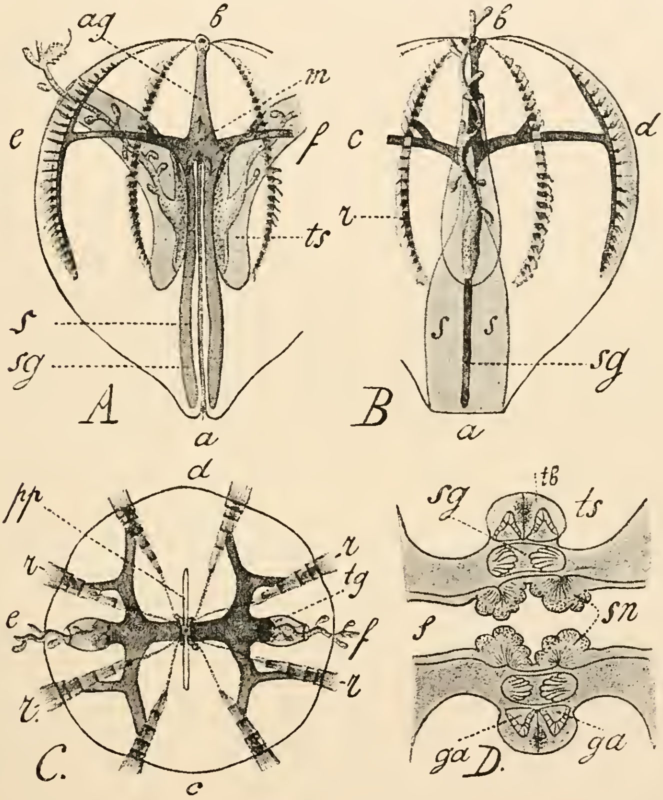

Fig. 68.—**Hormiphora plumosa**, after **Chun**. *A* and *B*, From the side: *A*, seen in the direction *c-d* in Fig. *C*; *B*, seen in the direction *c-f* in Fig. *C*. *C*, As viewed from the aboral or sensory pole. *a-b*, Chief axis; *c-d*, direction of the median plane; *e-f*, direction of the lateral plane; *a*, oral; *b*, aboral pole; *m*, stomach; *s*, œsophagus; *sg*, œsophageal vessels; *tg*, tentacular vessels; *ag*, aboral vessel; *r*, ribs; *ts*, tentacle sheath; *pp*, polar plates. *D*, Portion of a transverse section through the œsophagus (*s*); *tb*, tentacle base; *sw*, œsophageal papillæ; *ga*, branches of the tentacular vessel.

Between œsophagus and stomach on the one side and the outer integument on the other, there is a jelly which is strongly developed in most *Ctenophora*, and in which various tissue elements are imbedded.

Gastro-canals, lined with endoderm, similar to the radial canals of the *Medusæ* (or the radial gastric pouches of the *Corals*), branch out from the stomach in various directions through the jelly, reaching almost to the surface of the body. We can distinguish four kinds of these canals.

A. Four canals which to a certain extent rise interradially out of the stomach. Each of these canals branches dichotomously, and 8 adradial canals thus arise and run to the ribs, where they enter as many adradial **meridian** or **rib vessels**, which run under the ribs.

B. Two canals which run along the broad side of the œsophagus perradially and in the **lateral plane** (*i.e.* in the lateral perradii) towards the oral pole, where they end blindly; these are the **œsophageal vessels** ("gastric vessels" of authors) (*sg*).

C. Two canals which arise perradially and in the **lateral plane** (*i.e.* in the lateral perradii), and run to the walls of the tentacle sacs (**tentacular vessels**) (*tg*).

D. An **unpaired** canal (*ag*) running in the chief axis of the body towards the aboral pole, and dividing, under the sensory body into 2 branches, which lie in the median perradii. Each of these branches again divides into 2, and so 4 interradial small branches arise; 2 of these, which are diametrically opposite, generally open externally at the sensory pole, while the others, at right angles to the latter, end blindly. Less frequently all 4 branches open externally. The sensory body lies between these 4 branches of the aboral vessel ("funnel vessels" of authors).

In many *Ctenophora* there is a further development of two solid **pinnate tentacles**, into which the gastro-canal system is not continued. In quite young animals the tentacles lie near the aboral pole. At a later stage, however, they move towards the oral pole.

The tentacles are inserted at the base of sac-like depressions of the outer integument, the so-called tentacle sheaths (*ts*) into which they can be withdrawn. They lie in the lateral perradii. In many *Ctenophora* the body is round in transverse section; in others it is compressed either in the lateral or the median plane. The lateral compression is so great in the *Cestidæ* that the body appears drawn out into a long ribbon in the median plane.

If we now compare the Ctenophoral forms with other Cnidarian forms, we are at once struck by important distinctions between them. The *Ctenophora* depart in a peculiar manner, though in a direction different from that of the *Corals*, from the purely radiate fundamental form, the two cross axes being unequal. They agree with the *Scyphozoa* in the possession of an ectodermal œsophagus, but otherwise differ decidedly from them.

According to the opinion of some observers, the *Ctenophora* must be derived from *Craspedote Medusæ.* The transition from the one group to the other is made evident by an interesting *Cladonemid, Ctenaria Ctenophora.* In this animal the umbrella is much vaulted, the subumbrella much deepened; 4 radial canals rise out of the stomach and bifurcate into 8 adradial canals. There are only two pinnate, perradially placed tentacles. We need only say that the subumbrellar cavity of *Ctenaria* can be compared with the œsophageal cavity of the *Ctenophora*. The further homologies (or analogies ?) in the gastro-canal system and in the tentacles then follow of themselves.

II. The Body Epithelium.

It is not possible to carry out a sharp histological distinction between the ectodermal epithelium which clothes the whole exterior of the Cnidarian body and the endodermal gastro-canal epithelium. We here find the ectoderm and the endoderm, histologically, still in a rather undifferentiated condition; this is seen most clearly from the fact that the endoderm can in some groups supply nerve and muscle elements and stinging cells. These are tissue elements, which among the higher animals arise almost exclusively out of and in the ectoderm.

The close connection of the body epithelium of the *Cnidaria* with the nervous and muscular systems is characteristic. The cell-elements of these systems often take part with the other ectoderm cells in limiting the outer surface of the body; or they lie wedged in between them somewhat below the surface. Finally, we find them in many Cnidaria close under the body epithelium, but often still outside of the supporting membrane which divides the ectoderm from the endoderm.

The body epithelium is either naked, or may be covered with cilia or flagella over greater or smaller expanses. The **swimming** or **rowing plates**, which are arranged in eight meridional rows in the *Ctenophora*, arise out of cilia cemented together.

In the body epithelium of all *Cnidaria*, except the *Ctenophora*, the **stinging cells** are found as a very characteristic element (Fig. 69, *a*, *b*). These stinging cells contain a stinging capsule, with a spirally coiled filament, often bearing barbed hooks; when the skin is irritated this filament is evaginated and shot forward, and has the effect of a sting.

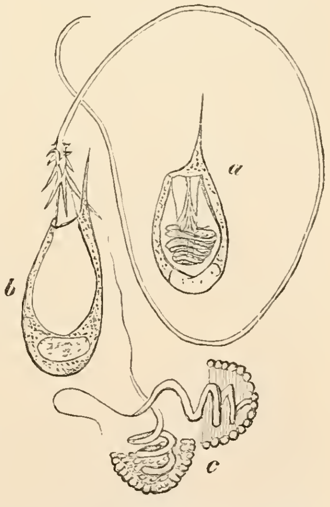

Fig. 69.—*a*, *b*, **Stinging cells of a Hydroid, Cordilophora, after F. E. Schulze.** *c*, **Seizing or adhesive cells of a Ctenophore, after Chun.**

The stinging capsules or nematocysts are microscopic adhesive organs, and are to the *Cnidaria* at the same time weapons of defence and of offence. They are particularly numerous in exposed parts of the body, and in organs which are used in seizing prey—round the mouth, on the tentacles, at the margin of the disc in the *Medusæ*. On the tentacles of *Hydro-* and *Scypho-medusæ*, and especially on the capturing filaments of the *Siphonophora*, they are assembled in masses, and form "stinging knobs" or "stinging batteries."

In the body epithelium of the *Ctenophora* we find peculiar adhesive cells (Fig. 69, *c*) with uneven and sticky surfaces. Their bases are prolonged into spirally coiled contractile filaments.

Besides the nerve cells, the sensory, muscle, stinging, flagellate, ciliated, and covering cells, various glandular cells and pigment cells are found in the body epithelium of many *Cnidaria*, and are especially numerous in the *Ctenophora*.

III. The Gastro-canal System.

The gastro-canal system in its general arrangement has already been mentioned in the general review. It is the most characteristic system of organs of the *Cnidaria*, and in some groups reaches a very high degree of complication. This complication stands in direct relation to the complication of other portions of the body, which fact is at once comprehensible when we learn that in the *Cnidaria* the gastro-canal system undertakes not only the digestion, but also the circulation. The more massive the body and the more numerous and complicated its organs, the more necessary is it that the nutrition of these organs should be provided for by gastro-canals or vessels.

From such a standpoint the complicated arrangement of the gastro-canal system of the *Medusæ* and *Ctenophora* is at once comprehensible. In the *Medusæ* the margin of the umbrella is distinguished by the possession of numerous organs (tentacles, velum, auditory vesicles, stinging cells, nerve ring, eye spots, and sensory bodies). The subumbrellar side is strongly muscular, while the exumbrella is devoid of organs. The jelly being so largely developed as a passive organ for motion and support, the special gastro-canals (radial vessels) must run near the subumbrella to convey food to the organs on the margin of the disc. This purpose is also served by the circumferential canal, into which they enter. The relations of the gastro-canals to the other organs of the body are just as clear in the case of those *Ctenophora* which have a massive gelatinous tissue between the ectoderm and endoderm. The most important organs of the body, apart from the sexual organs, are in this group: the sensory body of the aboral pole, the 8 ribs, and the 2 tentacles; answering to these, we find an aboral vessel, also 8 vessels running from the stomach to the ribs, and which enter 8 meridional vessels, and, further, 2 vessels which run to the base of the tentacles.

According to the ontogenetic origin of the gastro-canal system, two principal types can be distinguished in the *Cnidaria*. In one type, which is found among the *Hydrozoa*, the whole gastro-canal system rises out of the endodermal enteron of the larva. In the second type, which is characteristic of the *Scyphozoa* and *Ctenophora*, the gastro-canal system consists of an ectodermal and an endodermal portion. The former, which we call **stomodaeum** in embryos, larvæ, and generally in young transition stages, and **œsophagus** in adult animals, arises at the oral pole by a depression of the ectoderm into the body. This œsophagus is represented in the *Scyphomedusæ* by the inner lining of the oral or gastric peduncle as far as the point of insertion of the gastral filaments, in *Corals* by the tube which leads into the gastric cavity, and in the *Ctenophora* by the beginning of the gastro-canal system, hitherto unsuitably named the stomach. The **mouth** of the *Hydromedusæ* thus leads direct into the endodermal gastric cavity; whereas the mouth of the *Scyphomedusæ*, *Anthozoa*, and *Ctenophora* leads first into the ectodermal œsophagus, and from that through the **enteric aperture**, which corresponds with the mouth of the *Hydromedusæ*, into the endodermal gastro-canal system.

In all animals, from the *Cœlenterata* upwards, there is an ectodermal œsophagus.

The endodermal gastric cavity is met with in its simplest form in the *Hydroida* as a simple pouch adhering closely to the inner surface of the ectoderm, from which hollow or solid processes extend into the axes of the tentacles. In the long, or principal axis of the body, thickenings of the gastric wall, **gastric ridges**, which are occasionally 4 in number, regularly arranged crosswise, are commonly found.

We have already described the form of the gastric cavity of the *Scyphula* in the introduction; and we also there described the general arrangement of the gastro-canal system in the *Anthozoa*. We add here that the septa which separate the gastric pouches from each other round the œsophagus are occasionally broken through near the oral disc by an aperture, so that a sort of circumferential canal arises. The hollow processes of the gastro-canal system in the tentacle axes sometimes penetrate to the exterior at the tips of the tentacles through pores. The free edges of the septa, which are turned towards the principal axis of the *Coral* individual, are thickened, and are prolonged as **mesenterial filaments,** freely projecting into the gastric cavity. The epithelium of these filaments contains numerous gland cells, and sometimes stinging cells as well. Some of these filaments, the so-called **acontia,** are particularly long and vermiform, and can be quickly shot out of the body, either through the mouth, or through special pores in the body wall. These are found in the *Actinia*.

How the gastro-canal system of the *Craspedote Medusæ* (*Hydromedusæ*) can be traced back to the gastric cavity of the Hydrula form, and the gastro-canal system of the *Acraspeda* (*Scyphomedusæ*) to the gastric cavity of the Scyphula form, has already been shown in the general review.

The radial canals in the *Craspedote Medusæ* are comparatively seldom limited to the number 4. In most forms their number is greater, and in a few (*Æquoridæ*) they are very numerous (over 100) and run radially from the central stomach to the margin of the disc, and here enter the circumferential canal. There are also in a few *Craspedota*, near and between the radial canals, **centripetal canals,** which start from the circumferential canal and run a certain distance towards, but do not reach, the central stomach. The **radial canals** may be branched, and these branches may either end blindly or enter the circumferential canal. The **central stomach** may be divided, the divisions being superimposed one on another in the principal axis. The lowest division is the **oral stomach,** continued in the **oral** or **gastric peduncle,** which hangs down from the middle of the subumbrella. The gastric peduncle, at whose free end lies the mouth, may be very variously developed, from a short wide tube to a long tubular structure protruding far beyond the subumbrellar cavity. The mouth is either simple, square, or cross-shaped, or produced into 4 points or lobes, and sometimes supplied with oral tentacles, or with variously shaped papillæ. The edge of the mouth is generally well armed with nemato-cysts.

The gastro-canal system of the *Acraspeda* or *Scyphomedusæ* (Fig. 67, p. 77; Fig. 70) shows, in the arrangement of its single sections, a still more varied structure than that of the *Craspedota.* In some groups it is wonderfully complicated, and sometimes shows great similarity with the gastro-canal system of certain *Craspedota*; in such cases, when we further think of the great similarity in body form, it is difficult to believe that the *Acraspeda* and *Craspedota* are two sharply divided branches of the *Cnidaria.*

Let us first consider the **oral tube** or **oral peduncle,** which, unlike that of the *Craspedota*, contains the ectodermal œsophagus. The oral tube is usually short, and has either a simple square or cross-shaped aperture, or, as in most large *Acraspeda*, is produced into 4 long strong **oral arms.** These 4 perradial oral arms become, by means of a bisection so deep as to reach their bases, the 8 oral arms of the *Rhizostomæ*, which are distinguished by the following peculiar organisation.

Each oral arm becomes deeply furrowed on the side turned to the chief axis, forming a channel in the longitudinal direction. This inner **channel** corresponds with an externally projecting **mid-rib.** The channel becomes deeper, and the curled edges of the oral arm which border it unite over it and grow together, so that it now becomes a closed canal. Such concrescence is completed along the whole length of the oral arm to its base, and also spreads to the edges of the oral aperture lying at the base of the arms, and the canal thus becomes completely closed. The concrescence of the curled edges of the arm, however, takes place in such a way that numerous small open canals remain (**suctorial mouths**) (Fig. 70 *D*, *sm*); these lead from the exterior into the central canal of the arm. This again leads into the closed œsophagus. In all *Rhizostomæ* the original oral aperture is thus closed, and is replaced by the numerous suctorial mouths on the hollow oral arms.

In the endodermal gastro-canal system, here as among the *Craspedota*, we can distinguish a central or main intestine from the peripheral intestine (Kranzdarm). The main intestine can separate into two divisions, one lying above the other, the lower of which always communicates with the peripheral intestine.

On the wall of the main intestine of all *Acraspeda* (as opposed to the *Craspedota*), there are 4 interradial or 8 adradial mobile gastral filaments, or, usually, tufts (phacelli) of gastral filaments, whose bases define the boundary between the œsophagus and the endodermal main intestine. The peripheral intestine is very variously developed. In

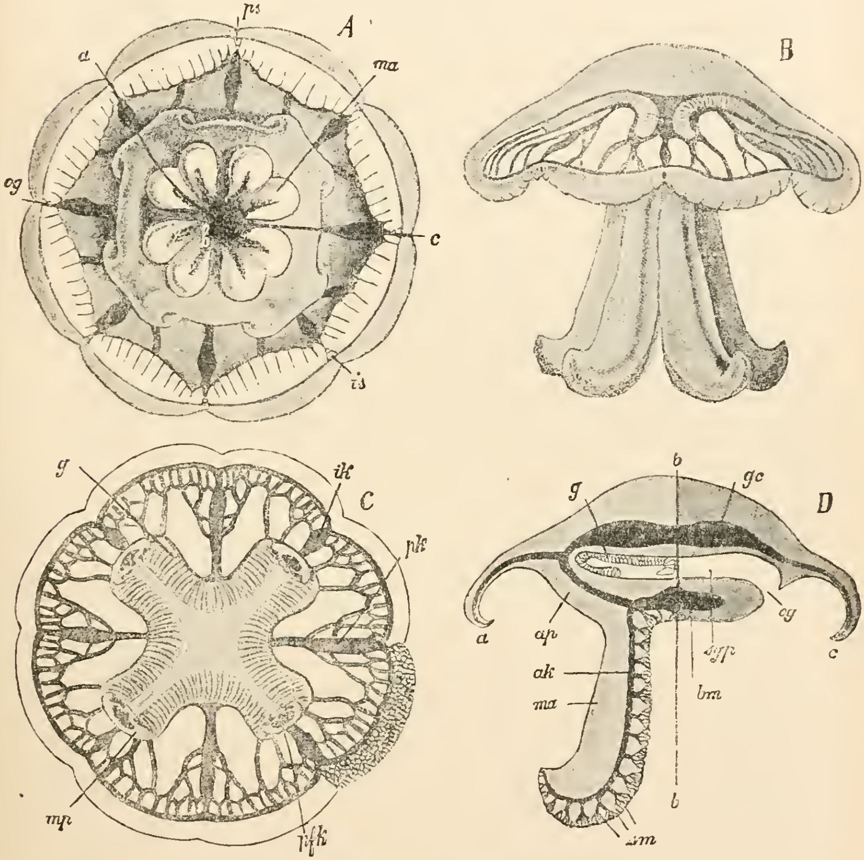

Fig. 70.—**Cannorhiza connexa**, after **Haeckel**. *A*, Seen from the subumbrella; *B*, from the side; *C*, from the subumbrella, after removal of the oral arms and buccal stomach by cutting through the oral pillars. *D*, Section in the direction of the principal axis and the line *abc* in Fig. *A*. *a-b*, Near an interradius; *b-c*, perradius; *og*, subgenital ostia; *ma*, oral arm; *ps*, perradial, *is*, interradial sensory body; *g*, gonades; *mp*, *ap*, oral pillars, arm pillars; *pfk*, pillar canals; *pk*, perradial; *ik*, interradial gastro-canal; *b-b*, principal axis; *sgp*, subgenital porticus; *bm*, buccal stomach; *ak*, arm canal; *sm*, suctorial mouths; *gc*, central stomach.

the lower *Acraspeda*, which also remind us of the *Scyphula* in their attachment by an aboral stalk (*Lucernaria*) and their cup-like shape, the peripheral intestine consists of 4 wide pouches divided by narrow septa, which communicate with the chief intestine and also open into a circumferential canal at the margin of the disc by means of breaches through these septa. If the septa are reduced to 4 small points of concrescence between the exumbrellar and subumbrellar walls of the peripheral intestine, directly on the circumference of the main intestine, the 4 pouches coalesce to form a spacious circular sinus, which commands the whole edge of the disc, and communicates with the principal gastric cavity between the points of concrescence. In the higher *Acraspeda* this circumferential sinus becomes divided, by the partial concrescence of its exumbrellar and subumbrellar walls, into 8, 16, 32, or more radial chambers or radial canals, which in many forms, by anastomosing or branching, form a very ornamental net-work of canals running towards the edge of the disc (Fig. 70, *C*).

Excretory pores of the gastro-canal system.—In various *Medusæ*, in *Acraspeda* as well as in *Craspedota*, small apertures have been observed at the margin of the disc; these often lie on the points of papillæ, and by means of them communication between the peripheral gastro-canal system and the outer world is established.

The gastro-canal system of the Ctenophora (Fig. 68, p. 79), in its general arrangement, has already been delineated. We add here that the meridional vessels in lobate *Ctenophora*, and also in the *Cestidæ* and *Beroidæ*, communicate with each other and with the œsophageal vessels at the oral portion of the body, and that in the *Beroidæ* they also send out numerous branching and anastomosing processes, some of which enter the jelly, or join to make a peripheral net-work. The nourishment of the often much-developed oral lobes of the lobate *Ctenophora* is provided for by the meridional vessels, which traverse the oral lobes in various arabesque-like patterns.

Histological.—Each epithelial cell of the gastro-canal system very commonly carries one single flagellum; these cells are thus flagellate cells. Among the epithelial cells there are gland cells, stinging cells, cells with various contents as products of metabolism, epithelial muscle cells, etc. Very often the gastric epithelial cells send out amœboid or pseudopodia-like processes on that side of them which is turned to the lumen of the gastro-canal system, and by the help of these they take into their cell bodies small particles of food in the manner of the *Rhizopoda* (intracellular ingestion of food).

IV. Musculature.

In the *Hydroida* and *Siphonophora* we find, in the first place, a system of longitudinal fibres which run, buried in the epithelium, from the oral to the aboral pole, and in the tentacles. These fibres, which correspond to the processes of the ectodermal neuro-muscular or epithelial muscular cells, serve for contracting the body and the tentacles. In these forms again, and especially in the *Siphonophora*, there is a system of circular fibres which run under the **endodermal** epithelium as processes of the endodermal epithelial muscular cells. By the contraction of these fibres the body and the tentacles are extended. In the medusoid swimming bells of the *Siphonophora*, just as in the *Craspedote Medusæ*, a layer of striated ectodermal circular muscle fibres is developed in the subumbrella and in the velum.

We find the two systems of muscles in the *Medusæ* also, the longitudinal and the circular, though the latter is here ectodermal. The longitudinal muscle fibres are generally smooth, the circular muscle fibres usually striated. The muscle fibres are mostly processes from the epithelial muscle cells; but there are also muscle bands and strands which quite detach themselves from the epithelium, and run in the gelatinous connective tissue as independent mesodermal muscles. The exumbrella is poor in muscles, sometimes even having none at all. In the remainder of the body, the longitudinal as well as the circular musculature falls into three systems: (1) into a system spreading over the gastric or oral peduncle; (2) a system spreading over the subumbrella from the base of the oral peduncle to the margin of the disc; (3) a system developed at the margin of the disc itself (musculature of the tentacles, the velum, and the velarium). In correspondence with this, the three systems of the longitudinal musculature are as follows:—

A. The longitudinal musculature of the oral peduncle (serving for its contraction and retraction).

B. The radial muscles, which run radially from the base of the oral peduncle towards the margin of the disc.

C. The longitudinal muscles of the tentacles and marginal lobes.

The three systems of the circular musculature are as follows:—

A. The circular musculature of the oral peduncle.

B. The circular musculature of the subumbrella, developed in the *Craspedota* over its whole extent, but in the *Acraspeda* generally forming a narrower but very strong **peripheral muscle** (Fig. 67, *m*, p. 77) near the circumference of the subumbrella.

C. The strong circular musculature of the Craspedote velum, and the circular musculature of the Acraspede marginal lobes and velarium.

In *Scyphostoma* and many lower *Acraspeda*, especially in attached forms, *e.g. Lucernaria*, there are 4 (seldom 8) interradial **septal** or **funnel** muscles (peduncular muscles) which, starting from near the oral disc, or that portion of the subumbrella which borders on the oral peduncle, run through the body as far as the aboral attached apex of the exumbrella. They lie in the 4 septa which separate the 4 gastric pouches on their axial sides, and then proceed upwards in the prolongations of the septa, *i.e.* in the 4 gastric ridges or tænioles. According to recent research, they arise in the ectodermal cells of a solid prolongation of the 4 interradial septal funnels, which grow towards the aboral pole; we shall speak of these septal funnels later.

The endodermal musculature of the *Corals*, in contradistinction to that of all the other *Cnidaria*, is at least as much if not more developed than the ectodermal. The musculature is most highly developed in those *Actinia* which have no skeleton. It shows in its arrangement much similarity with that of the *Scyphomedusæ*, *e.g.* the *Lucernaria*. We have an ectodermal longitudinal muscle system and an endodermal circular muscle system (leaving out of sight for the present the fact that single portions of the musculature detach themselves from the epithelial matrix and become mesodermal).

I. The ectodermal longitudinal muscular system forms (*a*) the longitudinal muscles of the tentacles and (*b*) the radial muscles of the oral disc. This system is wanting in the œsophagus, in the outer wall of the body, and in the pedal disc. Only in some forms, which possess no septal longitudinal muscles (*Cerianthus*), there are in the body wall strong ectodermal longitudinal muscles which serve as retractors of the body.

II. The endodermal circular muscular system extends all over the surfaces of the body, and forms a layer of circular fibres in the body wall, an inner circular muscular layer in the tentacles, a layer of concentric fibres on the oral disc, and a circular muscular layer round the œsophagus.

The **musculature of the septa** in *Corals* deserves special attention; it consists of a system of longitudinal and of a system of transverse muscles. The longitudinal muscles run along the septa from the pedal to the oral disc, and serve as retractors of the body. They are mostly so strongly developed that they form longitudinal thickenings on each septum in the space between it and the next septum (Fig. 66, p. 76). The transverse musculature is less strongly developed. It is attached on one side to the body wall, on the other to the pedal disc, the oral disc, and the œsophageal tube. The transverse muscles lie on one surface of each septum, the longitudinal on the other side. Their relative positions on the different septa varies in different divisions, and is always very characteristic. There is generally only **one plane**, which can be made to divide the body in such a way that the arrangement of the muscles on the septa on each side of it is exactly similar. This **median plane** runs in the principal axis in the direction of the flattened œsophagus or the slit-like oral aperture.

In most *Actinia* with numerous septa of various ages and sizes, septa of equal sizes always go in pairs. The longitudinal muscular thickenings of such a pair of septa are turned towards each other. The longitudinal muscles are therefore turned towards the space between the two septa of such a pair—the so-called **intraseptal space**—and the transverse muscle layers are turned towards the space between this pair and the next on each side—the **interseptal spaces.**

In those *Alcyonaria* which have 8 partition walls, the muscular thickenings of the 4 septa which lie on one side of the median plane are all directed towards one side (Fig. 66).

There are, besides these, other types of muscle and septal arrangement in the *Corals*.

The longitudinal muscles of the septa show a great analogy with the septal or peduncle muscles of the lower *Acraspeda*. The former appear, however, according to present knowledge, to be endodermal muscles.

The muscular elements of *Corals* are either epithelial muscle cells (endodermal musculature), or sub-epithelial muscle cells (ectodermal musculature), or mesodermal muscles (in some species at different parts of the body).

The following applies to the musculature of the *Medusæ*, *Siphonophora*, and *Corals*. If it is much developed in one part, the muscle lamella lays itself, for the purpose of superficial increase, in parallel folds like the leaves of a book (Fig. 71, *C*). These folds may again fold themselves in a more or less complicated manner, so as to have a feathered appearance in transverse section.

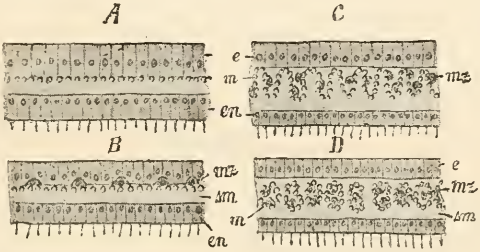

Fig. 71.—**Diagrammatic representation of the various arrangements of the ectodermal Cnidarian musculature in transverse sections through the body wall.** *e*, Ectoderm; *en*, endoderm; *m*, muscle lamella; *mz*, cell bodies of the muscle fibres; *sm*, supporting membrane, jelly.

The mesodermal supporting substance or supporting membrane takes part in the folding of the contiguous muscle lamellæ by itself running within the folds in the form of lamellæ.

When muscle folds completely detach themselves from their matrix, the epithelium, and when the free edges of each fold coalesce, there arise out of these sub-epithelial muscle folds mesodermal muscle tubes (*D*), which are then surrounded on all sides by the supporting substance.

In the musculature of the **Ctenophora**, we in the first place distinguish an ectodermal and a mesodermal portion, between which, however, no very sharp boundary can be made. The ectodermal musculature consists of elongated sub-epithelial fibres on the boundary between the epithelium and the jelly; these may have very various courses. Sometimes we can more or less clearly distinguish a system of longitudinal from a system of circular fibres. The ectodermal musculature is also continued on the œsophagus. The mesodermal musculature, which lies in the jelly, is more strongly developed than the ectodermal musculature; its fibres, which have an isolated course and are elegantly branched at each end (Fig. 47, *g*, p. 47), run in various directions, though usually radially, being stretched between the different parts of the gastro-canal system and the outer integument. The contraction of the tentacles and their lateral filaments is brought about by strands of longitudinal muscle fibrillæ which run in their solid axes and which may be partially striated. Longitudinal and circular muscle fibres have also been observed in the walls of the gastro-canals.

The **Velum** of the *Craspedote Medusæ* (Fig. 64, *B*, *v*, p. 73; Fig. 65, p. 74; Fig. 72, *v*, p. 95) is a thin membrane which projects from the margin of the disc like a diaphragm into the subumbrellar cavity. The gastro-canal system is never continued into this membrane, which consists of the following portions :—

1. A continuation of the epithelium of the exumbrella.
2. A continuation of the epithelium of the subumbrella. These two epithelia coalesce at the free inner edge of the velum. Under the former lies a thin supporting lamella, the continuation of the disc jelly; under the latter, a layer of ectodermal circular muscle fibres (*m*), a continuation of the circular musculature of the subumbrella.

V. Tentacles of the Cnidaria, Marginal Lobes of the Scyphomedusæ.

All Cnidaria (with the exception of the *Rhizostomæ* among the *Scyphomedusæ* and the *Amalthæidæ* among the *Craspedota*) possess **tentacles** arranged in a circle round the mouth, at a greater or less distance from it. These tentacles are evaginations of the body wall, into which (with the perhaps only apparent exception of the *Ctenophora*) hollow or solid processes of the endodermal gastro-canal system penetrate. The tentacles are pre-eminently organs for catching food, and at the same time sensory organs of touch. We shall see further on that some of them are partially transformed in the *Craspedote* and *Acraspede Medusæ* into specific sensory organs.

The structure of the tentacles, their number, their division and arrangement on the body, and their relation to the gastro-canal system, offer in the various divisions many modifications of great importance in classification.

Form of the tentacle.—The tentacles are, speaking generally, cylindrical filaments. In the *Hydroids* they are usually simply filamentous, less frequently knobbed at the free end, and still less frequently branched (*Cladocoryne*). Among the *Craspedote Medusæ* also we generally meet with filamentous tentacles. The family of the *Cladonemidæ* alone is distinguished by tentacles which are dichotomously branched, or feathered on one side (provided with collateral filaments), and often knobbed. The tentacles of the *Siphonophora* and the *Ctenophora* are also feathered on one side. The tentacles of the *Acraspeda* are simple. Among the *Anthozoa*, the *Alcyonaria* possess tentacles feathered in two rows, but all other divisions have simple filamentous or vermiform tentacles.

Number and arrangement of the tentacles.—Among the *Hydroida* the tentacles, in varying number, are either arranged in a circle at a short distance from the mouth (*e.g. Hydra*), or in two circles (*e.g. Tubularia*), or they are dispersed over the body of the individual, though not on its stalk (*e.g. Coryne*). In the *Scyphostoma* the tentacles (about 24 in number) are inserted at the edge of the oral disc of the cup-shaped body. In the *Craspedote* and *Acraspede Medusæ* the tentacles are invariably found on the margin of the disc. In the simplest case we find in the former 4 perradial, and in the latter 4 perradial and 4 interradial tentacles. In most Medusæ the number of tentacles increases in a regular manner—secondary, tertiary, etc., being inserted between the primary. Only in a few *Craspedota* the number is reduced to two tentacles, opposite one another, and less frequently to one single tentacle (in the sub-family of the *Euphysidæ* among the *Codonidæ*, and in the tentacle-bearing "persons" of one principal division of the *Siphonophora* (the *Siphonantha*). Complete loss of all tentacles is a distinguishing mark of the *Amalthæidæ* among *Craspedota* and the *Rhizostomæ* among *Acraspeda*. In a few Medusæ, especially among the *Narcomedusæ*, the points of insertion of the tentacles move up from the edge of the disc a greater or less distance on to the exumbrella.

In the *Corals* the number of tentacles inserted at the circumference of the oral aperture represents, in a general way, the number of gastric pouches separated by septa. Each tentacle lies above a gastric pouch, which is produced into it in the form of an axial canal. In the *Alcyonaria* we have 8, in the *Hexacorallia* 6 or 6*n*, in the *Tetracorallia* 4 or 4*n*, such corresponding tentacles.

The majority of the *Ctenophora* (*Tentaculata*) possess two solid tentacles or retractile filaments, feathered on one side, lying in the lateral plane; these can be withdrawn into special sacs or sheaths, and arise in the neighbourhood of the aboral pole; later, however, they generally move towards the oral pole.

Structure of the tentacles.—The tentacles of the *Hydromedusæ* and *Scyphomedusæ* consist: (1) of an ectodermal epithelium, generally with stinging knobs or batteries; (2) of a layer of ectodermal longitudinal muscle fibres lying directly under this; (3) of a structureless elastic supporting membrane; and (4) of an axis of endodermal cells. This axis is hollow in most forms, and the cavity is in open communication with the gastro-canal system of the body; or it is solid, and then consists chiefly of a single row of disc-like cells, which are superimposed like the coins in a roll of sovereigns (*e.g.* in *Obelia*, in many *Trachomedusæ*, *Narcomedusæ*, and the related *Hydroids*, also in *Stauromedusæ* and *Cannostomæ*). This axial pillar must serve as an elastic organ of support. The hollow tentacles are mostly far more mobile and more strongly contractile than the solid. The tentacles of *Corals* are also hollow; their structure differs considerably from that of the *Hydro-* and *Scypho-medusæ*. The ectoderm and endoderm in *Corals* are separated by a supporting substance which contains cells of connective tissue. Under the outer epithelium lies an ectodermal muscle layer, and under the inner epithelium a similar endodermal layer. In some cases muscles may also run within the supporting substance.

The tentacles of the *Ctenophora* are **solid.** They are generally provided with seizing or adhesive cells. Their axes are usually occupied by strongly developed longitudinal muscle-fibres. These fibres arise, as it appears, at an early stage out of special "mesodermal" elements, *i.e.* a group of cells which sever themselves from the primitive endoderm of the young gastrula larva. We ought therefore, perhaps, to compare the solid axis of the *Ctenophoran* tentacle with the solid endodermal axis of the tentacles of many *Medusæ.*

The marginal lobes of the Scyphomedusæ (Fig. 67, *rl*, p. 77; Fig. 70). The marginal lobes of the *Scyphomedusæ* or *Acraspeda* are just as characteristic of them as is the velum of the *Hydromedusæ* or *Craspedota.* As a real velum is wanting in all *Scyphomedusæ*, so are marginal lobes wanting in all *Hydromedusæ.* Like the tentacles, together with which they are found, the marginal lobes are processes of the body wall at the edge of the umbrella, into which the prolongations of the gastro-canal system extend. Unlike the tentacles, they are broad and flat, serving as rowing organs, with muscles on the concave subumbrellar side. In the simplest cases there are 8 adradial marginal lobes, mostly, however, there are 16 subradial lobes, and their numbers are often still further increased. In the *Cubomedusæ* and in many *Rhizostomæ* the lobes grow together to form a circular rim of varying width, the so-called **velarium** which, however, can always be easily distinguished from the true velum of the *Craspedota* by its supply of gastro-canals. The clusters of tentacles of the Lucernaria are secondary outgrowths of the marginal lobes, between which rudiments of the primary tentacles can sometimes be found.

VI. The Nervous System.

This, which appears in the *Cnidaria* for the first time in the animal kingdom as an independent system, is marked by a rather diffuse arrangement (want of definite centralisation), and by the close relation which it bears to the body epithelium during the whole life. In the *Hydra* the outwardly directed cell body of the so-called neuromuscular cells probably plays the part of an undifferentiated sensory nerve cell. But as early as the *Craspedote Medusæ* we find an independently developed nervous system, close under the epithelium, outside the supporting membrane or jelly; it forms a plexus of bipolar and multipolar ganglion cells with connecting fibrillæ. This plexus is connected by fibrillæ on the one hand with the epithelial sensory cells (tactile, auditory, visual, olfactory cells), on the other hand with muscle fibres. In correspondence with this, the nervous tissue is particularly strongly developed on the margin of the umbrella, which is so rich in sensory and locomotor organs. At this part in the *Craspedota* a central apparatus, in the form of a double nerve ring, is developed (Fig. 72, *A* and *B*, nr_1, nr_2, p. 95). One of these nerve rings, the upper one, is placed on the exumbrellar, the other on the subumbrellar margin, both close to the base of insertion of the velum. The first innervates chiefly the sensory organs of the umbrella margin, the latter the musculature of the velum; the two are connected by fibrillæ running through the supporting membrane. A peripheral nervous system is present in the form of a plexus of ganglion cells and fibres connected with the lower nerve ring, especially on the subumbrella; it supplies the musculature of this part with nerves. The aboral exumbrella, not only in the *Craspedota*, but also in the *Acraspeda*, is devoid of a nervous system, as also of sensory organs and musculature; this is explicable by the ontogenetic and phylogenetic derivation of these animals from a form attached by the aboral pole.

In the *Siphonophora* also a plexus of ganglion cells at various parts of the body has been demonstrated.

In the *Scyphomedusæ* or *Acraspeda* also a plexus of ganglion cells is developed in the subumbrella. It is connected with considerable central accumulations of nerve tissue on the subumbrellar margin. These are developed in the *Cubomedusæ* as 8 (4 perradial and 4 interradial) ganglia, connected together by a circular nerve, from which sensory nerves proceed to the rhopalia (sensory bodies) and to the tentacles, and motor nerves to the musculature. In the *Discomedusæ* there are also 8 ganglia at the bases of the 8 sensory bodies, but here there is no connecting nerve ring.

In the *Corals* a plexus of ganglion cells lying deep in the body epithelium has also been demonstrated. This is particularly strongly developed on the oral disc, and at the base of the tentacles.

In the nervous system of the *Ctenophora* we can, according to recent research, which still needs extension, distinguish the following parts: (1) a diffuse, ectodermal, ganglionic plexus under the body epithelium, which is spread over the whole surface of the body, and may be continued on to the wall of the œsophagus; (2) fine, branching, nucleated strands, which penetrate the jelly, and are connected with the muscles of the jelly by lateral branches—a connection between these strands and the ectoderm is not yet proved; (3) 8 meridional nerve strands, running under the 8 ribs, and ciliated bands (see description of sensory body),—the rib-nerves. It is a remarkable fact that it has till now been impossible to prove a connection between these three parts of the conjectural nervous system and the sensory body at the aboral pole.

A fact which deserves special mention is that, in the *Medusæ* and *Siphonophora*, and especially in the *Actinia*, a more or less extended plexus of ganglion cells may lie under the endodermal epithelium.

VII. The Sensory Organs.

We meet with special sensory organs for the first time in the animal kingdom among the *Cnidaria*. The development and distribution of these organs is directly related to the manner of life. In attached forms (*Hydroids*, *Corals*) there are only organs of touch (the tentacles); in free-swimming forms (*Acraspeda*, *Craspedota*, *Siphonophora*, *Ctenophora*) organs of smell, hearing, and sight may be added.

The **organs of touch** are primarily the tentacles of which we have already spoken. The sense of touch is due to special tactile cells belonging to the body epithelium; these are provided with a projecting tactile hair, which is either flexible, mobile, or stiff. The basal ends of such cells are continued into nervous processes which are connected with the nervous system. Tactile cells are to be found, not only in the tentacles of the *Cnidaria*, but in great numbers on the margin of the disc of the *Medusæ*, and especially in the *Ctenophora*, scattered over the whole free surface of the body.

As organs of **smell**, or perhaps rather **taste**, we have:

1. Small **club-shaped papillæ**, which in certain *Leptomedusæ* are found generally in great numbers at the edge of the umbrella between the tentacles, being attached to the margin by thin stalks. They contain a narrow blind canal, lined with thick cylindrical endodermal epithelium, which comes from the circumferential canal.

2. Pit-like depressions on the sensory bodies or rhopalia of the *Acraspeda*, lined with a sensory epithelium which is much folded and provided with long flagellate hairs.

Auditory organs (perhaps also organs for regulating the position of the body in the water) are found in *Craspedote* and *Acraspede Medusæ* and in the *Ctenophora*.

We can distinguish three types of auditory organs: (1) **auditory vesicles**, or marginal vesicles with ectodermal otoliths; (2) **tentaculocysts**, or auditory tentacles; and (3) the so-called **sensory body** of the *Ctenophora*.

I. The auditory or marginal vesicles are found in the division of the *Leptomedusæ* (*Vesiculatæ*). These are, in the simplest cases, open pit-like depressions of the subumbrellar epithelium near the base of insertion of the velum. Within these auditory pits are one or more otoliths, which have come from ectodermal cells, while the cells which form the base of the pit bear auditory hairs, on which the otoliths rest (*e.g. Mitrocoma*). Auditory vesicles rise out of these auditory pits by the closing of the pit, which moves towards the exumbrellar side of the base of insertion of the velum and here forms an externally rounded protuberance (Fig. 72, *A*). Auditory pits and auditory vesicles receive their nerves from the subumbrellar nerve ring. In the simplest cases we find 8 adradial auditory vesicles, but the number is often much greater, and mounts up to many hundreds.

II. **Tentaculocysts or auditory tentacles** are, among the *Medusæ*, the most widely spread organs of hearing. They are short transformed tentacles in which the solid endodermal axis in the *Craspedota* (*Tracho-* and *Narco-medusæ*, Fig. 72, *B*, *C*), or the peripheral distal end cells of the hollow tentacle-canal (*Acraspeda*, Fig. 73), form one or more otoliths, which are here, therefore, endodermal. The ectoderm of the tentaculocysts of the *Craspedota* and often also a sensory cushion round the base of the tentaculocyst carry long stiff auditory hairs. In many *Trachomedusæ* the sensory cushion rises round the base of the tentaculocyst into a circular wall (Fig. 72, *C*), which may even completely close over the tentaculocyst. Thus closed vesicular auditory organs again arise, but these have quite a different origin and morphological signification from the true marginal vesicles of the *Leptomedusæ*.

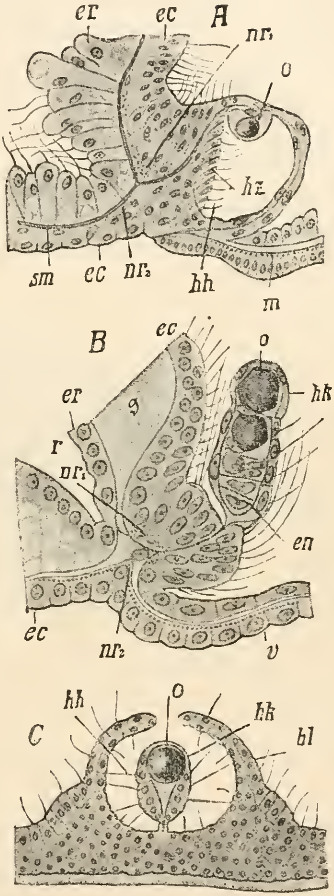

Fig. 72.—*A*. **Auditory vesicles of Æquorea Forskalea.** *B*, **Tentaculocysts of Cunina lativentris.** *C*, **Tentaculocysts of Rhopalonema velatum.** *A* and *B*, Transverse sections of the margin of the disc; *C*, section of the margin of the disc, after **Hertwig.** *ee*, Ectoderm; *er*, endoderm of the circumferential canal; nr_1, upper; nr_2, lower nerve ring; *r*, circumferential canal; *sm*, supporting membrane; *o*, otolith; *hh*, auditory hairs; *hz*, auditory cells; *hk*, tentaculocysts; *bl*, auditory vesicles; *g*, jelly; *m*, muscle lamellæ; *en*, endoderm cells of the tentaculocysts. In *A* and *B* the velum is bent centrifugally outwards.

Between the inner wall of the auditory vesicle and the tentaculocyst which it encloses, the auditory hairs are stretched like chords. The **tentaculocysts** always receive their nerves from the exumbrellar nerve ring. In the simplest cases we find 4 interradial tentaculocysts, but their number is often considerably greater.

The sensory bodies or rhopalia of the Acraspeda (Fig. 73) are compound sensory organs, of which the auditory organ is the principal factor. These are, at the same time, metamorphosed tentacles into which a hollow process of the gastro-canal system penetrates. The endodermal cells at the peripheral blind end of these processes produce an otolith or a mass of otoliths. The outer epithelium of the auditory body carries the auditory hairs. In it, also, on one side lie the eye or eyes; close to it also lie the olfactory pits. The whole epithelium round this compound sensory organ, which is protected in special indentations in the disc margin by lobes, is a sensory epithelium with a thick nerve plexus. There are either 4 or 8, less frequently 12, 16, or even more rhopalia on the margin of the *Acraspede* umbrella.

III. The **sensory body** at the aboral pole, so characteristic of the *Ctenophora*, is a compound sensory organ of a very peculiar kind, which, according to its structure, is an auditory organ, or rather, perhaps, an organ for regulating the movement of the swimming plates.

The sensory body is constructed as follows. It consists at first of a shallow pit-like depression between the 4 branches of the aboral so-called funnel vessel. The ciliated body epithelium which forms the base of this pit thickens considerably (Fig. 75, *se*). Its elements are thread-like cells. In this "sensory cushion" are found deposits of pigment, which perhaps represent simple organs of sight. Round the edge of the pit there rises a membrane which unites above in the shape of a bell, forming a sort of roof to the pit, which is thus transformed into a vesicle. The membrane is composed of the long cilia at the edge of the pit cemented together. It is broken through by slits at 6 places, and through these the sea water can freely reach the interior of the vesicle. Two of these slits, which are opposite each other, belong to the median plane. The other 4 lie interradially. On the sensory cushion within the vesicle rise 4 S-shaped radially-placed springs; these likewise consist of fused cilia, and their free upper ends enter a globular mass of otoliths, which they support.

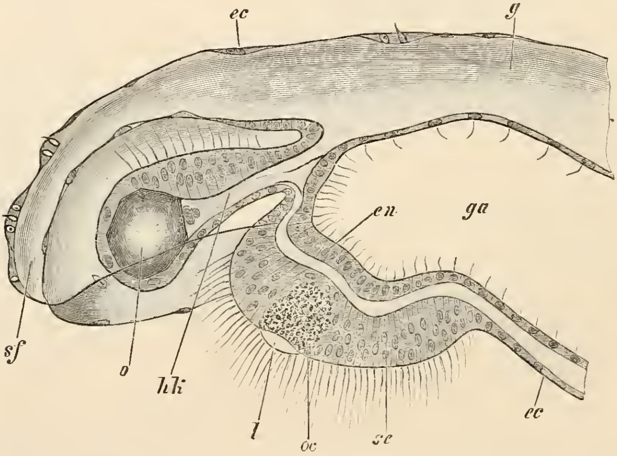

FIG. 73.—**Sensory bodies of Nausithoë**, after **Hertwig** (optical transverse section of the margin of the disc). *sf*, Sensory fold of the margin of the disc; *ec*, ectoderm; *en*, endoderm; *ga*, gastro-canal; *hk*, auditory body; *o*, otolith; *se*, sensory epithelium; *oc*, eye; *l*, lens; *g*, jelly.

From the 4 springs 4 rows of cilia run out through the 4 interradial slits in the bell-shaped roof. They divide into 8 adradial ciliated bands, which run along the aboral surface of the *Ctenophoran* body towards the upper end of the rows of swimming plates. Closely bordering on the sensory body are two ciliated epithelial bands, the so-called pole plates (Fig. 74, *pp*), whose edge is thickened. They lie in the median plane of the body; at the point where they come in contact with the sensory body are found the two above-mentioned median slits through the bell covering that body.

Organs of sight.—Simple organs of sight occur principally as pigment spots in such *Leptomedusæ* as possess no marginal vesicles

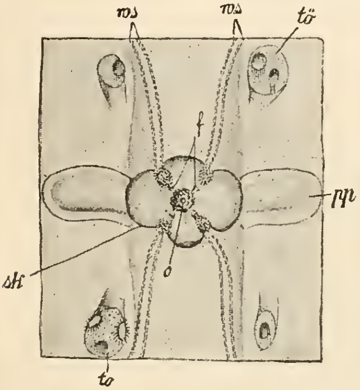

Fig. 74.—**Aboral pole of the body of Callianira, after Hertwig.** *ws*, Ciliated bands; *f*, springs carrying the mass of otoliths (*o*); *sk*, sensory body; *pp*, pole plates; *tö*, openings of the 4 branches of the aboral vessel or gastro-canal.

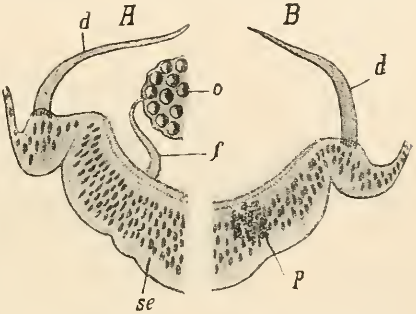

Fig. 75.—**Halves of two sections through the sensory body of Callianira, after Hertwig.** *A* passes through one of the 4 springs (*f*) which carry the otolith mass (*o*); *d*, roof of the sensory pit; *se*, sensory epithelium of the sensory body; *p*, pigment.

(*Ocellata*), and in *Anthomedusæ*. They consist of pigment cells and sensory cells, to which, in some cases, a cuticular thickening is added as lens. Such a lens is less often wanting in the visual organs of the *Acraspeda* (Fig. 73, *oc*, *l*), whose structure is occasionally considerably complicated; they form part of the marginal bodies. In the *Cubomedusæ* a vitreous body and a retina are developed between the lens and the pigment cup. In *Charybdea* there are compound eyes; each marginal body bears 2 large unpaired and 4 small paired eyes. Eye spots, sometimes with lenses, are found at the tips of the feelers in some *Siphonophora*. In the *Ctenophora* there are, as has already been mentioned, pigment spots in the sensory cushion of the sensory body.

VIII. Supporting Organs, Protective Organs, Skeleton.

The formations belonging to this category, which are very heterogeneous, can at once be divided into two principal groups, according to their ectodermal or mesodermal origin.

1. **Ectodermal supporting and protective organs.**—These are found in attached Cnidaria, and especially in those which form animal stocks by asexual reproduction (incomplete fission and gemmation). We can easily understand why such stocks, which in their natural state imitate trees, bushes, grass, feathers, crusts, leaves, etc., need special adaptations for holding the parts upright in the water, to support and at the same time to protect them. We also see why such supporting organs are of no use, or of very little use to attached Cnidaria which do not form colonies, and why they are often wanting, or only slightly developed in such forms. (Examples: *Hydra*, the attached *Scyphomedusæ*, and the *Actinia* among *Corals*.)

The ectodermal supporting formations are simplest in the *Hydroids*. Here the body epithelium generally secretes a chitinous cuticle (periderm) which surrounds the body like a tube. This tube surrounds either only the stem, the branches of the stock, and the stalks of the individuals, or, further, it widens out round the individuals into cups into which they can be withdrawn. In the division of the *Hydrocorallia* the periderm becomes calcified, and forms a framework of many tubes, arranged in a complicated manner, and reticulately bound together.

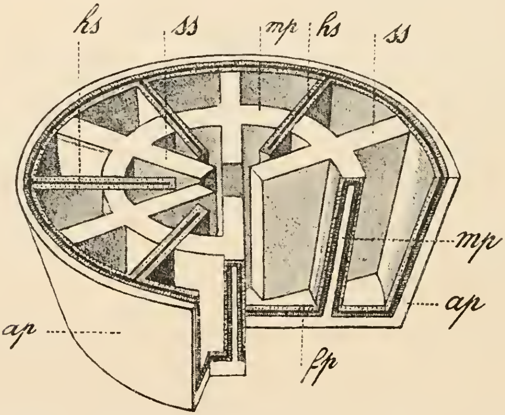

FIG. 76.—**Diagrammatic representation of the structure of a Stone Coral (Madreporarian), after v. Koch.** Only the lower aboral portion of the body is taken into consideration. *fp*, Footplate; *ap*, exotheca; *mp*, theca; *ss*, sklerosepta; *hs*, sarcosepta. White parts = calcareous skeleton. Streaked parts = ectoderm. Black parts = mesoderm. Dotted parts = endoderm.

The **calcareous skeletons** of the Stone-corals (*Hexacorallia*, *Madreporaria*), and the horny skeletons of the *Alcyonidæ* (*Octacorallia*) belong to the order of skeletons secreted by the ectoderm.

The origin of the calcareous skeleton of the Stone-corals (Fig. 76), and its relation to the soft parts of the body, are as follows:—

The young *Coral*, still devoid of skeleton, having attached itself by the aboral end of its body, secretes from the ectoderm of its pedal disc a **foot-plate** formed of globular calcareous grains, and thus connects the ectoderm of the foot with the surface to which the body is attached. Then from this foot-plate gradually arise, by calcareous secretion from the ectoderm, radially arranged perpendicular ridges, the **star-ridges** or **sklerosepta.** These are naturally covered on all sides with ectoderm, and they raise the pedal disc, in as many folds as there are ridges, into the gastric cavity. In the same way a calcareous tube, the **theca** (Mauerblatt), arises, partly by the coalescence of the ends of the star-ridges, and partly perhaps also by the rising of a circular wall out of the pedal disc; this again raises the basal body wall in folds into the gastric cavity, just as do the star-ridges. By the formation of this calcareous tube the gastric cavity is divided into a peripheral portion, lying outside the theca, and a central portion, the two being in open communication above its free upper edge.

In the axis of the *Coral* a calcareous pillar often rises from the pedal disc and projects into the gastric cavity; this is the **columella.** The star-ridges may fuse with this columella, they may also stand out above the before-mentioned tube as **ribs.** By a further calcareous secretion from the ectoderm round the base of the body wall, the **exotheca** arises; this is lined by ectoderm, and forms an outer circular calcareous wall of varying height above the pedal disc.

The peripheral ends of the star-ridges can also unite with the exotheca, though of course only by breaking through the body wall; indeed the theca may entirely or partially coalesce with the exotheca, displacing the intermediate soft portions.

Most *Madreporaria*, by incomplete fission or gemmation, form variously-shaped **Coral colonies,** in each individual of which the skeletal arrangement just described is repeated. Complications may arise by the complete or partial fusing, or else the complete disappearance of the thecæ of the various individuals, etc.

The star-ridges or **sklerosepta** never correspond in position with the ordinary septa or **sarcosepta,** but on the contrary alternate with them, so that a skleroseptum always lies between 2 sarcosepta, and a sarcoseptum between 2 sklerosepta. In consequence of this the sklerosepta imitate the sarcosepta in number and arrangement.

The skeletons of the *Madreporaria* are either massive and close (*M. aporosa*), or they are perforated by small cavities (*M. porifera*). The calcareous skeletons of the fossil *Rugosa* had probably an origin similar to that of the *Hexacorallia.*

The second kind of ectodermal *Coral* skeletons, the **horn skeletons,** which are found in many *Alcyonaria* and in the *Antipatharia*, are usually hollow axial skeletons; they run through the bodies of these colonial *Corals*, and thus take the shape of their often elegantly branched stocks. It seems at first paradoxical that these axial skeletons should be ectodermal. So as to explain this fact, we shall briefly describe the formation of the horn skeleton of *Gerardia.* The stocks of this *Coral* form a sort of crust over foreign bodies, preferring the axial skeleton of other dead *Alcyonaria*. The surface by which they adhere to these bodies, and which is of course ectodermal, puts forth externally, and thus between itself and the surface to which it adheres, a lamella of horn, which, together with the foreign body (axial skeleton of another *Alcyonid*), forms the axial skeleton of the whole stock. "Now, however, it not infrequently happens that the *Gerardia* colony tries later to spread out further than is allowed by the surface it rests on, and then growths which bear young polyps appear on its branches, and into these a new formation of horn enters, attached to the original horny secretion; this new formation has a similar origin with the first, but encloses no foreign body" (**v. Koch**). In the other *Alcyonaria* which have a horny axial skeleton, the formation of the skeleton is similar (Fig. 82, *B*, p. 107), but that part of the axial skeleton which is attached to a foreign substance is very much reduced, whereas the free part rising from it is considerably developed, and forms the generally much-branched principal mass of the skeleton. Horny axial skeletons are thus always lined with an ectodermal axial epithelium. In the axial skeleton of the *Alcyonaria*, lime may be found in larger or smaller quantities, and sometimes preponderates. In *Isis* horny joints alternate with calcareous. The mesoderm of the soft part of the *Coral* stocks which covers the axial skeleton often contains calcareous spicules. In such cases (*e.g. Gorgonia*) we have an ectodermal horny axial skeleton and a more peripheral mesodermal skeleton formed of calcareous spicules.

2. **Mesodermal supporting organs.**—The first of such organs which we shall consider is the thin structureless membrane, which, throughout the whole Hydroid body, separates the ectoderm from the endoderm. In the *Craspedote Medusæ* this membrane thickens into the more or less strongly developed structureless elastic disc jelly; it is retained as a thin membrane only in the tentacles, and generally also in the œsophageal tube. In the *Scyphomedusæ* the mesodermal supporting jelly begins to be more highly differentiated, connective tissue cells appearing in it, and fibres, which are either processes of such cells or differentiations of the intercellular substance (Fig. 36, p. 41). In the same way we find, in the *Corals*, a hyaline mesodermal layer throughout which cells are scattered. The membrane is everywhere reduced to a thinner layer in the tentacles. In many *Corals* (most *Alcyonidæ*) the skeletal elements are found in this layer. They consist of variously shaped calcareous spicules, which arise in special cells and are found in varying numbers. In the mesoderm of *Alcyonium*, and in the peripheral portions (the rind) of the stock of the *precious Corals* of commerce and other forms, they are isolated. Occasionally, however, a new calcareous substance is deposited between the calcareous spicules, cementing these into a firm mass, and leading to the formation of axial skeletons such as that of the *precious Coral* of commerce.

The greatest differentiation, histologically, within the Cnidaria is shown by the jelly which functions as supporting tissue in the *Ctenophora*, containing, as it does, nerve, muscle, and connective tissue elements. All these elements are usually represented by more or less branched fibres.

As to the origin of the various mesodermal supporting formations, we have the following remarks to make. The homogeneous supporting membrane of the *Hydroids*, and the corresponding jelly substance of the *Medusæ*, *Corals*, and *Ctenophora* is a product of secretion deposited between the ectoderm and endoderm. Whether both layers take part in this secretion or only one, and if so which, is a question difficult to decide. The cell elements which lie in the jelly, on the contrary, seem almost exclusively to arise by the immigration of cells from the ectoderm. In *Corals* the ectoderm soon becomes multi-laminar. The cells of the deeper layers become mesodermal connective tissue cells by the rise between them of homogeneous substance. Many observers, therefore, consider the *Coral* mesoderm as only a more deeply lying portion of the ectoderm.

IX. Funnel Cavities (Septal Funnels); Subgenital Cavities, Subgenital Chamber.

These formations, met with in many *Acraspeda* (analogous formations are very rarely found in *Craspedota*) are in the lower forms represented by 4 interradial funnel-shaped depressions of the subumbrella round the œsophagus (Fig. 99, *H*, *I*, *st*, *st'*, p. 130). They project more or less far into the gastric cavity, within the septa which separate the 4 gastric pouches. In *Discomedusæ* they become 4 somewhat flat interradial **subgenital cavities.** Their roof is close to the subumbrellar wall of the central gastric cavity in which the genital organs develop. The membrane which separates the two cavities thus becomes the **genital membrane.** In two families of the *Rhizostomæ*, (the *Versuridæ* and *Crambessidæ*), the 4 sub-genital cavities unite in the centre of the umbrella to form a spacious **sub-genital chamber** (*porticus subgenitalis*, Fig. 70 *D*, *sgp*, p. 85), which opens outward by four interradial apertures through the subumbrella into the umbrella cavity. The dorsal roof of the chamber is formed by the gastro-genital membrane, which separates it from the gastric cavity above it. The subgenital chamber separates the central gastric cavity from the œsophagus. The two remain connected only by the 4 canals which run perradially (*pfk*).

X. The Sexual Organs.

The Cnidaria are either sexually separate, like the *Hydrozoa* and the *Scyphozoa* (with a few exceptions, *e.g.* *Hydra* and a few *Cladonemidæ*, *Cerianthus*, *Chrysaora*), or hermaphrodite like the *Ctenophora*.

In the colonial Cnidaria we find male and female individuals either in the same stock (monœcious), and this is the rule; or on different stocks (diœcious).

Testes and ovaries are, taken as a whole, very simply constructed; they are vesicles or spheres, with numerous egg and sperm cells at different stages of development.

In *Hydra* both sorts of sexual products lie in the deeper part of the body epithelium. In the other colonial *Hydroids* they are met with in specially shaped so-called medusoid individuals, of which more will be said below, either being formed primarily in these individuals, or reaching such a position secondarily from the stem.

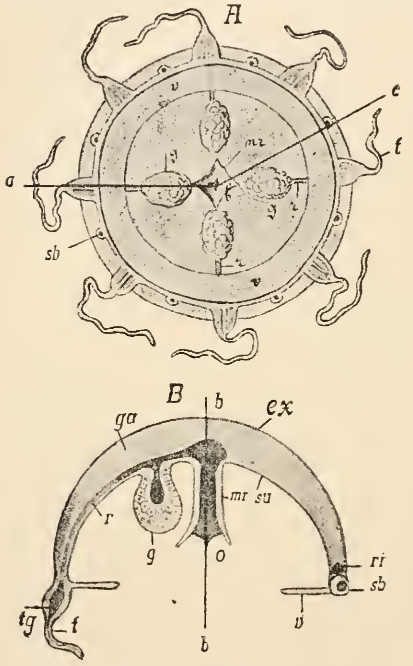

Fig. 77.—**Eucope campanulata**, partly after **Haeckel**. *A*, From the surface. *B*, Section in the direction *a-b-c* of Fig. *A*. *a-b*, Perradius; *b-c*, adradius; *t*, tentacle; *sb*, marginal vesicle; *g*, gonades; *mr*, gastric peduncle; *r*, radial canals; *v*, velum; *ri*, circumferential canal; *ex*, exumbrella; *su*, subumbrella; *ga*, jelly; *tg*, tentacular vessel; *b-b*, principal axis.

In all *Medusæ* the sexual glands or gonades show, by their position, a close relation to the nutritive gastro-canal system. In the *Craspedota* (Fig. 77), they lie in varying numbers either on the wall of the oral tube (*Narcomedusæ* and *Anthomedusæ*), or on the radial canals (*Leptomedusæ* and *Trachomedusæ*). Where there are 4 radial canals there are 4 gonades, and where there are 8 radial canals, 8 gonades. With increase in the number of radial canals there may also be increase in the number of gonades. In the *Acraspeda* 4 (less frequently 8) globular or band-like gonades are usually developed; these are sometimes folded, or curled, or clustered, and occasionally of considerable size; they lie in the subumbrellar wall of the gastro-canal system, sometimes nearer the circumference, at other times nearer the central gastric cavity. In the *Pelagidæ* and *Cyanidæ* the gonades hang down as 4 gastro-genital sacs from the subumbrella into the umbrella cavity; in the *Rhizostomæ* and *Aurelidæ*, on the contrary, they lie on the upper surface of the subgenital cavities or the subgenital porticus (Fig. 70, p. 85). In the *Craspedota* the ripe genital products pass directly out into the umbrella cavity by the bursting of the gonade; in the *Acraspeda* they pass inward into the cavity of the gastro-canal system, and reach the exterior thence through the mouth.

The sexual organs of *Corals* lie in the septa, near the free edges which project into the gastral cavity.

In the hermaphrodite *Ctenophora* we meet with them on or in the walls of the meridional vessels, in such a way that on the one wall of the meridional vessel the male elements lie, and on the opposite wall the female elements. These sexual glands are so arranged that in each of the 8 regions of the body, separated by the meridians, there are either 2 testes or 2 ovaries. The ripe sexual products fall into the meridional vessels, and through the gastro-canal system reach the stomach and œsophagus and pass out through the mouth.

In the Cnidaria no special ways of transmission for the sexual products, and no special copulatory organs, are developed.

Concerning the origin of the sexual products we may say, generally, that in very many *Hydrozoa* they are developed out of the ectoderm, but in the *Scyphozoa* out of the endoderm. Observers are not yet agreed about the origin of the sexual products in the *Ctenophora*.

Since in the one form, the *Hydroids*, the sexual products come from the ectoderm, and in a related form from the endoderm, too great significance should not be attached to the place of their origin.

XI. The "Stratification" of the Cnidarian Body.

In the lowest Cnidaria the body during life consists of two layers of epithelium separated by a supporting lamella; these two layers are similar to the two epithelial germinal layers of the gastrula larva. The musculature is formed by processes of the ordinary epithelial cells. Only the sexual products arise and continue to lie imbedded in the epithelium.

As the complication of the organism increases, there is a tendency for certain tissues and organs to detach themselves from the epithelium and to take up a position beneath it. This tendency is shown by the various tissues and organs approximately in the following order:—

1. **The sexual organs,** which in the lowest Cnidaria are already subepithelial, and in the higher Cnidaria come to lie altogether or partly in the jelly.

2. **Connective tissue elements,** which immigrate into the gelatinous supporting membrane.

3. **The musculature,** whose elements first arrange themselves into a subepithelial muscle layer, and then also move (partially at any rate) into the jelly.

4. The tendency to take up a position deep in the body affects the **nervous tissue** far less. In consequence of the inseparable connection of the nervous system, on the one hand with the sensory organs, which in accordance with their functions must remain at the surface, and on the other hand with the musculature which tends to sink below it, this system takes up an intermediate position.

We observe, then, in the Cnidaria the progressive development of an intermediate layer between the outer body epithelium and the inner intestinal epithelium, this intermediate layer being formed of heterogeneous elements of independent origin, connective tissue, musculature, nervous system, and sexual organs. The outer epithelium gives rise principally to the connective tissue and the nervous system, while the musculature and the sexual organs may be produced either by the outer or the inner epithelium.

It is evident that the development of such an intermediate layer, which we call mesoderm, is the necessary preliminary of a higher organological differentiation of the body.

XII. Reproduction.

Asexual reproduction by fission and gemmation—Stock formation—Division of labour and polymorphism.

Asexual reproduction is very common among the Cnidaria side by side with sexual reproduction. Among the *Ctenophora* alone it has not been observed. In *Hydra* we find asexual reproduction by gemmation side by side with sexual reproduction in adult animals. Buds are formed by hollow outgrowths of the body wall. These buds grow, and at the distal end a breach is formed—the oral aperture, round which the tentacles arise by means of new outgrowths. Such buds can detach

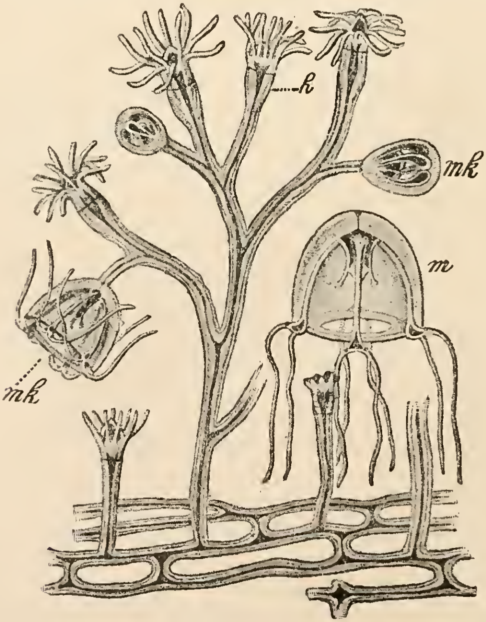

Fig. 78.—**Bougainvillea ramosa** (after **Allman**), with budding Medusæ. *h*, Nutritive polyps; *mk*, medusa buds; *m*, detached young Medusæ (**Margelis ramosa**).

themselves from the mother body, or they may in small numbers remain united with it for some time. In the last case small *Hydra* colonies composed of similar individuals arise.

In the same way elegant and richly branched colonies arise in most *Hydroids* (Fig. 78). The individuals of such stocks are, however, generally not similar, but, as a consequence of more or less division of labour, Dimorphism or Polymorphism takes place. We distinguish: (1) sterile **nutritive persons,** which remain on the level of the *Hydroid*, and undertake the feeding of the stock, the gastric cavities of all the individuals of the stock being in communication with one another; (2) **sexual persons,** which undertake the duty of ripening the sexual products, and also of planting them out and dispersing them, so that the young brood of *Hydroids* proceeding from the fertilised egg may attach themselves in new places and form new stocks. The sexual persons which are destined for a free-swimming life, and which are buds of the *Hydroid* stock, attain a structure corresponding with this manner of life, they become young *Craspedote Medusæ*, which detach themselves from the stock, swim away, and—often after longer or shorter metamorphoses—ripen the sexual products. That the *Craspedote Medusa* is only a metamorphosed *Hydroid* suited for a free-swimming manner of life has already been pointed out. In the accompanying illustrations (Fig. 79, *A-E*), we can see how a bud of a *Hydroid* stock develops into a *Craspedote Medusa*.

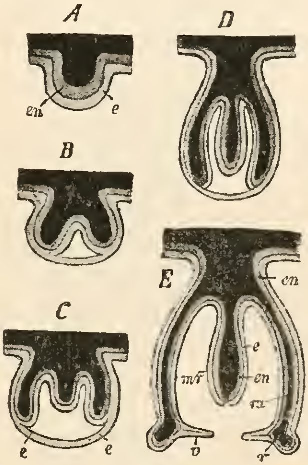

Fig. 79.—*A*, *B*, *C*, *D*, *E*, Diagrammatic representations of the formation of a Craspedote Medusa by budding from a Hydroid. Black portions = gastric cavities. *en*, Endoderm; *e*, ectoderm; *mr*, gastric peduncle; *v*, velum; *ra*, radial canal; *r*, circumferential canal.

The development of free-swimming sexual persons has also the further advantage that it makes cross-fertilisation possible.

In many *Hydroids*, however, there develop on the stock by budding sexual persons whose structure approaches more or less nearly to that of the *Medusa*, but does not reach it. Such **medusoid** sexual persons or **gonophores** (Fig. 80) do not detach themselves as free-swimming *Medusæ*, but develop the sexual products while remaining connected with the stock. It is not possible to define the various sorts of medusoid buds as stages in the development of the *Medusa* form, as we cannot see what advantage could be gained by the greater or less development of the *Medusa* form in these attached sexual persons. They should rather be regarded as so many stages of degeneration, due to the fact that the sexual buds no longer detach themselves from the stock as free-swimming *Medusæ*. Degeneration can go so far that the original *Medusa* organisation becomes quite unrecognisable (Fig. 80, *C*).

The division of labour among the persons of a stock goes still further in some *Hydroids*, and leads to the formation of polymorphic stocks. Besides the ordinary nutritive and sexual persons, **feelers** (tasters) devoid of mouth and tentacles, and thorn-like **protective persons** (guard polyps) provided with a hard periderm skeleton, may occur; between these latter the other persons can withdraw.

Reproduction by gemmation and fission is relatively rare in the *Medusæ* of the *Hydrozoa*, and in the *Craspedote Medusæ* generally. In the division of the *Anthomedusæ* gemmation has till now been observed only in the family of the *Sarsiadæ*. Here numerous buds are formed either at the edge of the umbrella, or on the very much lengthened gastric peduncle. These buds grow into young *Sarsiæ* like the mother animal, then detach themselves and swim about independently. Here we have formation of free-swimming **Medusa-stocks** without division of labour and without polymorphism of the individuals. The *Medusæ* attain full development only after their detachment from the mother animal.

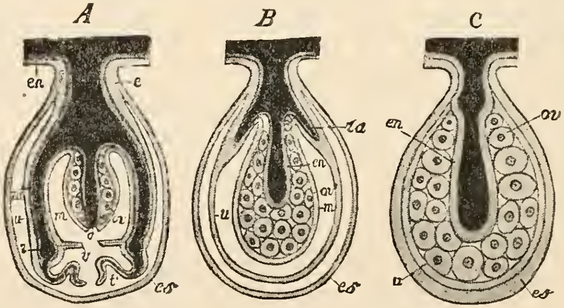

FIG. 80.—*A*, *B*, *C*, Three different types of gonophores from Hydrozoa. *e*, Ectoderm; *en*, endoderm; *es*, outer ectodermal envelope of the gonophore; *u*, umbrella; *ra*, radial canal; *r*, circumferential canal; *t*, tentacles; *m*, gastric peduncle; *o*, mouth; *ov*, gouade (ovary); *v*, velum.

Reproduction by repeated binary fission has also been observed in *Craspedote Medusæ*. In some cases (*Gastroblasta*) peculiar free-swimming *Medusa-stocks* arise which have the following structure. A single *Medusa* provided with tentacles and marginal vesicles carries on its subumbrella numerous gastric pouches. The number of these gastric pouches determines the number of persons in the stock, which are so far incompletely divided from each other that their discs never separate.

Asexual reproduction by a sort of fission occurs also in young forms of the *Discomedusæ* (*e.g. Aurelia*), *i.e.* in the young attached stage known as *Scyphistoma* and described above. In the simplest case

(monodisc Strobila) the disc of the *Scyphistoma* (*Ephyra*) constricts itself and separates from the peduncle, on which by regeneration a new disc is afterwards formed. New discs, however, are mostly formed between the peduncle and the older discs before the latter detach themselves; then we have the typical **polydisc Strobila** (Fig. 81).

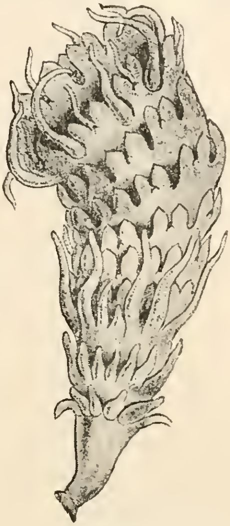

Fig. 81.—**Polydisc Strobila of Aurelia aurita, after Haeckel.**

In *Corals*, reproduction by gemmation and by incomplete fission is very wide spread. It is, however, rare in the naked *Actinia*. It leads to the formation of those occasionally very large *Coral-stocks* whose skeletons are well known as *Reef* or *Stone Coral*, the *Coral of commerce* and other *Alcyonaria*. The gemmation and stock formation of the *Alcyonaria* is the most fully investigated. At certain points of the mother-polyp outgrowths, the so-called stolons, make their appearance and are arranged on the mother-polyp in ways characteristic of each different group. They are either simple, or branched in a reticular manner. By new outgrowths, and local widenings of the endodermal canals which they contain, there arise, on these stolons, young daughter animals, in which the mouth, œsophageal tube, septa, and tentacles are formed. In this way arise

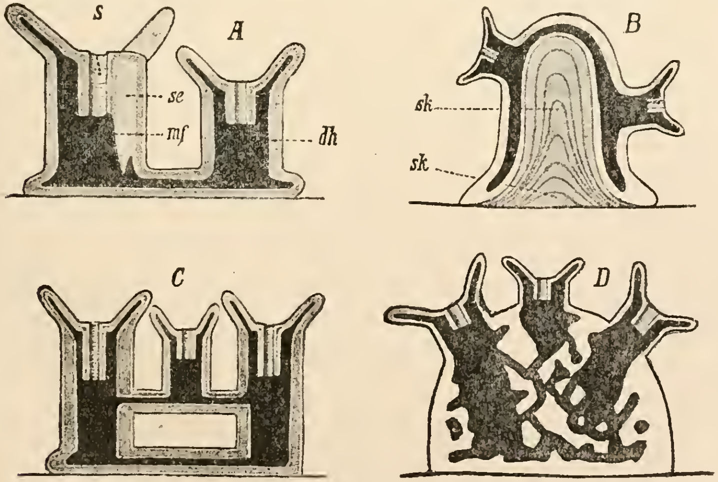

Fig. 82.—**Diagrams illustrative of gemmation and stock formation in various Alcyonaria.** *A*, General diagram. *B*, Gorgonia. *C*, Tubipora. *D*, Alcyonium. Black portions the cavities of the gastral system. *s*, Œsophagus; *se*, septa; *mf*, mesenterial thickenings; *dh*, gastric cavity; *sk*, axial skeleton, drawn in layers to illustrate the manner of its origin.

stocks formed of individuals whose gastric cavities remain connected, like those of the *Reef Coral*, by characteristic arrangements of the canal system. The above illustrations (Fig. 82, *A-C*) show diagrammatically the manner of gemmation and the beginning of stock formation in different *Alcyonaria*.

In the *Alcyonaria* also, division of labour takes place, with the resulting dimorphism or polymorphism of the persons (zooids). Thus, side by side with the normal persons there are other persons without tentacles and with septa reduced in number (two) whose chief function is the taking in of water into the canal system.

XIII. **Organisation of the Siphonophora.**

It is most suitable for our purpose here to describe the structure of the **Siphonophora**, as it can only be explained and understood by help of the phenomena of asexual reproduction by means of gemmation, of stock formation, and of the division of labour. The *Siphonophora* have actually been long considered by most investigators as polymorphic animal stocks, although zoologists had not agreed as to the significance of the separate parts.

The following description corresponds in general with the views recently put forth by Haeckel.

In the order of the *Siphonophora* two animal groups have till now been united, which, apart from the fact that both are *Medusa-stocks*, have nothing in common, and, in any case, have quite different origins. We shall therefore treat of these two groups—(1) the **Siphonanthe** and (2) the **Disconanthe**—separately.

I. **The Siphonanthe.**—These may be conceived of as colonies of *Craspedote Medusæ* by comparing their whole body with a *Craspedote Medusa* on whose gastric peduncle numerous young *Medusæ* have arisen by gemmation, somewhat in the same way as in *Sarsia siphonophora*. While, however, the mother *Medusa* of the *Sarsia* is radially constructed and all the daughter *Medusæ* are like each other and like the mother, the mother animal of a *Siphonanth* which is recognisable in its young or larval stage is a much metamorphosed *Medusa*. Its disc is mostly changed into an air vesicle, it possesses only one tentacle (which also occurs in the *Craspedota*), and its gastric peduncle is lengthened out into the generally very long "stem" of the *Siphonanth*. The daughter *Medusæ*, budding from the stem, are neither like one another nor like the mother animal. They divide between them the general work, and are consequently variously modified to suit their special functions.

If we now more closely consider the body of a *Siphonanth*, we must first bear specially in mind those parts which can be compared with parts or organs of the mother *Medusa* of a proliferous *Craspedote*.

A. The **pneumatophore** or **swim-bladder** (Fig. 83) lies at the upper end of the stem, and represents a metamorphosed *Medusa* umbrella. (It is wanting only in the order of *Calyconecta*, where the umbrella of the larval mother *Medusa* develops into the first provisional swimming-bell and is then thrown off.) At one point of the exumbrella an invagination forms at an early stage for secreting air, the **air vesicle**, which expands so much that it represents by far the largest portion of the original disc; it always remains in open communication with the exterior by means of the aperture of the invagination (the pore of the air vesicle). Around the air vesicle, in the bell which has been so much modified and has become more or less globular, there are 8 (less frequently 4 or 16) endodermal chambers divided by septa; these open under the air vesicle into each other and into the endodermal axial canal of the stem. These chambers correspond with the radial canals of the *Medusa*. The pneumatophore serves as a hydrostatic apparatus, which keeps the whole *Siphonophora* colony floating in the water. The air can be expelled through the pore of the air vesicle, and again secreted by the ectodermal glandular epithelium at its base.

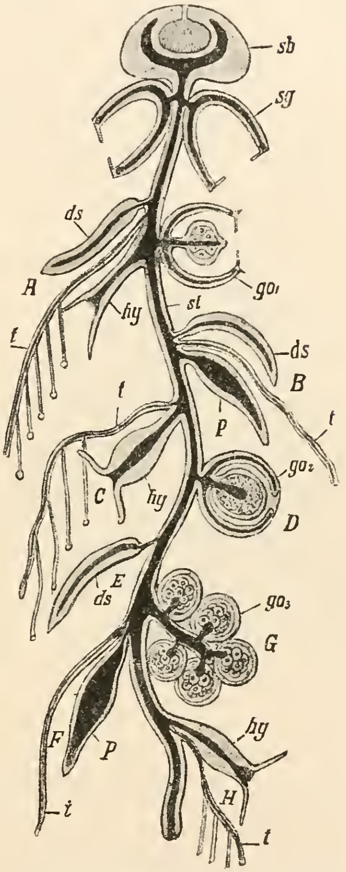

Fig. 83.—**Diagrammatic representation of the organisation of a Siphonanth stock.** *sb*, Pneumatophore; *sg*, swimming-bell; *ds*, bract; *t*, tentacles; go_1, go_2, go_3, gonophores; *hy*, oral or gastric peduncle (siphon); *p*, feeler or taster (palpon); *A*-*H*, various groups of appendages which are never found in this way together in any single Siphonanth. Black portion = gastric system.

B. Only one of the **tentacles** is fully developed. This is moved from the margin of the disc on to the subumbrella to the base of the stem, and is probably usually thrown off at an early stage.

C. The **stem** of the *Siphonanth*, which is generally long, tubular, and contractile, more rarely short and flat, answers to the gastric peduncle of a *Medusa*. An aperture (primary oral aperture) is but rarely found at its lower end. The view that these three parts together are equivalent to a *Medusa* is supported by ontogenetic observation, as is to a certain extent evident from what has already been said. The gastrula which develops from the fertilised egg grows into a *Siphonanth* larva, such a larva possessing at first only these three parts—umbrella, tentacle, and gastric peduncle. This medusoid larva is bilaterally symmetrical. Its umbrella has a deep cleft, it possesses only one tentacle, its gastric peduncle is filled with yolk. The *Siphonophora* colony arises on the gastric peduncle by gemmation.

Let us now consider the polymorphic appendages of the *Siphonanth* stem, which we compared with the daughter *Medusæ* budding on the gastric peduncle of *Sarsia siphonophora.* All these appendages are arranged on the stem in a line whose position is called ventral. The line generally becomes a spiral, because of the spiral twisting of the stem. Highest up on the stem under the pneumatophore (when one is present) the so-called **swimming-bells** or **nectophores** are inserted; these are wanting only in the *Cystonecta.* The swimming-bells exclusively and alone provide for the locomotion of the whole stock. They have lost all those *Medusa* organs which were of no use to or even hindered the fulfilment of this function, first of all therefore, mouth, gastric peduncle, and tentacles. The locomotory organ of the *Medusa*, the disc or umbrella, however, is all the more strongly developed; it is much vaulted with a strong circular muscular layer in the subumbrella. Its edge projects in the shape of a true velum. At the base of the velum runs the circumferential canal, into which 4 radial canals enter. The swimming-bells are so inserted on the stem by their

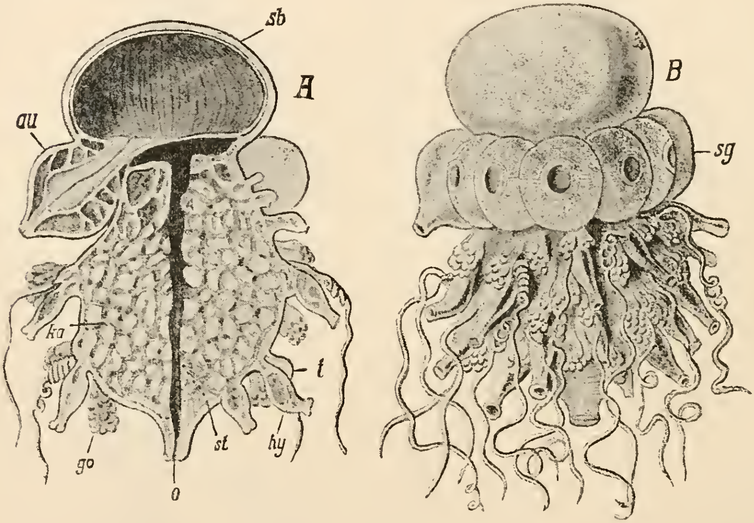

FIG. 84.—**Stephalia corona**, after **Haeckel.** *A*, Halved longitudinally. *B*, From life. *sb*, Swim-bladder; *au*, aurophore; *sg*, swimming-bells; *ka*, canal system of the stem (chief stomach, *st*); *go*, gonophore clusters; *o*, aperture (mouth) of the peduncle (chief gastric tube, *st*); *hy*, gastric tubes (siphons); *t*, tentacles.

aboral or apical poles, that the aperture of the bell is turned downwards and outwards, away from the apex of the stem.

When the swimming-bells contract, and so expel the water downwards out of their subumbrellar cavities, the whole stock is propelled by the recoil in the opposite direction, *i.e.* upwards. The swimming-bells are not regularly, but bilaterally symmetrical, which is explicable by their insertion on the stem, and by the position they have to assume to effect the motion forward of the whole stock. As to the number and arrangement of the swimming-bells, we find either one or two opposite each other, or several, or often very many, arranged in two or many rows in circles round the stem. The points of insertion of the bells, however, always lie in a spiral, which is sometimes much extended, sometimes much compressed. The direction in which this spiral is twisted is the opposite of that in which the other appendages are arranged. The radial vessels of each swimming-bell, which unite at its apical pole, are in open communication with the endodermal axial canal of the stem.

Fig. 85.—**Praya galea**, after **Haeckel**.

Beneath the swimming-bells the stem carries the following different kinds of appendages, which we may also consider as modified *Medusæ*:

A. The gonophores or reproductive persons (Fig. 83, go_1, go_2, go_3).—To these belong exclusively the function of forming the sexual products. They are either male or female. The typical organisation of a *Craspedote Medusa* is still more or less faithfully maintained in them. They possess a bell-shaped umbrella with velum, circumferential canal and radial canals, and, further, a gastric peduncle which projects into the subumbrellar cavity (occasionally with an oral aperture in addition), and in whose wall, as in the *Codonidæ* among the *Craspedote Medusæ*, the sexual products arise. The umbrella is here, probably, a protective apparatus. Occasionally the rudiments of tentacles are still found on the margin of the disc. Sometimes, however, the whole *Medusa* form is considerably degenerated.

B. Sterile persons.—These perform the functions of taking in food, and digestion, of protection, touch, etc. The *Medusa* structure in them is always obscured, and often so much so as to be unrecognisable. The following different kinds of such sterile persons may be distinguished:

a. Persons in which the following typical organs of a *Medusa* may still be recognised: (1) a variously-shaped **protective** or **bract** as metamorphosed umbrella. It serves as umbrella or shield, and affords protection, not only to the other parts of the same person, but also to the neighbouring persons, which can withdraw under it. (2) The **oral** or **gastric** peduncle (siphon), the chief organ for taking in food and digestion. The siphon is often stalked, and the edge of the mouth widened into a funnel, or produced into 4 points, or prolonged like a proboscis. (3) A very contractile **tentacle** or **capturing filament**, which is placed at the base of the gastric tube. The tentacle is feathered on one side, *i.e.* it is provided with one row of lateral branches, whose ends are armed with stinging batteries. Such a sterile person simultaneously performs the functions of taking in food and of protection (Fig. 83, *A*).

b. Persons distinguished from those just described by the fact that the contractile hollow siphon has lost its mouth, and so appears changed into a **taster** or **feeler** (palpons). The tentacle at the base of the feeler becomes an unfeathered, long, and very retractile sensory filament (Fig. 83, *B*).

c. Persons in which the umbrella is completely degenerated, and which consist of nothing but siphon and tentacle (Fig. 83, *C*).

d. Persons which have retained exclusively the function of protection, and in whom the umbrella alone, in the form of a bract, has attained development, while the formation of siphon and capturing filament has been suppressed (Fig. 83, *E*).

e. Persons reduced to tasters, without bracts and without sensory filaments.

C. Special swimming-bells.—Nectophores, agreeing in structure with the ordinary swimming bells developed at the upper end of the stem are found in some *Siphonanths* on other parts of the stem as well.

These various appendages, or heteromorphic persons (**A-C**), of which several may be wanting, occur in different and often very characteristic order and manner of division on the stem. They are, in the first place, arranged in many *Siphonanths* in distinct groups, repeated at regular intervals and separated by internodes of the stem.

The following are the chief modifications which occur in the composition of such a group, which is known as a **cormidium**:

A. The cormidium consists of (1) a gonophore and (2) a sterile person with bract, siphon, and capturing filament (Fig. 86).

B. To these two persons a third person, a special swimming-bell, is added.

C. The cormidium consists of (1) one or more gonophores, (2) one sterile person with siphon and tentacle, but without bract.

D. It consists of (1) one or more gonophores, (2) one siphon with tentacle but without bract, (3) one or more palpons with tentacle but without bract.

E. It consists of (1) a group of gonophores, (2) a siphon together with a tentacle, (3) one or more palpons without tentacle, (4) several bracts, some of which perhaps belong to the palpons and to the siphon.

Less frequently we find in the cormidium several siphons with tentacles.

The cormidia described under **A** and **B** can detach themselves from the stem, and only when they are thus free-swimming *Eudoxiæ* (**A**) or *Ersææ* (**B**) do they ripen the sexual products in their gonophores. From the fertilised egg a medusoid *Siphonophoran* larva is then produced, and from this, by budding, comes the polymorphic *Siphonanth* stock.

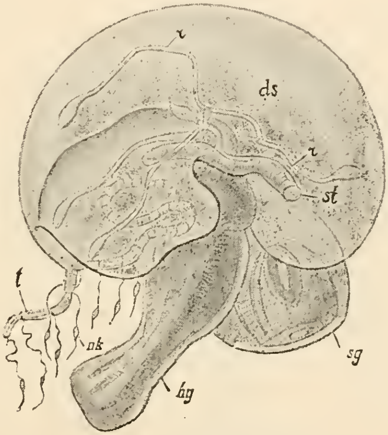

Fig. 86.—**Single Cormidium (Eudoxia) from Praya galea,** after **Haeckel.** *ds*, Protective or bract ; *r*, radial canals of the same ; *st*, portion of the stem ; *hy*, siphon or gastric peduncle ; *t*, tentacle ; *nk*, stinging knobs ; *sg*, gonophore.

In many *Siphonanths* the arrangement of the heteromorphic persons in special cormidia is either more or less obscured (*e.g. Rhizophysa*, several *Agalmidæ* and *Forskalidæ*) or quite suppressed, so that the persons are irregularly distributed on the stem (*Physalia, Agalmopsis*). In this case the persons are generally appendages, in which, apart from the gonophores standing in groups or clusters, the medusoid structure is more or less completely degenerated : *i.e.* siphons with tentacle, taster with or without sensory filament, or isolated bracts.

This dispersed arrangement is to be explained in this way : the parts belonging to a sterile person, such as siphon or taster, bract or tentacle, become detached, and move away from each other, and stand separately on the stem. These dislocated portions or organs are able to multiply independently.

II. **The Disconanthe (Discalia, Porpeta, Porpalia, Velella).**—These have to be interpreted quite differently from the *Siphonanthe*. According to the harmonious and convincing teaching of ontogeny and comparative anatomy, these animals must be considered as *Medusæ* with marginal tentacles. These *Medusæ* have a gastric tube with mouth (principal siphon) in the centre of the subumbrella in the typical way, but also produce secondary siphons or palpons, by gemmation, on the subumbrella (just as in the *Gastroblasta*); out of the wall of these secondary siphons the *Medusa*-shaped gonophores bud (Fig. 87). All the tentacles belong to the margin of the undivided persistent *Medusa* umbrella. In the umbrella (on which in *Velella* a vertical crest, generally placed diagonally, rises) an air vesicle is developed on the exumbrellar side; this is often of very complicated structure, many chambered, and originally octoradiate; the chambers communicate with the exterior through numerous pores. The young stages of the *Disconanthe* are typical *Medusæ*, with 8 (later 16) tentacles at the disc margin, and with one central gastric peduncle or siphon. The gonophores detach themselves as free-swimming medusoid sexual persons, and only ripen the sexual products after their separation.

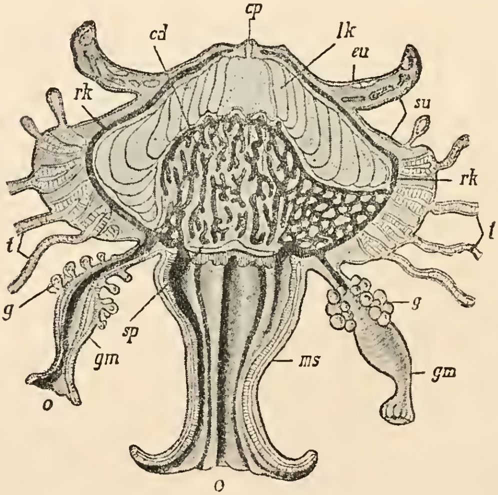

FIG. 87.—**Porpalia prunella**, after **Haeckel**. *cd*, Central gland; *lk*, air chamber; *cp*, central pore of the same; *rk*, radial canal; *sp*, supporting plate; *eu*, exumbrella; *su*, subumbrella; *t*, tentacles; *g*, gonades; *o*, mouth; *ms*, principal siphon; *gm*, accessory siphons.

The view of the *Siphonophoran* body here brought forward takes up a position intermediate between two diametrically opposed theories, each of which has long had its supporters. According to one theory, the whole *Siphonophoran* body represents a single *Medusa* person, and all its separate appendages—the nectophores, siphons, tasters, tentacles and gonophores—are nothing but displaced organs of this *Medusa*, whose number increases by multiplication. According to the other theory, the *Siphonophoran* body is a free-swimming polymorphic *Hydroid* stock, and each of the appendages just enumerated, even each tentacle, is to be considered as a more or less modified person, suited to some special function, in consequence of an extreme division of labour, either, therefore, as a metamorphosed *Hydroid*, or (as *e.g.* the nectophores and gonophores) as a metamorphosed *Medusa*.

XIV. **Life-history of the Cnidaria, Alternation of Generations.**

We shall return later to the special ontogeny of the *Cnidaria*, the arrangement of the layers of the body, and the development of the organs. Here we shall restrict ourselves to depicting the general course of their life-history.

Hydra multiply both asexually by gemmation, and sexually by means of fertilised eggs. From the latter, by a gradual course of development, *Hydra* again arise.

In very many *Hydromedusæ* an attached *Hydroid* form arises out of the fertilised egg, out of which, by budding, comes a *Hydroid* stock, which is at least dimorphic and often polymorphic. Some buds become sterile nutritive persons, others sexual persons. The latter detach themselves from the stock as free-swimming *Craspedote Medusæ* (Fig. 78, *m*, p. 104) and form the sexual products. From the fertilised egg an attached *Hydroid* may again be produced. We thus find here, in the cycle of development, two consecutive generations, as it were, intercalated: (1) the dimorphic or polymorphic *Hydroid* stock which reproduces by gemmation; and (2) the *Medusa* which arises by gemmation, detaches itself, swims about, and reproduces itself sexually. Such an alternation of differently formed generations which multiply in different ways is called **alternation of generations (metagenesis)**. It follows from our description that this alternation of generations is the result of division of labour between the single persons of a *Hydroid* stock. Each *Medusa* is originally equivalent to a nutritive person, and it owes its structure to adaptation to the special function of forming the sexual products and of dispersing them by means of its free locomotion.

We must not, therefore, consider the *Hydroid* form as a young stage of the *Medusa* form. Nutritive polyp and *Medusa* are sisters. The one sister develops further than the other and reproduces sexually, while the latter remains sterile.

There are two other methods of development to be derived from the alternation of generations of the *Hydro-Medusæ*. There are *Hydroid* stocks in which the sexual persons do not detach themselves from the stock, but remain connected with it as medusoid gonophores. From the fertilised eggs of such *Hydroids* other *Hydroids* are produced. On the other hand there are *Hydro-Medusæ* in whose whole life cycle no attached *Hydroid* stock is developed. From the fertilised egg of such a *Craspedote Medusa* another sexual *Medusa* is produced, often after a series of metamorphoses.

In the *Discomedusæ* also a kind of alternation of generations occurs. The fertilised egg may develop into a young attached *Medusa*, which reproduces asexually by **axial budding (strobilation,** Fig. 81, p. 107) or by **lateral budding**. The constricted young *Medusæ* (ephyræ), whose organisation, but for absence of gonades, is essentially the same as that of *Nausithoë* (Fig. 88), undergo a more or less complicated metamorphosis, till they again become adult sexually mature *Medusæ*. Here, however, the organism which multiplies asexually is really a young stage of the sexually differentiated *Medusa*, not a sister as in the *Hydro-Medusæ*. The young *Scyphistoma* does not need to multiply asexually. It can detach itself from the stem and develop direct into a *Medusa*. There are also very many free-swimming *Scypho-Medusæ* from whose fertilised eggs a new *Medusa* is produced again direct without the intervention of an attached stage in which multiplication is asexual. This direct development is usually accompanied by meta-

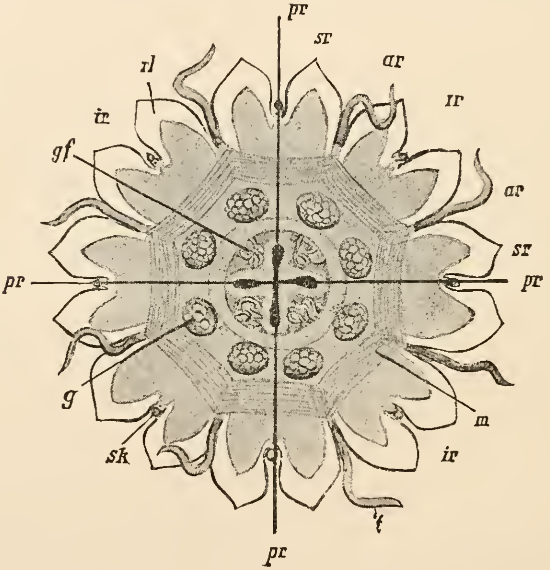

Fig. 88.—**Nausithoë.** *pr*, Perradii; *ir*, interradii; *ar*, adradii; *sr*, subradii; *rl*, marginal lobes; *t*, tentacles; *gf*, gastral filaments; *m*, circular muscle of the subumbrella; *sk*, sensory bodies (rhopalia); *g*, sexual glands (gonades); in the middle the oral cross.

morphosis. Development with alternation of generations and without it can occur in the same species.

In *Corals* a free-swimming larva is produced from the fertilised egg, and this attaches itself and develops into a *Coral*, which either remains a single individual or produces a *Coral-stock* by means of gemmation and incomplete fission.

The *Ctenophora*, without exception, develop direct.

From the fertilised egg of the *Siphonophora* a medusoid organism arises, which, by budding, yields the polymorphic animal stock. Here also (*Physalia*, *Disconanthe*) the medusoid gonophores can detach themselves from the stock and lead a free life as sexual individuals. In many *Siphonanthe* groups of persons, the already mentioned *Eudoxiæ* and *Ersææ*, detach themselves from the stock, and swim about freely as minute new animal stocks. In their gonophores the sexual products are developed. From the fertilised egg a medusoid organism arises, which by gemmation again becomes the polymorphic animal stock. We thus have here again to do with a sort of alternation of generations.

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The fundamental law of Biogenesis.—Egg segmentation and the development of the two primary germinal layers of the Metazoa (gastrulation)—The ontogeny of the Cnidaria.

Every Metazoon is, at the commencement of individual existence, a simple cell, an egg cell; *i.e.* its development starts from a point at which the Protozoon remains during its whole life. Further, by the repeated division of the fertilised egg of every Metazoon, a germ is produced, whose structure repeats in a general way the structure of a simple *Cœlenterate.* This germ, which is known as the **gastrula**, consists of two cell layers, the **ectoderm** and the **endoderm**, which may be compared with the two layers composing the body of a simple adult *Cœlenterate.*

Fundamental law of Biogenesis.—The frequently observed parallelism between the consecutive stages of individual, or ontogenetic development, and the grades of development presented by the animal kingdom, is thus explained by the theory of descent. Every animal, in its ontogeny, passes through, in an extraordinarily abbreviated and concise manner, the long series of its ancestral forms. "**Ontogeny, or the history of the development of the individual, is a short recapitulation of the history of the race, or phylogeny.**" This sentence, in which the fundamental law of Biogenesis is formulated, contains a generalisation of the fact that every animal passes on to its descendants by **inheritance**, not only its organisation at an adult stage, but also its own course of development.

In the course of time adaptation, *i.e.* the survival of the fittest in the struggle for existence, interferes with the action of heredity, so that species do not remain constant, but change according to circumstances. In the same way, the ontogenetic process of development also, *i.e.* the series of consecutive stages of development of a species, may be subject to such modification that it no longer faithfully recapitulates the process of development of its ancestors. The repetition of ancestral development caused by inheritance is called "**palingenetic**"; the modifications of ancestral development caused by adaptation are "**cænogenetic.**"

It is extremely difficult to determine in a concrete case what is palingenetic and what is cænogenetic. It is at once evident that a purely palingenetic course of development never occurs anywhere. It is only by the discovery of similarity between one stage of development in an animal and another adult animal, that we can decide that that stage has something palingenetic in it. When a comparison of a stage of development in one species with other species in an adult condition is not possible, we have no sure means of judging what is palingenetic in it and what cænogenetic. For instance, we know of no adult animal with which the Echinoderm larva can be compared; and we cannot consequently know whether these larvæ have in any way retained the organisation of their primitive Echinoderm ancestors.

Our justification, again, for holding that a stage of development is probably palingenetic, when other organisms in adult condition possess essentially the organisation of that stage of development, stands or falls with the assumption that in the course of the earth's history some lower animal forms have remained very little altered by the side of others which have developed into higher organisms, and that it is not the case that nearly all lower animals living to-day are the degenerate descendants of ancestors once highly developed. Palæontology teaches us, in fact, that during those epochs of the earth's history which are accessible to investigation, and among those organisms which we know in a fossilised condition, many forms and groups of forms have remained unaltered for immensely long periods, while other forms on the contrary have progressed. On the other hand, we cannot doubt that retrogressions in the development of the organic world are by no means rare phenomena. The acquisition of a stationary manner of life, for example, and still more of parasitism, necessitate such retrogressions. In many cases, in consequence of new conditions, sexual maturity may be shifted to an earlier stage of development, better suited for competition, and the "adult" form may gradually cease to be developed. The *Axolotl*, for instance, generally becomes sexually mature at a stage with external gills—a so-called larval stage—and reproduces itself at that stage. It only rarely develops into the "adult" animal. If, in consequence of certain conditions, the development into an adult animal were altogether and always to cease to take place, we should have before us a case in which an animal, according to the common conception more lowly organised, descended from one more highly developed. If we wish, therefore, to compare the developmental stages of an animal with the final stages of other animal forms, in order to demonstrate their palingenetic meaning, we must always be able to bring forward good reasons for believing that these animal forms are not simplified or degenerated.

If the distinction between palingenesis and cænogenesis is difficult, even when we can illustrate it by adult animals, the difficulty increases when the comparison remains purely ontogenetic; *i.e.* when we can only compare developmental stages of one animal with developmental stages of other animals. It is now accepted, that when two animal groups have similar larval forms, these groups are racially related. The larva of *Balanoglossus* agrees in many important points with the larva of the *Echinoderm*; *Balanoglossus* is therefore considered to be related to the *Echinoderms*. It is possible that this view is correct; but we cannot say that this relation is probable; for we can bring forward no reason to show that either of these larval forms has any palingenetic significance.

In dealing with ontogenetic problems we have to take into account another series of considerations, which are partly a simple result of a consistent carrying out of the Darwinian principles. We give only the most important.

1. We are more likely to be justified in considering an ontogenetic process of development palingenetic, when it exhibits from first to last an unbroken series of self-supporting stages of development, so that we can imagine the larva at each stage to be an adult sexually mature animal. But we certainly do not find such a method of development entirely realised anywhere in the animal world.

2. It is an advantage for an animal whose organisation is adapted to its conditions, *i.e.* which maintains with success the struggle for existence, to reach its adult form, not only as directly and as quickly as possible, but economically, *i.e.* without the development of parts which have become useless.

3. Such a direct and abbreviated development can take place only when the developing animal is from first to last provided with nourishment by means of which it can develop. This occurs either by the egg receiving from the mother body nutritive yolk to help in its development, or by its being nourished, as in viviparous animals, direct from the mother body. Everything that is connected with such

nourishment of the developing animal is a secondary addition to the original development. We cannot think either of a bird embryo at the time of incubation, or of a mammalian embryo in its egg envelopes as an independent and self-feeding animal.

4. Direct development may occur together with gradual development or metamorphosis in the ontogenetic development of the animal. Of all the original independent stages of development, often only one or a few are preserved, viz. those which are specially capable of competition, whilst all the others disappear in the direct development. Thus the insect egg develops direct into the caterpillar or larva by the help of the nutritive yolk. The larva at this stage of development, being suited for competition, procures food for itself independently, grows vigorously, and then again develops direct (pupal stage) by the help of the stored-up food into the adult winged insect.

5. The effect of the struggle for existence on the larvæ at the various stages of development, and especially on those which feed independently, is just the same as on adult animals. It is therefore to be expected that the different manners of life (attached, free-swimming, parasitic, etc.) during the stages of development should determine adaptations and modifications in the larval organisation similar to those in adult animals. Such modifications, however, have a limit not clearly known to us, just because the stages they affect are stages of development whose purpose is to produce an adult sexually mature animal.

6. The more important organs or systems of organs are, the earlier do they begin to form in the larva; or, in other words, the order of their development in time is in direct correspondence with their importance to the adult animal. Whatever holds good for the adult animal also naturally holds good for every organ and for every adaptation; its development becomes more and more direct, and more and more abbreviated; it adapts itself more and more to the purpose of reaching as soon as possible the form and arrangement which belong to the adult animal. Increasingly defined localisation of the developing parts is a necessary consequence of their earlier commencement.

We see from the above that in phylogenetic investigations it is perhaps still more difficult to decide the true bearing of ontogenetic than of anatomical facts. We can only attain to phylogenetic conclusions of a certain degree of probability when comparative anatomy and comparative ontogeny go hand in hand, when comparative anatomy takes into account the developing organs, and when comparative ontogeny does not leave out of consideration the last stages of development.

Segmentation and gastrulation.—When we come to investigate in what manner the bi-laminar germ, the gastrula of the Metazoon, arises out of the fertilised egg, we find what appear to be very different methods of development. Numerous thorough investigations have proved that this variety of methods is almost exclusively caused by the **quantity and distribution of the nutritive yolk** in the egg. If we assign to the influence of the nutritive yolk the importance that is due to it, we shall be convinced that one single process underlies all these different phenomena. We must keep well in view, (1) that the **nutritive yolk**, or **deutoplasm**, is an inert, lifeless nutritive material deposited in the egg cell, and (2) that the **formative yolk**, or the **protoplasm**, with the nucleus it encloses, is the only living active portion.

We have already spoken of the variations in amount and distribution of the deutoplasm in the egg. We shall now describe the first appearance of **segmentation** or **furrowing** in the different kinds of eggs. The following are the types of eggs whose segmentation we propose to describe:—

Holoblastic alecithal egg. Holoblastic telolecithal eggs, with varying quantity of nutritive yolk: *Eupomatus* (*Annelid*), *Discocelis* (*Polyclad*), *Bonellia* (*Echiurid*), *Ctenophora.* Holoblastic centrolecithal eggs: *Geryonia* (*Craspedote Medusa*). Meroblastic telolecithal eggs: *Shark.* Meroblastic centrolecithal eggs: *Insects.*

The first divisions occur in directions which seem to be identical in the eggs of most animals. The first plane of division which, after previous nuclear division, separates the two daughter cells of the egg, *i.e.* the first two **segmentation spheres,** or **blastomeres,** runs in the direction of the principal axis of the egg, from the animal to the vegetative pole. By the animal pole we mean that portion of the surface of the egg at which the spermatozoon entered, and near which, in telolecithal eggs, the chief mass of the formative yolk lies. The point lying diametrically opposite to this we call the vegetative pole. The first plane of division is, therefore, with relation to the two poles, **meridional.**

The **holoblastic alecithal** egg falls at the first division into two similar blastomeres, each of which has a nucleus in its centre.

The **holoblastic telolecithal** egg falls generally into two blastomeres, each of which repeats the structure of the undivided egg. Each blastomere shows polar differentiation—at the animal pole lies the greatest mass of formative yolk with the nucleus, at the vegetative pole the greatest mass of nutritive yolk (Fig. 89, *B*, *C*).

The **holoblastic centrolecithal** egg (*Geryonia*) falls into two blastomeres, each of which repeats the structure of a telolecithal egg, the formative yolk only appearing at the free surface of the blastomere, and not at the side which is directed towards the plane of division. The nucleus of each blastomere lies superficially in the formative yolk (Fig. 89, *D*).

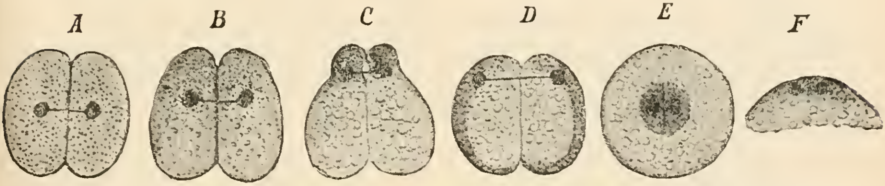

FIG. 89.—**2-Blastomere stage of different eggs.**—These are placed in this and all following illustrations, so that the animal pole is directed upwards, and the vegetative pole downwards. The nucleus is black, the formative yolk dark, the nutritive yolk light and granulated. *F* represents merely a portion from the animal pole of an egg.

In the **meroblastic telolecithal** egg the inert lifeless nutritive yolk is so strongly developed in comparison with the living active formative yolk, that the formative yolk when dividing is not able to effect the division of the whole of the nutritive yolk. The former only therefore divides, the latter remaining undivided. We have thus a large sphere of nutritive yolk, with two masses of formative yolk divided by a meridional furrow at the animal pole, in each of which lies a nucleus (Fig. 89, *F*).

In the **meroblastic centrolecithal,** or rather **mesolecithal,** egg the central formative yolk again alone is able to divide under the influence of the nucleus, while the remaining portions of the egg continue at first undivided (Fig. 89, *E*).

The **second plane of division** is also meridional and stands at right angles to the first. It divides each of the first blastomeres into two halves exactly in the same way as the first plane divided the whole egg.

The **third plane of division** seems to be pretty generally **equatorial.** It is visible on the exterior of the egg as an **equatorial furrow.** It stands at right angles to the first two planes of division and to the chief axis of the egg, and divides the first 4 blastomeres into 8, of which the 4 animal portions form the animal part of the germ, and the 4 vegetative portions its vegetative part.

In the **holoblastic alecithal** germ the 8 blastomeres are of equal size, and the third plane of division shows itself outwardly as a strictly equatorial circular furrow (Fig. 90, *A*).

In **holoblastic telolecithal** germs each of the 4 blastomeres divides into a smaller animal blastomere, consisting almost exclusively of formative yolk, and a larger vegetative blastomere containing the nutritive yolk and a small quantity of formative yolk. The greater part of the latter lies towards the animal pole of the blastomere and contains the nucleus. Each vegetative blastomere of the germ of 8 blastomeres thus repeats the structure of a blastomere of the germ at the 4-blastomere stage. The more considerable the quantity of nutritive yolk in the germ, the larger is the vegetative blastomere as compared with the animal. The smaller blastomeres are called **micromeres,** the larger **macromeres.** The division of the 4 blastomeres into 4 micromeres and 4 macromeres looks as if the former budded from the latter (Fig. 90, *B*, *C*).

In the **holoblastic centrolecithal** (*Geryonid*) germ, after the appearance of the third plane of division, which is here strictly equatorial, the 8 blastomeres are of equal size. Each blastomere has a peripheral layer of formative yolk, with a nucleus imbedded in it, and a mass of nutritive yolk towards the centre of the spherical germ (Fig. 90, *D*).

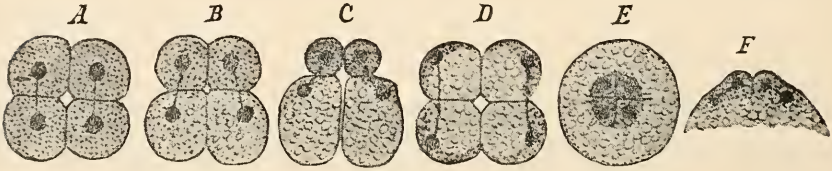

Fig. 90.—*A*, *F*, **Diagrams showing the 8-blastomere stage of different eggs.**

The germ of the *Ctenophora* departs from the usual arrangement of the telolecithal holoblastic germ, since the third process of division is not equatorial. Each of the 4 blastomeres divides, in a plane slantingly meridional, so that the germ consists of 8 approximately equal blastomeres, of which 4 lie rather nearer the animal pole than the other 4. The 8 blastomeres are grouped round a central space, which lies in the principal axis of the germ. Each blastomere shows the structure of the original *Ctenophoran* egg, the formative yolk lying chiefly at the animal pole of the blastomere, and the more considerable nutritive yolk forming its larger vegetative part.

In the **meroblastic telolecithal** germ, in consequence of the great development of the nutritive yolk, the "equatorial" division takes place quite near the animal pole. Exteriorly this division is visible as a circular furrow (polar circle) which divides the 4 prominences of formative yolk into 4 smaller central prominences with nuclei, and 4 peripheral prominences also with nuclei. The 4 central and the 4 peripheral prominences are not completely separated below the surface, either from each other or from the subjacent nutritive yolk (Fig. 90, *F*).

In the **meroblastic mesolecithal** germ the 8 central masses of formative yolk, each provided with a nucleus, are not separated from the great mass of nutritive yolk surrounding them (Fig. 90, *E*).

No general rule can be given for further divisions. Many meridional, equatorial, and cross divisions follow. The determination of the processes in detail is the more difficult in that divisions occur simultaneously at different points of the germ, and the number of blastomeres considerably increases. Starting with the 8-blastomere stage, we will further follow the course of development of each germ type.

1. In the **holoblastic alecithal** germ (Fig. 91), out of the 8 blastomeres, by repeated meridional and equatorial division, 16, 32, etc., blastomeres of about equal size are produced, which together form the uni-laminar wall of a sphere, which becomes hollow by the formation of a cavity (**segmentation cavity, blastocœl**) (total equal furrowing). At this stage the germ is called **blastula**, or **cœloblastula**, because it is hollow. During repeated division of the blastomeres the blastula becomes flattened at the vegetative pole (*C*), the flattened part sinks into the segmentation cavity more and more, so that the invaginated portion, which consists of vegetative blastomeres, approaches the non-invaginated part by means of complete or partial reduction of the cavity. We now have before us a germ consisting of two layers of blastomeres, which have become epithelial. The outer layer is the **ectoderm**, the inner the **endoderm**. At the edge of the **aperture of invagination** or **blastopore** the two layers pass into each other. The endodermal blastomeres or cells form together a hollow sac, the **arch-enteron**, the cavity of which opens externally through the blastopore. At this stage the germ is called **gastrula**, and in this case **cœlogastrula**, because the blastopore leads into an open enteric cavity. This process, by which a blastula becomes a gastrula, is called **invagination** or **embole**.

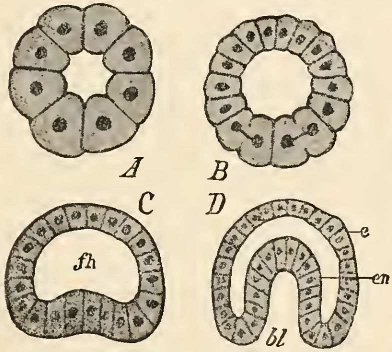

Fig. 91.—**Segmentation and gastrulation of a holoblastic alecithal germ.** *B*, Blastula. *D*, gastrula. *fh*, Segmentation cavity; *e*, ectoderm; *en*, endoderm; *bl*, blastopore.

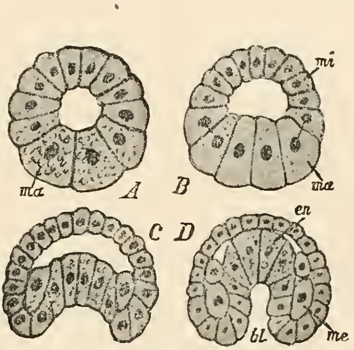

Fig. 92.—**Segmentation and gastrulation of a telolecithal egg with little nutritive yolk** (of **Eupomatus**). *mi*, Micromeres; *ma*, macromeres; *en*, endoderm; *me*, mesoderm; *bl*, blastopore.

2. In the **holoblastic telolecithal** germs, the phenomena of blastula and gastrula formation are at least apparently different according to the presence of much or little nutritive yolk. Let us first consider a germ with little nutritive yolk, as, for example, that of *Eupomatus* (Fig. 92). It consists of 4 animal micromeres and 4 vegetative macromeres. The difference in their sizes is not very great, because of the small mass of nutritive yolk, and the third plane of division lies near the true equator. First the 4 micromeres divide, then the 4 macromeres. We thus now have 8 micromeres and 8 macromeres. The micromeres continue to divide, and the macromeres follow at a slower rate. While, however, the micromeres always divide into two cells or blastomeres of pretty equal size, the **equatorial** divisions of the macromeres are such that each divides into a micromere, which is directed towards the animal side of the germ and contains less nutritive yolk, and into a macromere, turned towards the vegetative pole and containing more nutritive yolk.

The number of micromeres thus increases, as in the first place they themselves divide, and in the second place new micromeres, produced by macromeres, become added to them. This process of the continual production of micromeres is extremely important for the comprehension of all following types of segmentation and gastrulation. The furrowing is **total**, but already a little **unequal.** The blastula which results is a cœloblastula, with a cap-like cover of micromeres and a lower part formed of a few yolk-containing macromeres. In consequence of the considerable size of the macromeres the segmentation cavity is somewhat narrowed. The gastrula is formed by invagination, and looks as if the layer of macromeres which sinks in were grown round on all sides by micromeres. The gastrula is a cœlogastrula, and the arch-enteric cavity appears narrowed in consequence of the large size of the macromeres.

Closely connected with the segmentation and germ-layer formation just described is another process, an example of which is afforded by the developing germ of *Bonellia* (Fig. 93). The process is essentially the same; the apparent variations are explicable by the fact that the mass of nutritive yolk is more considerable. The 4 large macromeres, burdened with yolk, appear in consequence of their size as the fixed resting-point round which the processes of development take place. At first, as before, the 4 micromeres divide. The 4 macromeres are telolecithal blastomeres. The chief mass of the formative yolk left after the first division or budding no longer lies in the direction of the animal pole, but at some distance from it, towards the outer edge of the 4 micromeres. The division or budding of these 4 macromeres leads to the formation of 4 micromeres, which take up a position externally, side by side with those already formed (*A*). The 4 macromeres still contain a remnant of formative yolk, which, as it always lies at the edge of the micromere cap, moves along the surface of the germ from the animal side of the macromeres towards the vegetative pole of the germ. Thus the process goes on (*B*, *C*). As the micromeres divide, and as their number increases by the constant formation of new micromeres from macromeres, the macromeres are at last surrounded, everywhere except at a small space at the vegetative pole. This process is called **epibole**; it is the growth of micromeres over a resting mass of very large macromeres. It will be seen from the above description that this process and that of invagination are fundamentally identical. The gastrula which is formed is a solid **sterrogastrula,** whose enteric cavity is almost filled up by the large size of the yolk-laden macromeres. The micromeres present at this stage form the ectoderm; the macromeres represent the rudiments of the endoderm and of a part of the mesoderm. The blastula stage of this method of development is unrecognisable.

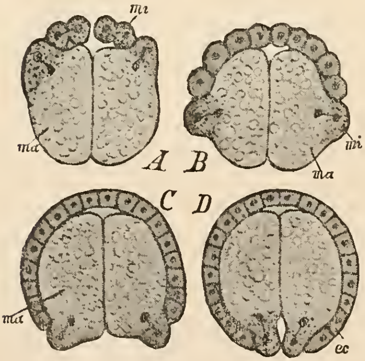

Fig. 93.—**Segmentation and gastrulation of the egg of Bonellia,** after **Spengel.** *mi*, Micromeres; *ma*, macromeres; *ec*, ectoderm.

From the type of segmentation exemplified by *Bonellia* we pass on to one nearly related which occurs in the *Polyclada* (Fig. 94). The formation of micromeres, and their growth over the macromeres, is just as in *Bonellia*. But here the 4 micromeres which are first constricted yield, by division, the whole ectoderm. The micromeres, which become constricted off from the macromeres in the second (and third) order, yield a great part of the mesoderm (musculature, sexual organs, connective tissue), and are overgrown by the ectoderm micromeres. All micromeres which are detached later belong to the endoderm. We have here before us a typical case of the tendency to shift back formations to very early stages of development. A typical gastrula is not developed in the *Polyclada*, since the separation of ectoderm and endoderm occurs as early as the 8-blastomere stage. We shall return to this later.

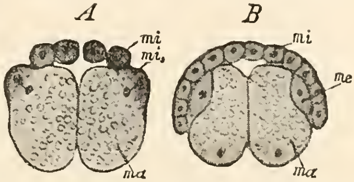

Fig. 94.—**Segmentation of a Polyclad egg (of Discocelis).** *mi*, First generation of micromeres (ectoderm-forming cells); mi_1, second generation of micromeres (mesoderm micromeres); *ma*, macromeres.

The *Ctenophora* exhibit an interesting process of segmentation and gastrulation intermediate between the gastrulation by means of epibole of the telolecithal holoblastic eggs and the gastrulation by delamination of the centrolecithal eggs to be spoken of later. The 8-blastomere stage of these animals has been described above. All the 8 blastomeres are telolecithal, with the formative yolk directed towards the animal pole. What occurs at the 4-blastomere stage of the telolecithal holoblastic eggs hitherto described, viz. the constriction of the 4 micromeres from the 4 macromeres, here takes place one stage later, at the 8-blastomere stage. The 8 blastomeres in fact give off 8 micromeres towards the aboral pole (Fig. 95, *A*). The further segmentation is quite similar to that of *Bonellia*. The micromeres increase in number (1) by division, (2) by the continual addition of new micromeres towards the vegetative pole, by constriction from the macromeres (*B*, *C*). After the micromeres have thus grown round the macromeres, leaving a large region at the vegetative pole in which the macromeres come freely to the surface, the formation of micromeres does not cease, as in the *Polyclada*. The already formed micromeres, however, yield exclusively ectoderm; the remaining macromeres, part of the mesoderm and the endoderm. Here also no very recognisable gastrula is developed.

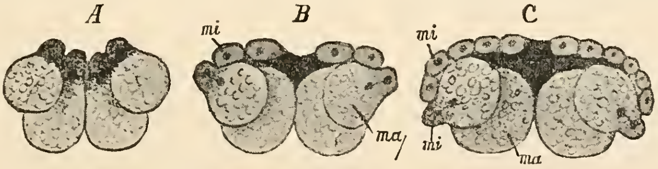

Fig. 95.—**Three stages in the segmentation of a Ctenophoran egg.** *mi*, Micromeres; *ma*, macromeres.

In all processes of the formation of micromeres the following is to be specially noted. After a macromere has constricted off a micromere, or, what is the same thing, after a blastomere has divided into a small micromere with little or no nutritive yolk, and into a large macromere with much nutritive yolk, the portion of formative yolk or protoplasm which remains in the macromere grows evidently by the assimilation of nutritive yolk before the macromere can again divide.

3. Segmentation and gastrulation of the **holoblastic centrolecithal** germ. We give as an example of this the *Geryonid* germ which has been the most carefully investigated and is the best understood (Fig. 96). We are already acquainted with the 8-blastomere stage. Each blastomere is telolecithal, with deutoplasm directed towards the centre of the germ and protoplasm towards the circumference. The 8 blastomeres divide into 16, and then into 32 blastomeres of equal size, which

all remain telolecithal in the same way as in the 8-blastomere stage. The 32 blastomeres of the spherical germ form a single layer round a considerable central cavity. A blastula-like stage thus occurs, though the germ has really another significance, as the central cavity does not represent the segmentation cavity of the alecithal germ, but, as we shall see, the enteric cavity.

When 32 blastomeres are formed, the formation of **micromeres** follows. From each blastomere a micromere is constricted off on the outer side, so that the germ now represents a double-layered hollow sphere, whose outer layer is formed of micromeres, and whose inner layer consists of macromeres. The micromeres increase in number (1) by themselves dividing, (2) by the formation once more of micromeres which are constricted off on the outer side of the macromeres. The micromeres form the ectoderm, the macromeres the endoderm, which surrounds a completely closed cavity—the enteric cavity. The germ thus represents a cœlogastrula without blastopore. We call this a **cœloplanula.** The formation of the two germ layers in the manner described above is called **delamination.** It must appear clear from our description that this cannot be sharply distinguished from **epibole.** Both processes rest on the formation of micromeres. In *Bonellia* and the *Polyclada* the first formation of micromeres, or delamination, takes place at the 4-blastomere stage, in the *Ctenophora* at the 8-blastomere stage, and in *Geryonia* at the 32-blastomere stage.

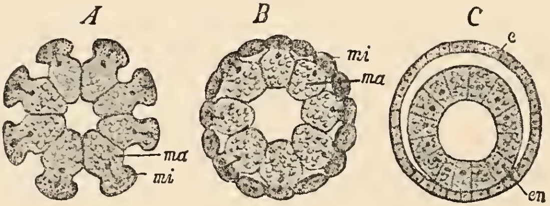

FIG. 96.—**Segmentation and gastrulation of the Geryonid egg.** *mi*, Micromeres; *ma*, macromeres; *e*, ectoderm; *en*, endoderm.

4. The **meroblastic mesolecithal** germ was left at the stage where the formative yolk or protoplasm was divided into 8 small masses, each with a nucleus, in the centre of the undivided nutritive yolk. If we compare this stage with the 8-blastomere stage of the *Geryonid* germ, we shall see that these 8 masses of formative yolk correspond with the 8 portions of protoplasm of the latter germ, only that in the former, in consequence of the originally different arrangement of the nutritive yolk, the masses of protoplasm lie at the centre, while in the latter they are peripheral. In the meroblastic germ the nutritive yolk is undivided, the formative yolk being incapable, at the time of division, of effecting the division at the same time of so large a mass; in the holoblastic egg the formative yolk controls the whole less massive nutritive yolk.

The 8 central nucleated masses of protoplasm of the meroblastic mesolecithal germ (Fig. 97) we shall call **merocytes.** They are often branched, and have amœboid movements. Their processes penetrate the surrounding mass of yolk, and are also connected with the thin layer of protoplasm which is found at the surface of the germ. They feed at the expense of the deutoplasm.

The 8 merocytes divide into 16, 32, and so on, and move at the same time centrifugally through the yolk to the surface of the germ, where they form a simple continuous layer. It is this layer of merocytes which is called the **blastoderm.** The germ has now become centrolecithal, and agrees in its structure with the *Geryonid* germ before the formation of micromeres or delamination, except that the central nutritive yolk is here still undivided.

The further development of the germ has unfortunately not yet been thoroughly investigated. Some observations tend to show that at this point, as in the *Geryonid* germ, delamination or formation of micromeres takes place. The merocytes at the surface divide in such a way that the outer portion separates off completely as a nucleated micromere layer detached on all sides, while the inner portion remains in the nutritive yolk as a nucleated merocyte layer. Thus the two germ layers are formed; the outer micromere layer represents the ectoderm; the central mass of nutritive yolk with the merocytes which belong to it probably represents the endoderm.

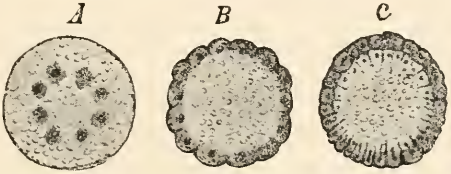

FIG. 97.—**Segmentation and formation of blastoderm in the egg of an Insect.**

The merocytes by increasing in number and feeding at the expense of the nutritive yolk, become able at last to overpower and incorporate it, *i.e.* they can divide it.

The gastrula is here a solid **sterroplanula.**

It has been observed in many cases that in the partial segmentation, *i.e.* in the multiplication of the central merocytes, only some of them move towards the surface, there to form the blastoderm, while the others remain in the yolk.

5. The **meroblastic telolecithal** germ (Fig. 98). We left this germ at the 8-blastomere stage, with undivided mass of nutritive yolk. We may here also call the masses of protoplasm **merocytes.** They stand in exactly the same relation to the collection of protoplasm at the animal pole of the blastomeres of the holoblastic telolecithal egg as do the merocytes of the mesolecithal meroblastic germ to the protoplasmic portion of the blastomeres of the *Geryonid* germ.

The 8 primary merocytes divide in the following manner. The 4 central merocytes divide into 4 secondary central merocytes in contact with one another at the animal pole, and 4 secondary peripheral merocytes. The former are now entirely severed from each other and from the nutritive yolk as **micromeres.** The latter remain connected with the yolk as merocytes. The primary peripheral merocytes also divide, but their descendants remain connected with the yolk as merocytes. Some of them even sink into the nutritive yolk as branched and probably amœboid merocytes.

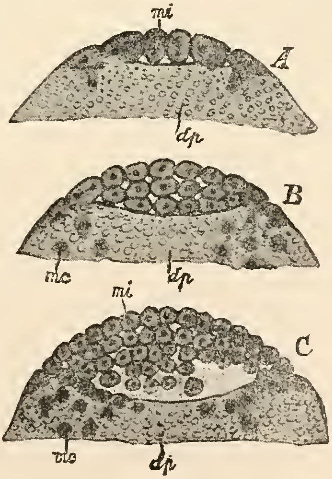

FIG. 98.—**Segmentation of a meroblastic telolecithal egg (of a shark), after Rückert.** *mi*, Micromeres; *dp*, deutoplasm; *mc*, merocytes.

The region at the animal pole of the germ (egg) in which the micromeres and some of the merocytes are visible is called the **germ or germinal disc**.

The further course of segmentation is as follows:—

1. The micromeres already formed continue to divide independently.

2. Towards the edge of the germ disc new micromeres are constricted off from the merocytes, and then associate themselves to those already existing, so that the area of the micromere region, or germ disc, increases.

3. The merocytes at the edge of the germ disc, as well as those which lie deep in the nutritive yolk, constantly divide, so that not only does the germ disc grow at its edge, but the nutritive yolk becomes more and more crowded with merocytes, which penetrate further and further into it.

Finally, the germ shows the following structure: at the animal pole, in the middle of the germ disc, lies a flat mass of micromeres consisting of several layers, the rudimentary ectoderm. Lying at the edge of the germ disc, and imbedded in the yolk, are merocytes. The greater number of these merocytes yield the material from which, by the formation of micromeres in a way hereafter to be described, a large part of the mesoderm and the endoderm are built up. By the constriction of micromeres from merocytes at the edge of the germ disc, and by division of the already formed ectoderm cells, the cap of ectoderm increases still more, so that it grows more and more round the germ as the blastoderm.

We see that in the development of the meroblastic telolecithal egg the gastrula form is unusually indistinct, because of the enormous mass of the nutritive yolk. The micromere-cap respresents the ectoderm; the yolk with the merocytes the endoderm and part of the mesoderm. If a blastopore is sought for, this can only be represented by that portion of the germ which is not covered by the ectoderm cap, where the nutritive yolk comes to the surface. The edges of the blastopore are represented by the edges of the ectoderm cap. The gastrula formation here also occurs by means of **epibole**; the gastrula is a solid **discogastrula**.

In the above description only the most important types of segmentation and formation of the two primitive germ layers have been brought forward. The processes in the animal kingdom are in reality extremely varied, yet most of them can be included without much difficulty under one or other of our heads. The great majority of investigations are still insufficient; because in some cases, as in the meroblastic eggs, observation is very difficult. The difficulty is to establish quite clearly the distribution of the formative yolk in the egg, and to follow the division of the blastomeres in detail.

The method of gastrulation does not afford any means of recognising the relationships of animals, as it is determined by the quantity and distribution of the nutritive yolk, and this may be quite dissimilar in animals nearly related, and similar in widely separated forms.

The question, which sort of segmentation and gastrulation is the original, has been much discussed. Most authorities hold, not without reason, total equal furrowing, the formation of a cœloblastula, and the subsequent formation of a cœlogastrula by invagination to be the original method. This view is supported chiefly by the following facts:—(1) the want of a nutritive yolk, which cannot have been present in corresponding racial forms; (2) the similarity of the blastula with certain Protozoan colonies (*Magosphæra*, *Volvox*); (3) the similarity of the cœlogastrula with the simplest *Cœlenterata* (*Olynthus*, *Hydroids*). Just this similarity makes it possible for us the more easily to imagine these germ forms as independent adult animals.

The free-swimming gastrula, which is usually ciliated on the outer surface, possesses a mouth (blastopore) through which it can or could take food into the enteric cavity.

It is important to note that in most of the higher bilaterally symmetrical animals the bilateral symmetry appears very early. The gastrula of these animals is **bilaterally symmetrical**, *i.e.* only one plane can be made to cut it into **two exactly similar halves.** We can consequently distinguish in the gastrula upper and lower, anterior and posterior, right and left. The gastrula of the radiate *Cœlenterata*, on the contrary, is radiate or rather uniaxial. There is one principal axis round which all the elements of the body are arranged in circles. This principal axis has unlike poles; at one pole, the vegetative, lies the blastopore; the other, the animal pole, is closed.

Bilateral symmetry is shifted back in many bilaterally symmetrical animals to much younger stages of development—to the blastula or the segmentation stages. In a few cases even the egg is bilaterally symmetrical, and the position of the future principal regions of the body can be determined even in it.

In the uniaxial gastrula the blastopore is round and closes to a point. In the bilateral gastrula, however, it has become slit-like, and closes either from front to back or *vice versa*, in a line lying in the plane of symmetry or median plane of the body.

Ontogeny of the Cnidaria.—The segmentation is everywhere complete. The formation of the gastrula occurs by invagination, epibole, or delamination. In the last case a **cœloplanula** arises direct. Where a cœlogastrula or a sterrogastrula occurs it changes, in all cases except the *Ctenophora*, into a **planula** by the closing of the blastopore. This is generally free-swimming and ciliated, and has a tuft of long, mostly immobile sensory hairs at the original animal pole, which we now call aboral. A *Hydroid* arises out of the blastula by the formation of the definite oral aperture by means of a breach where the blastopore closed, the animal having attached itself by the aboral end of the body. Round the mouth, the tentacles bud out as hollow outgrowths of the ectoderm and endoderm.

The direct development of a *Craspedote Medusa* from the fertilised egg is best known in *Geryonia*, with whose blastula we are already acquainted.

Between ectoderm and endoderm a jelly is formed, which constantly increases in mass, so that the ectoderm sac is separated by a great interval from the endoderm sac which it encloses. At one point only, the future oral pole, which probably agrees with the vegetative pole, the endoderm sac remains in contact with the ectoderm sac. The permanent mouth is formed at this point of junction by means of a breach, while at the same time, at some distance from the mouth, the velum arises as a circular thickening of the ectoderm, and the 6 tentacles as buds, into whose axes solid processes of the endodermal sac grow. The connection of the endodermal tentacle axis with the gastral sac soon ceases. The oral surface of the larva, which is surrounded by the tentacles and the velum, sinks in and becomes the concave subumbrella. The *Medusa* form thus gradually comes into existence. How the radial vessels are formed in *Geryonia* has not been investigated.

A **Scyphopolyp** (*Scyphula of the Acraspeda, Coral polyp*) arises out of a planula in the following way (Fig. 99). The planula (*A*) attaches itself by the animal or aboral end of its body (*B*). At the oral end the body of the ectoderm sinks in in the shape of a pit and forms the ectodermal œsophagus with the external mouth (*C*). The base of the œsophagus then breaks through in the direction of the gastral cavity (*D*), and so arises the enteric aperture. The œsophagus of the Scyphula is at first not a round but a flatly compressed tube (*F*). On each side of it a prolongation of the enteron penetrates between it and the ectodermal body wall—the first 2 gastric pouches. Crosswise to these there is a further growth of 2 new pouch-shaped invaginations of the enteron between the œsophagus and body wall. Thus arise around the œsophagus the 4 gastric pouches of the Scyphula (*G*, *mt*). The neighbouring endodermal walls of every 2 gastric pouches apply themselves to each other and form the partition walls or septa (*H*, *se*), which are continued also, with free axial edges, into the central gastric cavity, and there form the so-called gastric ridges. The first 4 tentacles (*E*, *t*), arise around the oral disc as outgrowths of the ectoderm and endoderm. The endoderm forms a solid axis in the tentacles, which arise over the 4 gastric pouches, and which increase in number later.

In the *Coral polyps* the formation of the tentacles, gastric pouches, and partition walls, if not exactly like the above, is still similar, and the endodermal axes of the tentacles are hollow from the first.

The most important facts about the development of the Scyphula into the *Acraspede Medusa* have already been given on pp. 77, 106, 107, and 116.

The direct development of the *Acraspede Medusa* out of the egg is not yet sufficiently known. Compare what was said of the development of the mesoderm of the *Coral* (p. 100).

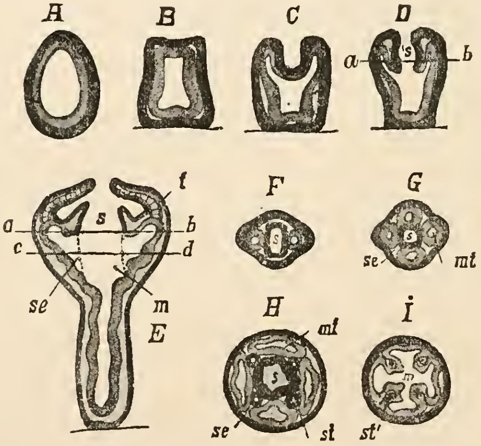

Fig. 99.—**Development of the Scyphula of Aurelia Aurita out of the Planula,** after **Götte.** *A*, Planula. *B*, The same after it has attached itself. *C*, Invagination of the œsophagus. *D*, Breaking through of the enteric aperture. *E*, Scyphula. *F*, Transverse section through the stage *C*. *G*, The same through stage *D* at the level of the line *a-b*. *H*, Transverse section through the Scyphula (*E*) at the level *a-b*. *I*, the same at the level *c-d*. Black, ectoderm; streaked, endoderm. *s*, Œsophagus; *se*, septa; *mt*, gastric pouches; *t*, tentacle; *m*, gastric cavity; *st'*, *st*, septal funnels.

The development of the *Ctenophora* is in a certain way opposed to that of all other *Cnidaria*. The total unequal furrowing of the telolecithal egg has already been described, as also the formation of a two-layered germ by epibole. We here again resume our account of the development.

After the 8 macromeres have formed a cap of micromeres which yield the whole ectoderm, they themselves divide into 16 macromeres, which arrange themselves as a plate on the vegetative side of the germ. Thereupon each of the 16 macromeres constricts off one micromere on the under side, *i.e.* towards the vegetative surface of the germ (Fig. 100). The 16 micromeres so formed are a part of the mesodermal rudiment, the rudiment at any rate of the tentacle mesoderm. They may be considered, perhaps, as part of the endoderm, as an early product of separation from it. The mesodermal axis of the *Ctenophoran* tentacle might then be compared with the endodermal tentacle canals or tentacle axes of the other *Cnidaria.*

After the 16 mesoderm micromeres (*me*) have been formed, the macromere plate becomes depressed, while, at the same time, the ectoderm cap spreads out more and more towards the vegetative pole. A cœlogastrula thus arises, in which we can already observe, besides the two primitive germ layers, a mesodermal rudiment (*B*). The latter, by the invagination of the 16 macromeres which represent the rudiment of the endodermal gastro-canal systems, come to lie inside, towards the gastric cavity. Later on it reaches a position quite at the animal pole, beneath the ectoderm (*C*), its elements at the same time increasing by division. The ectoderm at the vegetative pole becomes depressed inwards round the blastopore, and thus forms a stomodæum (*st*), the rudiment of the œsophagus (erroneously stomach) of the adult *Ctenophore.* The mesoderm at the aboral pole, viewed from this pole, assumes the shape of a cross. Two opposite limbs of the cross stretch out into the rudiments of the two tentacles, which appear as outgrowths of the ectoderm. The ectoderm thickens at the aboral pole to form the sensory body (Fig. 101, *sk*). Swimming plates appear as fused cilia in 8 meridians, arranged in pairs at the surface of the ectoderm. At first only a few swimming plates are formed in each row, but their number gradually increases. The hollow spaces of the gastro-canals appear as fissures penetrating from the gastric cavity to the circumference. Between the endoderm and the stomodæum on the one side, and the ectoderm on the other, a clear mass of jelly is secreted. The various elements which in the *Ctenophora* occupy the jelly are, according to some investigators, derived from cells migrating inwards from the ectoderm; according to others they are yielded by the rudimentary mesoblast, which has been described above.

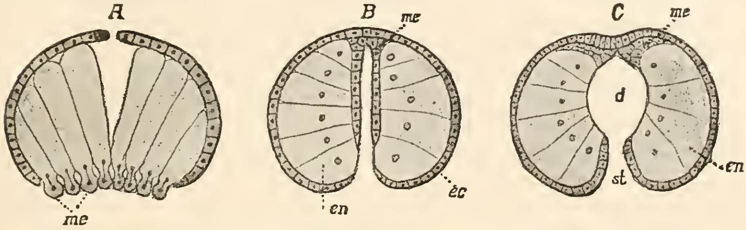

Fig. 100.—**Three early stages of development of a Ctenophore (Callianira), after Metschnikoff,** somewhat diagrammatic. *ec*, Ectoderm; *en*, endoderm; *me*, mesoderm; *d*, gastric cavity; *st*, œsophagus (stomodæum).

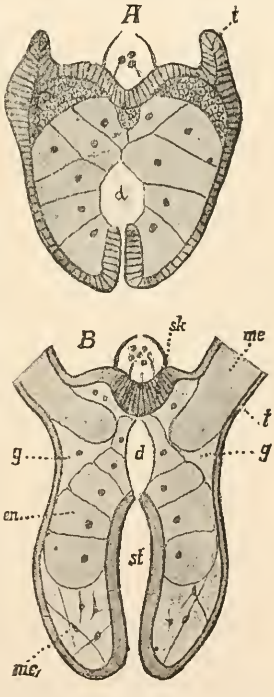

Fig. 101.—**Two further stages of development of Callianira, after Metschnikoff.** *en*, Endoderm; *me*, mesoderm; me_1, mesenchyme; *t*, tentacle; *sk*, sensory body; *d*, gastric cavity; *st*, œsophagus (stomodæum); *g*, jelly.

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Compare further the bibliography on p. 117.

CHAPTER III

The organisation of the Flatworms—The life-history of the Cestoda and Trematoda—The development of the Marine Planaria—The influence of Parasitism.

THE THIRD RACE OR PHYLUM OF THE ANIMAL KINGDOM.

PLATODES—FLATWORMS.

Systematic Review.

Class I. **Turbellaria.**

Free-living Platodes, with ciliated body epithelium.

Order I. **Polycladidæ, Marine Planaria.**

Large *Turbellaria* with flat, leaf-shaped body, with numerous ovaries and testes, without vitellaria, mostly with 2 separate genital apertures. The intestine very much branched, the branches anastomosing.

Tribe 1. **Cotylea.**

With ventral sucker. Mouth and pharynx in the middle of the body or further forward. Tentacles wanting or found at the anterior edge of the body. *Anonymus, Thysanozoon, Yungia, Cycloporus, Stylostomum, Eurylepta, Prosthiostomum.*

Tribe 2. **Acotylea.**

Without sucker. Mouth and pharynx in the middle of the body or further back. Tentacles wanting, or 2 dorsal neck-tentacles present. *Planocera, Leptoplana, Trigonoporus, Cestoplana.*

Order II. **Tricladidæ (Fresh-water, Land, and Marine Planaria).**

The generally large body is long and flat. Mouth and tubular pharynx behind the middle of the body. One common external genital aperture with 2 germaria and numerous testes and vitellaria. The alimentary canal consists of an anterior unpaired portion and of two lateral posterior limbs, which are again provided with side branches. *Planaria, Dendrocœlum* (in fresh water), *Geodesmus, Bipalium* (on land), *Gunda segmentata* (marine).

Order III. **Rhabdocœlidæ.**

In fresh and salt water. Small forms. Intestine, when clearly distinguishable, a straight tubular cæcum without or with very slightly pronounced lateral branches. Body elongate, mostly cylindrical, more rarely flatly compressed.

Tribe 1. **Alloiocœla.**

Intestine sharply separated from the parenchyma, often with short lateral sacs. Numerous small testes. Female germ glands either 2 ovaries or 2 germ-vitellaria, or separate germaria and vitellaria. *Monotus, Plagiostoma, Vorticeros.*

Tribe 2. **Rhabdocœla.**

Intestine sharply separated from the parenchyma, without lateral diverticula. In the parenchyma there occur spaces, generally of considerable size, filled with fluid, which form a sort of cœlome. 2 large testes. Female germ glands either 1 or 2 ovaries, or 1 or 2 germaria and vitellaria, or 2 germ-vitellaria. *Vortex, Graffilla* (parasitic), *Macrorhynchus, Mesostoma, Prorhynchus, Microstoma* and *Stenostoma* (in these two genera the sexes are separate), *Macrostoma.*

Tribe 3. **Acœla.**

Without distinct intestinal canal; with digesting parenchyma. Without excretory organs; with numerous very small testes, and 2 ovaries. *Nadina, Convoluta.*

Class II. **Trematoda.**

Parasitic unsegmented Platodes, without covering of cilia, mostly with forked intestine. Mouth and pharynx at the anterior end of the body. 2 testes, 1 germarium, and 2 vitellaria branched or divided into numerous lobes.

Order I. **Ectoparasitica (monogenetic).**

With at least 3 suckers. Development direct, without alternation of generations, or heterogeny; life-history simple. *Tristomum, Diplozoon* (two young, not yet sexually mature animals early fuse in the shape of a cross, and only become sexually mature in this condition) *Polystomum, Gyrodactylus.*

Order II. **Endoparasitica (digenetic).**

With at the most 2 suckers. Life-history with heterogeny. *Distoma hepaticum* (life-history, p. 169, Fig. 119), *D. lanceolatum*, both in the bile ducts of the sheep. *Distoma isostomum, Gynæcophorus hæmatobius*, in the blood in the portal veins of man (in Africa), sexually separate; the male with a channel on the ventral side for the reception of the female. *Amphistoma, Monostomum.* The sporocysts and rediæ usually live in water snails; the sexual generation mostly in the intestines of vertebrates.

Class III. **Cestoda (Tapeworm).**

Endoparasitic Platodes without cilia and without intestine, with numerous testes, 2 germaria, and 1 or 2 vitellaria broken up into lobes. With organs of adhesion only at the front end of the body.

Order I. **Monozoa.**

Unsegmented individuals. *Amphilina, Caryophyllæus, Archigetes.*

Order II. **Polyzoa.**

Cestode stocks arising by strobilation: segmented tapeworms. With scolex and chain of proglottides. *Phyllobothrium, Tetrarhynchus, Ligula* (very indistinctly segmented). *Bothriocephalus latus*; broad tapeworm (Fig. 117, *C*, p. 164) in human intestine. Over 3000 proglottides. With 2 pit-like suckers in the head. Genital apertures on the flat surfaces. Larva ciliated in water. Scolex-like young form in flesh of the Pike, of the Burbot, and perhaps of other fish. *Schistocephalus. Triænophorus. Tænia*; with 4 suckers. *T. Saginata* (*mediocanellata*) (Fig. 117, *A*,

p. 164), without hooks on the rostellum, with over 1000 proglottides, sexual apertures placed on the edge; in the human intestine. The finn, a *Cysticercus*, lives in the muscles of the ox. *T. solium* (Fig. 117, *B*, p. 164), with double circle of hooks on the rostellum. Sexual apertures placed on the edge. About 800 proglottides. Finn: *Cysticercus cellulosæ* in flesh of the pig (Fig. 120, p. 172). *T. serrata*, in intestine of the dog. Finn: *Cysticercus pisiformis*, in the liver of rabbits and hares. *T. crassicollis*, in the intestine of the domestic cat and of other Felidæ. Finn: *Cysticercus fasciolaris*, in the liver of the mouse. *T. cucumerina*, in intestine of the dog, and scolex-like finn in the body cavity of the dog-louse. *T. cœnurus*, in intestine of the dog. Finn: *Cœnurus cerebralis*, in brain and spinal marrow of the sheep, causing "staggers." *T. echinococcus*, in the small intestine of the dog; finn, *Echinococcus veterinorum* in the liver of man and in that of different domesticated ungulates.

I. General Remarks.

The race of the Platodes forms a very natural division of the animal kingdom, containing the three classes of the *Turbellaria*, the *Trematoda*, and the *Cestoda*. Their fullest development is shown in the organisation of the free living *Turbellaria*, which move forward by creeping or gliding, while in the *Trematoda* and *Cestoda* many degenerations and simplifications have taken place in consequence of parasitism. The organisation of the *Turbellaria* more than any other therefore supplies us with the clue to understand the systematic position of the Platodes and their affinities.

Of all *Metazoa* it is the Platodes, and especially the *Turbellaria*, whose general structure most agrees with that of the *Cœlenterata*, *i.e.* of the *Cnidaria*. They might almost be placed near the *Ctenophora* as creeping *Cnidaria*.

On account of the **absence of a cœlome** between the alimentary canal and the integument, and of a separate blood-vascular system, the function of circulation is performed, as in the *Cnidaria*, by the digestive system as gastro-canal apparatus. An anus is wanting here as there. The Platodes show, however, on the other hand, many essential differentiations of organisation which we miss in the *Cnidaria*, and which are in great part to be referred to the creeping mode of life. All the Platodes are bilaterally symmetrical; we can distinguish in their bodies an anterior and posterior, an upper and lower, a right and left. The aboral surface of the body of the *Cnidaria* becomes in the Platodes the dorsal surface, the oral the ventral surface, in whose centre the mouth originally lies. The sensory organs collect chiefly at that part of the body which goes first in creeping, *i.e.* at the anterior end, and the principal part of the central nervous system also, the brain, which originally lay at the aboral pole, *i.e.* at the centre of the dorsal surface, has, following the sensory organs, moved more or less far forward.

Those organs and systems of organs which, in the *Cœlenterata*, showed the tendency to leave the body epithelium and deposit themselves below it, forming a middle layer, have in the Platodes become markedly mesodermal, viz. (apart from the connective tissue) the sexual organs, the musculature, and the nervous system. The musculature is arranged under the body epithelium in a muscle layer whose elements have transverse, longitudinal, and diagonal courses. Dorso-ventral muscle fibres stretch between the ventral and dorsal surfaces. The whole arrangement of the musculature seems adapted for the creeping motion. The nervous system forms a plexus of nerves lying in or on the muscle layer, which is more strongly developed on the ventral than on the dorsal side. In this plexus single stronger nerve trunks are more clearly developed, and they meet together from various directions in one central point, the brain. In very many Platodes this nerve plexus forms the so-called ladder nervous system, in which we distinguish the following parts:—(1) the brain, lying at the anterior end of the body; (2) the two principal longitudinal trunks proceeding out of it and running on the ventral side; (3) transverse commissures which connect these latter.

The so-called **water-vascular system** is very characteristic of the Platodes. It is a system of fine canals, on the one hand ramifying in the mesoderm, and on the other emerging externally, which has certainly an excretory, and perhaps at the same time a respiratory purpose. In the *Cnidaria* no such system has been observed.

The Platodes are hermaphrodite. Besides the sexual reproduction by means of fertilised eggs, there is also (in *Trematoda*) parthenogenetic reproduction and (in *Turbellaria* and *Cestoda*) asexual multiplication by fission or gemmation.

For the comprehension of the relation of the Platodes to the *Cnidaria*, the knowledge of two animal forms, which have been considered to be intermediate forms between the *Ctenophora* and the *Turbellaria* (*Polyclada*), is necessary. Only one specimen of each has till now been described. One of these forms is *Cœloplana Mecznikowi*, the other *Ctenoplana Kowalevskii.* Unfortunately our knowledge, especially of the first form, is very insufficient. Their sexual organs and their development are unknown, so that we cannot be sure whether we have to do with young stages or with adult animals. But in any case both forms are of the greatest interest.

Cœloplana is a little animal about $\frac{1}{4}$ of an inch long and $\frac{1}{8}$ broad, whose appearance quite coincides with that of a *Polyclad.* The body is flatly compressed and ciliated all over; it creeps on the ventral surface. In the centre of the dorsal surface lies a vesicle with a mass of otoliths. Near it on each side, right and left, is a long tentacle feathered on one side, which can be withdrawn into a special sheath. In the middle of the ventral side lies the mouth. The gastro-canal system consists of the quadruply-lobed stomach and numerous anastomosing canals radiating from it. From the stomach 2 canals rise towards the dorsal surface of the body, where they apparently end blindly in front of and behind the otolith vesicle.

Ctenoplana has in general the same body form as *Cœloplana*; but besides the general ciliation this animal also has on the dorsal surface eight short rows of stiff plates arranged like a rosette; these correspond with the ciliated or rowing plates of the *Ctenophora*, and lie in special grooves, out of which they can be protruded. The arrangement of the gastro-canal apparatus is like that in the *Cœloplana*. In the middle of the dorsal surface occurs a formation similar to the sensory body of the *Ctenophora*. At the base of the depression containing the otoliths there is on each side a nerve centre with nerves proceeding from it, and near these on each side a solid tentacle with short lateral branches. In the neighbourhood of the tentacle on each side is found an aperture leading into a system of canals which branch in the body parenchyma, and which the discoverer of *Ctenoplana* compares with the water vascular system of the Platodes. Under the body epithelium lies a basal or skeletal membrane, under this a layer of longitudinal muscles, and under this again a layer of transverse muscles. Besides these there are dorso-ventral muscular fibres branched at both ends, which adhere on one side to the dorsal, and on the other to the ventral basal membrane. There are special bundles of muscular fibres for the protrusion and withdrawal of the ciliated plates.

These two forms agree with the *Ctenophora* chiefly :

1. In the possession of an aboral sensory body.
2. In the possession of 8 rows of ciliated plates (*Ctenoplana*).
3. In the possession of feathered tentacles.
4. In the general structure of the body.

Cœloplana and *Ctenoplana* are not yet bilaterally symmetrical. The chief axis runs, as in the *Ctenophora*, from mouth to sensory body. It is very much shortened. The lateral plane runs through both tentacles ; the median or sagittal plane stands at right angles to it. Each of these planes divides the body into 2 similar halves. If such forms were always to move forwards in the direction say of its median plane, and if at this end special sensory organs were to develop, or the sensory body come more forward, they would become bilaterally symmetrical. Only one plane, viz. the median plane, would divide the body into 2 exactly similar halves. We could then not only distinguish upper and lower, but anterior and posterior regions of the body.

Cœloplana and *Ctenoplana* agree with the *Polyclada* :—

1. In the flatly compressed form of body, and in the capacity of moving forward by creeping.
2. In the general ciliation of the body.
3. In the possession of a skeletal membrane (*Ctenoplana*).
4. In the possession of a dermal musculature, consisting of a longitudinal and a circular layer.
5. In the possession of dorso-ventral muscle fibres branched at both ends.
6. In the general arrangement of the gastro-canals.
7. In the possession of 2 (in *Polyclada*, however, unfeathered) dorsal tentacles and of a dorsal nerve centre (?).
8. In the possession of a water-vascular system (*Ctenoplana ?*).

The peculiarities mentioned under 1-5 may be considered as due to the creeping mode of life.

Cœloplana and *Ctenoplana* are distinguished both from the *Ctenophora* and the *Polyclada* by the want of an ectodermal œsophagus,—at least no such œsophagus has been described.

II. The Body Form.

Most of the Platodes are, as their name indicates, more or less flat. The *Polyclada* are leaf-shaped. In these all intermediate forms between the broad oval and the long ribbon occur. The *Triclada* are mostly long, lancet-shaped, with dorsal surfaces slightly arched. Among the land *Triclada* forms occur of great length. In the *Rhabdocœla* great variety prevails ; there are flat, disc-shaped, plano-convex, and often spindle-shaped animals. Among the *Trematoda* the ectoparasites and a few small endoparasites (*e.g. Distoma hepaticum*, *D. lanceolatum*) are flat and compressed. Most of the endoparasitic *Distoma* species, on the contrary, are more or less cylindrical. The *Cestoda* or tapeworms are ribbon-like, and consist chiefly of a row of consecutive segments progressively increasing in size posteriorly (proglottides). In front, where the body thins away, the segmentation is indistinct. The thin neck portion swells into a knot-like tapeworm-head (scolex), which is provided with organs of adhesion.

III. The Outer Body Epithelium.

A distinct body epithelium occurs only in the *Turbellaria*. In the *Trematoda* and *Cestoda* it is replaced by a resistant, elastic, cuticular membrane, which is generally perforated by very fine pores. It is indeed not impossible that this integument itself is a much modified epithelium. The body epithelium of the *Turbellaria* is ciliated. The ciliary motion serves principally (1) for **Respiration** (by the maintenance of a constant circulation of the water over the naked surface of the soft animal) and (2) for **Locomotion** (especially of the smaller forms).

Unicellular **dermal glands** open in the skin. In special glandular cells of the skin the so-called rod or rhabdite cells, spindle-shaped glandular secretions occur; the so-called **rods** or **rhabdites**, although found in other divisions, are specially characteristic of the *Turbellaria*. Whereas the rod-glandular cells in most *Polyclada* lie in the epithelium itself, in most *Triclada* and *Rhabdocœlidæ* they sink deep into the parenchyma, and only remain connected with the epithelium by means of long thin processes (rod-passages) in which the rhabdites are conveyed outwards and deposited in the epithelium. Typical stinging capsules also occur in the epithelium of many *Turbellaria*. There are besides numerous intermediate forms between true rhabdites and true nematocysts.

IV. The Gastro-canal System.

This has entirely disappeared in the *Cestoda*. These endoparasites are nourished endosmotically by the juices which surround them.

In the other Platodes the gastro-canal system is well developed, and shows in a few divisions modifications almost as important and characteristic as those in the *Cnidaria*. We can everywhere distinguish in it two principal parts: (1) an **œsophagus** or **pharyngeal apparatus**, which comes from a depression of the outer integument and is consequently lined with ectodermal epithelium; and (2) the endodermal **intestine** or **gastral apparatus**. We will treat of these two parts separately.

I. The **pharyngeal apparatus**. This opens externally through the mouth, and internally through an enteric aperture into the gastral apparatus.

The position of the mouth is in no animal race so extraordinarily variable as in the Platodes. We hold that the original position of the mouth is the central one, in accordance with the views set forth in the general remarks, and with its position in *Ctenoplana* and *Cœloplana*. This position is found only in *Turbellaria*, *i.e.* among the *Polyclada* in the families of the *Anonymidæ*, *Planoceridæ*, and most *Leptoplanidæ*, and among the *Rhabdocœlidæ* in a few *Acœla* and *Mesostomidæ*. In the remaining Platodes the mouth is placed either more to the front or to the back, without in any case reaching the extreme anterior or posterior end of the body. The mouth lies somewhat further forward than the middle among the *Polyclada* in the *Pseudoceridæ*, among the *Rhabdocœlidæ* in many *Acœla*, and also in *Mesostomidæ*, *Proboscidea*, and *Plagiostomidæ*. It is found near the anterior end of the body in the *Euryleptidæ* and *Prosthiostomidæ*, among the *Polyclada*, in many *Rhabdocœla*, and all *Trematoda*. It lies somewhat behind the middle in a few *Leptoplanidæ* among the *Polyclada*, all *Triclada*, and many *Rhabdocœlidæ* (especially in the *Monotidæ*). It is met with near the posterior end of the body in the *Cestoplanidæ* among the *Polyclada*, and in many *Plagiostomidæ* among the *Alloiocœla*.

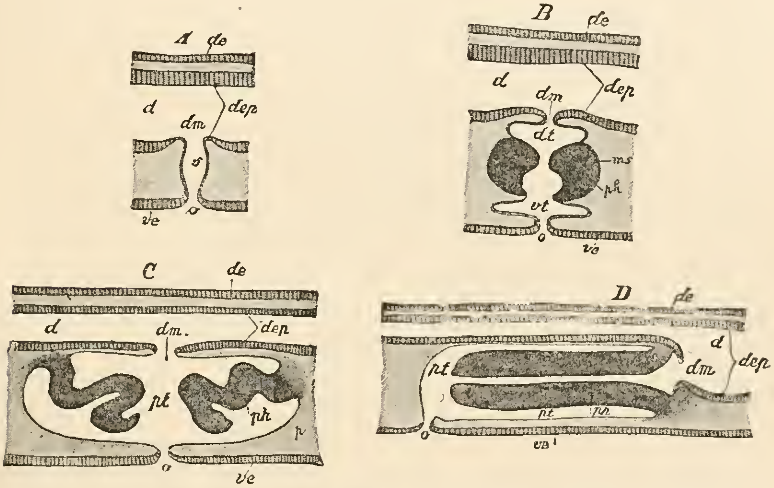

Fig. 102.—*A-D*, **Diagrammatic representation of the Pharyngeal Apparatus of the Turbellaria.** *A*, **Of Convoluta**; *B*, **of Mesostoma**; *C*, **of Planocera**; *D*, **of Prosthiostomum.** *de*, Dorsal body epithelium; *ve*, ventral body epithelium; *o*, mouth; *dm*, entrance to intestine; *pt*, pharyngeal pouch; *ph*, pharynx; *d*, intestine; *dep*, intestinal epithelium; *s*, œsophagus; *p*, parenchyma; *dt*, dorsal œsophageal pouch; *vt*, ventral œsophageal pouch; *ms*, muscular lamella.

The structure of the pharyngeal apparatus is very varied in the Platodes. We can only briefly describe the chief types.

The pharyngeal apparatus of the *Convolutidæ*, the *Microstomidæ*, and *Macrostomidæ* among the *Rhabdocœlidæ*, is distinguished by its great simplicity and its embryonic condition (in most *Acœla* it is even entirely wanting). In the 3 families mentioned it consists of a simple œsophageal tube between mouth and intestine (Pharynx simplex, Fig. 102, *A*). This simple œsophagus becomes at first complicated by the massing of definitely arranged muscles around it. The muscular wall of the œsophagus, then, almost always projects in various ways more or less far into the lumen of the œsophagus, so that we can now distinguish in the pharyngeal apparatus 2 chief parts: (1) the œsophageal or pharyngeal pouch, and (2) the muscular **œsophageal bulb** or **pharynx** which projects into it. When the œsophageal pouch is not spacious, and the pharynx with its free inner surface projects only a short way into it, the latter is generally round or barrel-shaped, and is sharply marked off from the body parenchyma which surrounds it by a layer of muscle (**Pharynx bulbosus**, Fig. 102, *B*). In this form we meet it in nearly all *Rhabdocœla*, in the *Plagiostomidæ* among the *Alloiocœla*, and further in all *Trematoda*.

In very many *Turbellaria* the pharynx projects as a circular fold into the mostly spacious pharyngeal sheath or pouch, and takes, like the latter, very various shapes; it is in this case never sharply severed from the surrounding parenchyma by a muscle layer (**Pharynx plicatus**). In all *Polyclada*, with the exception of *Euryleptidæ* and *Prosthiostomidæ*, the pharyngeal pouch is very spacious, and often has secondary pouches, which again are occasionally branched; and the pharynx is a flat and broad band which hangs as a circular fold from the sides of the pouch (Fig. 102, *C*). Such a pharynx can be extended through the oral aperture, and, spreading out, envelop its prey on all sides, as in a sheet. In the *Euryleptidæ* and *Prosthiostomidæ* among the *Polyclada*, and in all the *Triclada*, and in the *Monotidæ* among the *Alloiocœla*, this circular fold becomes a more or less extended cylindrical muscular tube, which projects freely into the equally cylindrical pharyngeal pouch from its base. By contraction of the circular musculature this tube elongates and passes out through the oral aperture (Fig. 102, *D*).

The relation of the pharynx plicatus to the pharyngeal sac is similar to that of the variously-shaped oral or gastric peduncle of the *Acraspede Medusa* to the subumbrellar cavity into which it projects.

The musculature of the Platode pharynx consists of one or more longitudinal and circular muscular layers, and of muscle fibres arranged radially round the axis of the pharynx.

All over the free surface of the pharynx, and chiefly at its free end, unicellular glands (salivary glands) open. These glands lie either in the pharynx itself, as in the pharynx bulbosus, which is sharply marked off from the parenchyma, or, as in the pharynx plicatus, scattered about in the parenchyma round the place of insertion of the pharynx. In the latter case they send only their long and thin processes (efferent ducts) into the pharynx.

The following is the rule for the position of the pharynx and the pharyngeal sac. When the mouth lies in the middle of the body the enteric aperture is found directly above it. The axis of the pharynx and its pouch then stand perpendicularly to the ventral surface. If the mouth lies to the front the enteric aperture lies behind it;

the free end of the pharynx is directed forwards and is extended forwards. The opposite is the case when the mouth lies behind the middle of the body. The generally narrow round enteric aperture leads out of the pharynx or pharyngeal pouch into the endodermal gastral system.

II. The **endodermal gastral system** must be separately described for the various divisions of the Platodes.

An **anus** is everywhere wanting, as in the Cnidaria.

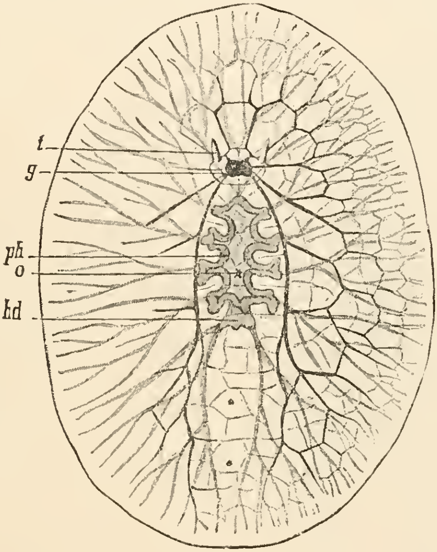

FIG. 103.—**Intestinal and nervous systems of the Planocera.** *t*, Tentacle; *g*, brain; *ph*, pharynx; *o*, mouth; *hd*, posterior end of the main intestine, the greater part of which is covered by the pharynx.

Turbellaria.

A. Polyclada (Fig. 103).—The gastral system here is very similar to that of the higher *Cnidaria* (*Medusæ* and *Ctenophora*). It consists of (1) the main intestine and (2) the gastro-canals or intestinal branches. The longer the body the longer is the generally spacious main or stomach intestine. Where the pharyngeal apparatus is found in the middle of the body, the main intestine lies just above it; where the pharynx lies behind, the intestine in almost every case is found in front of it. If the pharynx is placed in front the main intestine lies nearly always behind it. From the stomach intestine the gastro-canals arise in varying numbers. They perforate the body parenchyma, penetrating towards the edge of the body in a horizontal direction on all sides, and freely branching or anastomosing with each other on the way. Pairs of gastro-canals can be distinguished, and there is one unpaired canal. The paired are found in 4 pairs at least, and often, especially in long forms, in very numerous pairs. The unpaired canal runs forward from the front end of the stomach intestine in the middle line of the body.

In a few *Polyclada* the gastro-canals open on the dorsal surface of the body (*Yungia*) through pores, or else on the edge of the body (*Cycloporus*). In *Thysanozoon* diverticula of the intestinal branches run into the lobate processes of the dorsal surface.

B. Triclada (Fig. 104).—A distinction between main intestine and intestinal branches cannot here be made. Three gastro-canals start direct from the intestinal aperture; 1 unpaired, which runs forward in the median line and often possesses lateral offshoots which again branch, and 2 paired, which run backward at the sides of the pharyngeal pouch and give off lateral branches towards the exterior.

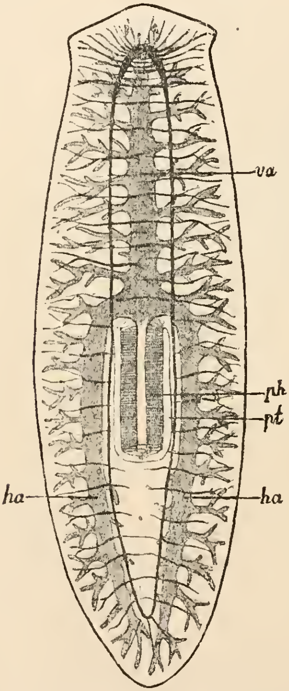

Fig. 104.—**Intestinal and nervous systems of a fresh-water Triclade.** *va*, Anterior median intestinal branch; *ha*, posterior intestinal branches; *ph*, pharynx; *pt*, pharyngeal pouch.

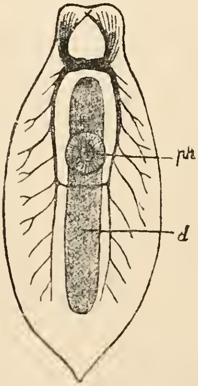

Fig. 105.—**Intestinal and nervous systems of Mesostoma (Rhabdocœle).** *ph*, Pharynx; *d*, intestine.

C. Rhabdocœlidæ.—The gastro-canal system is reduced to a simple sac-like or tubular intestine (Fig. 105), which runs in the middle line of the body. This occasionally (especially in the *Monotidæ*) has numerous short lateral diverticula.

In the so-called *Acœla* the alimentary canal is represented by a mass of star-shaped branched cells, in which no intestinal cavity can be demonstrated. Food enters this mass direct through the mouth or œsophagus; it has been described as "digesting parenchyma."

Trematoda.—The gastro-canal system of the **Trematoda** most resembles that of the *Triclada*. Since the mouth and pharynx lie to the front, the intestinal aperture leads into the anterior end of a short unpaired median portion of the intestine called the œsophagus; this soon splits into two forked branches which run backward (Fig. 106). In the broad leaf-shaped *Trematoda* to which most of the ectoparasitic forms and also the liver fluke belong, lateral branches, which again divide, run mostly outwards from these forked branches.

In certain forms (*Stichocotyle*, *Aspidogaster*) the intestine runs back as an unpaired median cæcum. When a median sucker is developed at the anterior end (oral sucker) the mouth lies in its base.

The intestinal epithelium of the *Turbellaria* is covered, over larger or smaller areas, with cilia. Intracellular taking in of food is very common in the *Turbellaria*. The musculature of the gastro-canal system is on the whole very feebly developed, and consists of longitudinal and circular fibres. In the *Polyclada* single circular muscle fibres succeed each other on the intestinal branches at regular intervals, so that in consequence of the constrictions thus formed the intestinal branches assume the aspect of strings of beads.

As an anus is wanting, the fæcal masses are emptied out through the mouth. The gastro-canal system of the *Turbellaria* may, besides the functions of digestion and circulation, also have a respiratory significance.

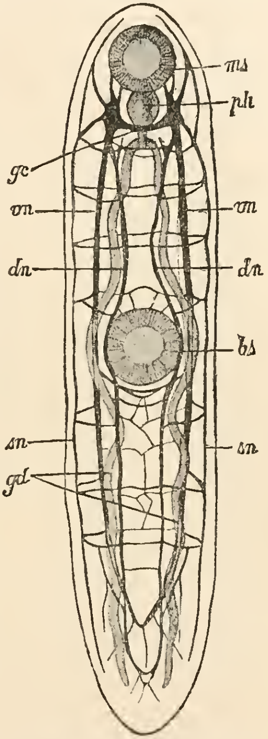

Fig. 106.—**Intestinal and nervous systems of Distoma isostomum (Trematode), after Gaffron.** *ms*, Oral sucker; *ph*, pharynx; *gd*, forked branches of the intestinal canal; *gc*, cerebral commissure; *dn*, dorsal longitudinal nerves; *sn*, lateral longitudinal nerves; *vn*, ventral longitudinal nerves; *bs*, ventral sucker.

V. Supporting Organs, Passive Organs of Locomotion.

These are in most soft and delicate Platodes little developed. In the *Turbellaria*, at least in the *Polyclada*, the basal membrane, which is resistant and tolerably firm and elastic, plays the part of a supporting membrane, to which the dermal musculature is closely applied, and in which the dorso-ventral muscle fibres are inserted. The same part is also certainly played by the cuticle of the *Trematoda* and *Cestoda*. Besides this, the more or less compact parenchyma lends the body a firmer structure and a greater consistency, like the gelatinous tissue in the *Cnidaria*.

VI. The Musculature.

The collective muscle elements of the Platodes may be brought into 2 chief groups: (1) the general body musculature, and (2) the special musculature of the organs, *e.g.* of the intestinal canal of the copulatory organs, etc. The latter cannot here be taken into consideration, as the musculature is adapted in every one of the extraordinarily numerous cases to the special activities of the organ.

The body musculature also is by no means so uniform throughout the race as to make a generally applicable scheme possible. It again falls into (1) the dermal musculature and (2) the dorso-ventral musculature. The first lies under the basal membrane of the integument or under the outer cuticle, the second runs transversely through the parenchyma between the various organs and connects opposite points of the basal membrane or the cuticle.

1. The **dermal musculature** is composed of layers, which are generally clearly separated. In each of these layers all the fibres run in a certain direction. We can distinguish longitudinal, tranverse, and diagonal fibre layers. The diagonal fibre layer is naturally always double. The longitudinal and the transverse layers may also be double. We find the largest number of layers—5 or 6—in the *Polyclada*; in the *Triclada* their number is smaller, we here find outer circular and inner longitudinal fibres, between which diagonal fibres may be intercalated. The same is the case in the *Rhabdocœlidæ*, in which the musculature is weaker than in any other *Turbellaria*. It is generally much weaker on the dorsal than on the ventral side, on which the animals creep. Certain dorsal muscle layers may be altogether wanting. In the *Turbellaria* the diagonal muscle layer seems always to lie between the others.

The sequence of layers in the dermal musculature of the *Trematoda* is as follows: the circular or tranverse muscle layer lies externally; then follows a strong longitudinal muscle layer; and inside comes the diagonal muscle layer. In the *Cestoda* the diagonal muscle layer is replaced by a strong inner circular muscle layer, lying pretty deep under the skin, and divided from the outer circular layer and the longitudinal muscle layer by a layer of parenchyma.

2. The **Dorso-ventral** or **Sagittal Musculature.**—Its fibres are branched at both ends (Fig. 47, *d*, p. 47), and run through the parenchyma from the dorsal to the ventral surface. Where intestinal diverticula are developed, the fibres naturally run between them as muscle septa, filling up the spaces. Where, as in the broad disc-shaped *Polyclada*, the ramifying intestinal branches of the stomach intestine radiate out towards the circumference on all sides, the septa project more or less far from the latter towards the former, and where

numerous pairs of lateral intestinal branches succeed each other more or less regularly, they are separated by equally regular muscle septa or dissepiments. This is the case in elongated *Polyclada* and *Triclada*, and especially in the marine *Triclada* (*Gunda*), in which the lateral intestinal diverticula are unbranched. In all cases, when sexual maturity is attained, the formation of septa is more or less obliterated by the development of male and female germ glands, which are generally placed between the intestinal branches.

VII. Organs of Adhesion.

These are very widely spread among the *Platodes*. One division of the *Polyclada*, that of the *Cotylea*, is characterised by the possession of a muscular sucker, which lies about the middle of the ventral surface, always behind the mouth and the genital apertures. By means of this sucker the *Cotylea* often temporarily attach themselves to some object on the sea bottom. Besides this, very many *Turbellaria* of the most various divisions, possess special adhesive cells with rough surfaces which serve for attachment.

In the parasitic *Trematoda* and *Cestoda* the organs for adhesion are specially strong and variously developed. They here serve to fasten the body either outwardly to the skin, or inwardly to the intestinal wall of the animal inhabited, or host. They are principally pit- and disc-like suckers, with or without stalks, whose number, form, and arrangement are of the greatest importance in classification. We select only the most important.

In the **digenetic Trematoda** there are at the most 2 pit-like suckers (Fig. 106), one of which, in whose base the mouth nearly always lies, is found at the front end of the body as oral sucker (*ms*). The other is either wanting (*Monostoma*), or lies at a variable distance from the anterior end on the ventral side (*bs*) (*Distoma*), or at the posterior end of the body (*Amphistoma*).

In the **monogenetic Trematoda** there are often 2 suckers or sucker-pits on each side of the mouth. Besides these, at the posterior end of the body, there is a very large stalked ventral sucker (*Tristoma*); or the hinder portion of the body becomes transformed into a large sucker-disc, which again may carry sucker-pits in varying numbers and in symmetrical or asymmetrical arrangements (*Polystoma*).

In the class of the *Cestoda* also the presence of suckers or sucker-pits is the rule (Fig. 117, p. 164). They here always lie at the foremost end of the body, singly (*Amphilina*), two in number (*Bothriocephalus*, *Schistocephalus*, *Triænophorus*), or four in number (*Tæniadæ*, *Tetrarhynchidæ*, *Tetraphyllidæ*). In the *Tetraphyllidæ* they often have long stalks.

As a further strengthening of the apparatus for adhesion there are often hooks, ridges, teeth, etc., as in the ventral suckers or on the adhesive discs of many monogenetic *Trematoda*, in the suckers of many

Tetraphyllidæ, or at the foremost end of the body, the apical cone, or rostellum of many *Tæniadæ*.

In the *Tetrarhynchidæ* at the foremost end of the body there are 4 proboscides furnished with barbed hooks, which can be protruded from special proboscis sheaths and withdrawn again by special muscular retractors.

VIII. The Nervous System.

The nervous system in the *Platodes* is completely detached from the body epithelium. Nearly all its elements lie in or close under the dermal musculature.

In the *Polyclada* (Fig. 103, p. 141) it consists of a close network of finer or coarser nerves, which is spread in or under the dermal musculature over the whole body, and which, like the musculature, is less developed on the dorsal than on the ventral side. In this plexus specially strong nerves occur, which, converging from all sides and thus growing thicker, unite in a nervous centre, the **brain**, which lies deep in the parenchyma under the anterior median intestinal branch between the middle and the front of the body. The more elongated the *Polyclada* are, the nearer the brain lies to the anterior end, and the more conspicuously do the longitudinal nerve trunks stand out among the nerves converging towards the brain. The most strongly developed of these longitudinal nerves are, in order of importance, 2 inner nerves, which run on both sides of the median line, 2 lateral and 2 dorsal. From the brain special nerves proceed to the sensory organs.

The brain in all *Polyclada* (with one single exception) lies in front of the mouth. Only in *Oligocladus* (*Euroleptidæ*) does it lie behind the mouth over the beginning of the pharyngeal pouch. The two inner longitudinal trunks in this genus embrace the front end of the pharyngeal pouch, and are connected only behind the same by means of a web of commissures. The brain, the first part of the longitudinal trunks, and the first transverse commissure between these, thus form together a ring which surrounds the anterior portion of the pharyngeal pouch.

In the *Triclada* (Fig. 104, p. 142) the brain always lies far forward. The ventral inner longitudinal trunks are always specially strongly developed, and are on the one side connected together by a web of commissures, and on the other give off anastomosing branches outwards. In *Gunda* both the branches which proceed outwards and the commissures are very simple and regular, and correspond in number with the successive pairs of lateral branches of the intestine. We thus have here a typical ladder nervous system.

In the *Rhabdocœlidæ* (Fig. 105, p. 142) we generally meet with the nervous system in a simpler form. It consists of the brain, which lies in the anterior portion of the body, and, proceeding from it, of the two ventral longitudinal nerves, and of several smaller nerves which spread out in the anterior part of the body. Commissures between the longitudinal nerves appear in larger numbers only in the *Monotidæ* among the *Alloiocœla*, which show near relationship to the *Triclada* in other points also. In *Mesostoma Ehrenbergii* there is a tranverse commissure behind the pharynx; in *Microstoma lineare* two other nerves besides the longitudinal nerves proceed backwards from the brain, surround the pharynx, and unite behind it.

In the *Acœla*, according to earlier investigators, a nervous system was wanting; but lately a somewhat complicated nervous system has been proved to exist. It consists of 2 ganglia lying one behind the other in the anterior part of the body (the front ganglion being the smaller), and six longitudinal nerves, 2 inner, 2 middle, and 2 lateral which run along the edge of the body. The 2 inner arise from the posterior ganglion, the 2 middle and the 2 outer from the front ganglion. All these 6 nerves are connected by transverse commissures which go off at right angles and themselves again anastomose.

The nervous system of the *Trematoda* (Fig. 106, p. 143) is closely connected with that of the *Triclada* and *Polyclada*. It consists of a brain, from which proceed, besides small nerves which run to the sides and the front, 6 nerve trunks running backwards, viz. 2 dorsal, 2 inner ventral, and 2 outer ventral or lateral. The 2 ventral are connected together and with the lateral by more or less numerous transverse commissures, as are the lateral with the dorsal, and the dorsal again together; these tranverse commissures may again anastomose with each other.

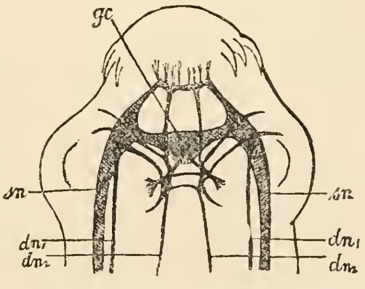

Fig. 107.—**Nervous System in the Scolex of a Tapeworm (Tænia serrata)** after Niemic. Of the 8 weaker longitudinal nerves only the 4 on one side (dn_1, dn_2) are depicted. *sn*, Lateral nerves; *gc*, chief or cerebral commissure.

The nervous system assumes this form especially in ectoparasitic *Trematoda* (*Tristoma*) and in *Distoma isostomum*. In many other *Trematoda*, however, perhaps in most species of *Distoma*, the commissural system appears to have degenerated; and of the 6 longitudinal nerves only the inner ventral nerves seem to be strongly developed, as in the *Rhabdocœla*.

The brain lies above the mouth in all *Trematoda*; when the mouth is placed in the pit of the oral sucker, the brain extends as a transverse bridge over the front part of the pharynx.

The nervous system of *Amphilina* quite agrees with that of the *Distomidæ*.

The nervous system of the typical *Cestoda* (Fig. 107) consists of two lateral longitudinal trunks, which pass through the whole body and are connected by means of a chief commissure (brain commissure) at the foremost end in the scolex. There are generally several more besides, often 8 longitudinal nerves, which, however, do not stretch backwards beyond the scolex, and further other nerves, which proceed to the suckers, the hooks, and in the *Tetrarhynchidæ* to the 4 muscular proboscides, etc. Apart from the brain commissure, all these nerves in the scolex are connected together in a complicated way by circular square, polygonal, or cross-shaped commissures. In the segments (proglottides) no commissures between the longitudinal trunks have yet been observed.

The brain (cerebral ganglion, cerebral commissure) of the Platodes is not to be considered exclusively as a central nervous system, since more or less numerous ganglion cells exist in the larger nerve trunks also, at those points where the nerves and commissures branch off. Thus the ganglion cells in many *Triclada* are found in the ventral longitudinal trunks of the ladder nervous system, principally at the points of departure of the transverse commissures. We are thus led to conjecture that the double ganglia of the ventral ganglionic chain of the *Vermes* have proceeded from these points in a ladder nervous system.

The nervous system of the Platodes is in our opinion of the greatest significance from the point of view of comparative anatomy, because it joins on to that of the *Cnidaria* on one hand, and on the other is, in many groups, modified in a direction which points to the nervous system of the *Vermes*, and also perhaps of the lowest Molluscs. If we consider the matter without prejudice the following seems characteristic of the nervous system of the *Turbellaria* and *Trematoda*. (1) The arrangement of the nervous system in the form of a nerve plexus all over under the skin, dorsally as well as ventrally, in close connection with the musculature which has to be innervated. In this condition we recognise a great similarity to the higher *Cnidaria*. (2) The development of a central organ (brain). We have seen in the *Cnidaria* that nerve centres are formed in close connection with the sensory organs, which is comprehensible *a priori*, since it is in the nerve centres that the junction of the sensory nerves with the motor nerves or nerve fibres takes place. Now the finer structure of the brain of the Platodes shows, most unmistakably, that the brain is nothing more than a specially developed part of the nerve plexus, in which motor and sensory nerves unite. The sensory organs become, in connection with the development of bilateral symmetry, more and more localised in the anterior end of the body, *i.e.* in the end which goes first in creeping; and therefore the centralised nerve plexus (or in other words the brain), in which the motor and the sensory fibres unite, must, following the sensory organs, shift more and more towards the anterior end of the body.

In *Acœla* we find 2 cerebral centres; in *Cestoda* the many often very complicated commissures between the nerves in the scolex must collectively be considered as the brain; in certain land *Triclada* the only part which can be called the brain is a not very sharply demarcated tract of the longitudinal trunks at the anterior end of the body, in which the transverse commissures lie specially crowded together, and into which also the sensory nerves enter.

Bearing in mind the fact that in the *Ctenophora*, in *Cœloplana*, and in *Ctenoplana* the sensory body is developed in the middle of the dorsal surface, we must consider this as the original position of the brain. As a necessary result of the development of this central portion, the peripheral nerves, the nearer they approach to this part, unite into increasingly massive trunks, which finally enter the brain. In consequence of the position of the brain at the anterior end of the body, the nerves proceeding backward are always the thicker nerves, while the lateral and front nerves are the shorter and thinner. The greater development of the musculature on the creeping surface has as a consequence the greater development of the ventral trunks. The elongation of the body further causes a retrogression of the outer longitudinal nerve trunks, so that finally the 2 inner longitudinal trunks remain as the main trunks, which from the first are very strong, since they have to innervate the most important muscular organs which lie in the median line between them (pharynx, copulatory apparatus, suckers). Thus in the end the regular ladder nervous system of *Gunda* is deducible from a general nerve plexus in the integument, determined by the elongation of the body, the localisation of the sensory organs at its anterior end, and the strong development of the musculature on the ventral surface.

The brain in the Platodes appears the more evidently to consist of 2 lateral halves or ganglia connected by a bridge of fibres, the more strongly the 2 longitudinal trunks of the nervous system are developed in comparison with the whole nervous system.

IX. The Sensory Organs.

The Platodes possess sensory organs, which according to their structure may be described as eyes, auditory organs, or organs of touch. To these belong also ciliated pits, whose function is unknown. Many consider them to be olfactory organs. The development of the sensory organs stands in direct relation to the mode of life. They are best developed in the free-living *Turbellaria*. In the parasitic *Tremadota* their degeneration begins, and the *Cestoda* no longer possess any specific sensory organs.

A. Eyes.

These are found in most *Turbellaria* and ectoparasitic *Trematoda*. They are wanting in adult endoparasitic *Trematoda*, but, on the other hand, are found in their young stages, which are free-living, at least for a time.

All *Polyclada* possess eyes in large numbers, often as many as several hundreds. In their arrangement the following points are worthy of note. A group of eyes is always found above the brain and in the tentacles. Many forms possess, besides these, other eyes at the anterior margin of the body or all round the margin. In the *Triclada* there are either 2 eyes near the anterior end, or numerous eyes along the margin of the whole body, or along its anterior margin. In the *Rhabdocœlidæ* there are generally 2 or 4 eyes (less frequently one unpaired eye) directly on or over the brain; this is also the position of the 4 eyes of the ectoparasitic *Trematoda* and the 2 eyes of the free-living larvæ of the endoparasitic *Trematoda*.

In all the Platodes (except the *Acœla* and *Microstomidæ*) the eyes lie under the epithelium in the parenchyma; in the *Rhabdocœla* and *Trematoda* directly on or in the brain. Yet in the case of the *Polyclada* at least, it can be ontogenetically proved that the eyes at their first appearance arise in the ectoderm of the embryo and only secondarily sink below the surface.

The eyes are simple pigment spots in many *Rhabdocœlidæ*; in others a refractive body is added. The eyes of the *Triclada*, *Polyclada*, and ectoparasitic *Trematoda* are somewhat more complicated. They consist of a pigment cup (often unicellular), at whose aperture lie one or more nerve or retinal cells as perceiving elements. In the cavity of the eye-cup lie homogeneous non-nucleated rods or clubs, apparently processes of the retinal cells. A fine optic nerve is connected with the group of retinal cells. In the *Polyclada*, where there are numerous eyes, the sensory nerves from the brain branch, sending a single branch to each eye.

B. Auditory Organs.

These are not widely spread among the Platodes. They are only found in the *Rhabdocœlidæ*, and there almost exclusively in the division of the *Acœla*, and among the *Alloiocœla* in the family of the *Monotidæ*. They are always found singly, and lie on the brain, and consist of a small spherical vesicle filled with fluid; an otolith or auditory stone (composed of carbonate of lime and an organic substratum) is also enclosed in this vesicle.

C. Organs of Touch.

These are universal in the *Turbellaria*. In the first place the skin is everywhere very sensitive. This sensitiveness is caused by the presence of delicate tactile hairs or tufts of immobile tactile hairs, which are found in great numbers principally at the exposed parts of the body, especially at the anterior edge and on the tentacles. The tentacles may be considered in a special manner to be organs of touch; they are present in very many *Polyclada*, but less frequently in *Triclada* and *Rhabdocœlidæ*. In the *Polycladan* family of the *Planoceridæ* we find on the dorsal surface, between the middle and the anterior end, two lateral, mobile, stylet-shaped, solid tentacles (Fig. 103, *t*, p. 141), which can occasionally be withdrawn into temporary depressions of the skin. They may be directly compared with the tentacles of *Cœlo-* and *Ctenoplana*, but are distinguished from these and from the contractile tentacles of the *Ctenophora* (1) in that they have moved from the middle of the back more or less far towards the front, and (2) in that they have no lateral branches. In the *Pseudoceridæ* and *Euroleptidæ* there are at the anterior edge tentacular folds of the leaf-shaped body, into which branches of the intestine generally penetrate. In a few *Triclada* also, and in *Vorticeros* among the *Rhabdocœlidæ*, feeler-like projections or thickenings at the anterior margin of the body have been described.

The so-called proboscis is a highly developed specific organ of touch which distinguishes a *Rhabdocœlan* family, the *Proboscidea*. The anterior end of the body of many *Turbellaria* is very retractile; in *Mesostoma rostratum* it can be telescopically withdrawn and protruded. The permanent arrangement in the *Proboscidea* can be deduced from such a condition. The proboscidal apparatus of such an animal consists of an invagination at the anterior end of the body, on to which the outer epithelium is continued. This invagination can be evaginated and again withdrawn by means of special retractors. The invagination, as well as the retractors which are inserted in it, are surrounded by a sac-like muscular integument, by whose contraction the proboscis is protruded. Fig. 108, *A*, *B*, *C*, represents the proboscis in various stages of protrusion. The whole apparatus shows in every detail a similarity which cannot be ignored to the 4 proboscides of the *Tetrarhynchidæ* and the proboscis of the *Nemertina* to be described later.

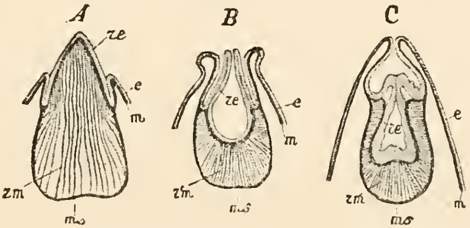

Fig. 108.—**Proboscis of Macrorhynchus croceus.** *A*, In a protruded condition; *B*, half protruded; *C*, withdrawn (after **v. Graff**). *re*, Proboscis epithelium, which is a continuation of the body epithelium (*e*); *ms*, muscular envelope which divides the proboscis from the body parenchyma; *m*, dermal muscle layer; *rm*, muscles for withdrawing the proboscis.

In the *Trematoda* the sensation of touch seems specially localised in the suckers.

D. Ciliated Pits.

In certain *Rhabdocœlidæ*, viz. in the *Microstomidæ*, *Prorhynchidæ*, and *Plagiostomidæ*, there are 2 paired strongly ciliated integumental pits which lie laterally on a level with the brain, and are supplied with a nerve ring by the brain. They have been regarded as olfactory pits. In the *Triclada*, also, similar strongly ciliated parts of the epithelium of the end of the head have been observed, to which special sensory nerves proceed. In *Bipalium*, a land *Triclad*, there are pits supplied with special nerves in large numbers at the anterior margin of the body which is broadened out in the shape of a crescent. Whether the ciliated furrow which in all *Polyclada* runs along the anterior margin of the body in the epithelium of the ventral side belongs to the formation here described cannot yet be decided.

X. The Body Parenchyma (Reticulum).

The whole space between the body wall and the gastro-canal system, as far as it is not filled by specific organs, is occupied by a cellular connective tissue, the details of whose structure are very various. This connective tissue, which corresponds with the gelatinous tissue of the higher *Cnidaria*, is called parenchyma or reticulum. It often becomes finely lacunar by the formation of many vacuoles filled with fluid. The lacunæ may coalesce in sinuses which conduct fluid, which, however, generally remain small; but in a few *Rhabdocœla* they become large hollow spaces filled with a perivisceral fluid. In such cases the body parenchyma can assume the constitution of a membrane, covering the inner organs like an epithelium. In the *Acœla*, where there is no parenchyma separate from the intestine, the former, composed of star-shaped cells filling the whole body apart from the specific organs, may be described as **digesting parenchyma.**

XI. The Excretory or Water-vascular System.

This is very characteristic of the Platodes, and as yet has been found to be wanting only in the *Acœla* among the *Rhabdocœlidæ*. It consists of a system of very fine transparent canals (excretory capillaries) which branch out in the parenchyma and between the muscles, and which enter into a system of wider, equally transparent canals, which open externally in various ways. In the formation of the extremely thin walls of the capillaries only a few cells take part, so that the nuclei lying in the wall occur at long intervals, and in a transverse section of a canal the wall enclosing the central lumen belongs to a single cell. The capillaries thus represent perforations of linear rows of cells, and are described as intracellular. The wider canals, on the other hand, in the *Cestoda* at any rate, appear lined by a thin epithelium, and are thus intercellular. The blind end of each excretory capillary is formed by one cell (Fig. 109), which possesses fine protoplasmic processes running into the parenchyma. In this cell, which, on the surface turned to the lumen of the capillary, carries a tuft of fine vibrating cilia (the flame) projecting into the lumen, excretory products (drops, granules, etc.) collect and are emptied out of the cell into the capillary. The excretory products are forwarded out of the capillaries into the wider vessels partly by the motion of the above-mentioned cilia, and partly perhaps by the independent contractions of the canals, and thence reach the exterior. Sometimes also in the lateral walls of the capillaries and larger canals flames are found which belong to the excretory cells in those walls. The larger canals sometimes have a continuous lining of cilia. It is not impossible that the greater part of the transparent fluid which fills the canals is water taken in from outside. If so, it is occasionally emptied out and again taken in. In this way the water-vascular system may also perform a respiratory function.

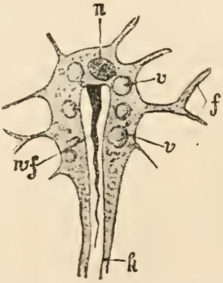

FIG. 109.—**Excretory cell at the end of a fine excretory canal** (*k*) **of a Turbellarian.** *n*, Nucleus; *v*, vacuole; *f*, processes of the cell; *wf*, flame.

The whole water-vascular system shows a decided similarity to a greatly developed dermal gland which has sunk deep under the skin, as is often the case in the Platodes (dermal mucus glands, rod glands, accessory glands of the copulatory apparatus). The excretory cells must then be considered as glandular cells, and the canals as glandular efferent ducts. We can actually regard the water-vascular system as a dermal gland, which has undertaken the special function of excretion. In consequence of the strong development of the parenchyma, and especially of the middle layer of the body, and because of the absence of a body cavity, this gland is obliged to search for the products of excretion all over the body—hence its great ramification.

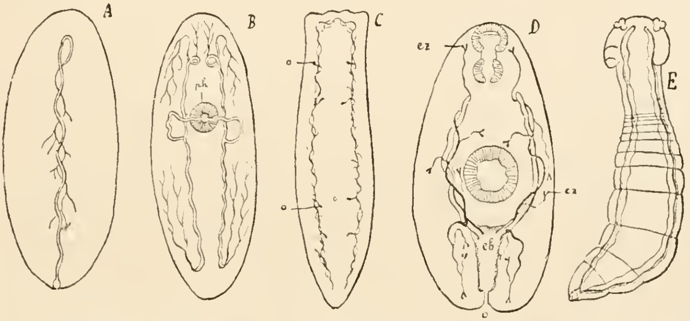

FIG. 110.—**Water-vascular system of various Platodes.** *A*, of **Stenostoma**; *B*, of **Mesostoma**, after **v. Graff**; *C*, **Dendrocœlum**, after **Ijima**; *D*, **Distomum divergens**, after **Fraipont**; *E*, **Phyllacanthide**, after **Pintner**. *ph*, Pharynx; *o*, external aperture; *ez*, excretory cells (terminal cell); *eb*, contractile vesicle.

Concerning the arrangement of the principal canals and their external apertures (Fig. 110) the following is noteworthy.

We have no sufficient information as to the water-vascular system of the *Polyclada*.

In the *Triclada* (Fig. 110, *C*) a main canal runs on each side of the body (*Gunda* has two such canals on each side, a ventral and a dorsal, bound together by canals), and these open externally on the dorsal side of the body by means of somewhat numerous special branches and excretory pores placed one behind another. These pores are arranged pretty regularly, in *Gunda* at least, and correspond in number with the lateral intestinal diverticula—the transverse commissures of the nervous system,—in short with the number of those organs which are regularly paired from one end of the body to the other.

In the *Rhabdocœlidæ* we can distinguish 3 principal types.

A. There are 2 lateral principal vessels, which have separate external openings on the ventral side, either (*a*) at the middle or the front part of the body by special branches opening externally direct (*Prorhynchidæ*), or (*b*) by 2 cross branches which enter the pharyngeal pouch (Fig. 110, *B*, *Mesostomidæ*, *Vortex?*), or (*c*) direct by two openings lying at the posterior end of the body.

B. There are 2 longitudinal trunks which open externally at the posterior end of the body by means of a common terminal piece (many *Vorticidæ*, *Proboscidea*).

C. There is a single median principal branch with an opening at the posterior end of the body (*Stenostoma* among the *Microstomidæ*, Fig. 110, *A*).

In the *Trematoda* also we find typically 2 longitudinal trunks which open externally, either together through a common contractile terminal vesicle of very varying size at the posterior end of the body (digenetic *Trematoda*, *Distoma*, *Monostoma*, Fig. 110, *D*), or separately, anteriorly and dorsally, by means of 2 widened terminal portions.

In *Distoma hepaticum* there is a wider and larger median longitudinal trunk, which stretches pretty far forward, and into which collecting canals enter from all sides. The external aperture lies at the extreme posterior end of the body.

In the *Cestoda* (Fig. 110, *E*) in the simplest cases there are on each side 2 longitudinal trunks running through the whole body, which are united anteriorly in the scolex by a loop. At the extreme posterior end of the body (at the end of the oldest segment) all the four branches open outwardly by means of a contractile vesicle (*Tæniadæ*, *Tetrabothridæ*, *Tetrarhynchidæ*). In the *Bothriocephalidæ*, *Caryophyllidæ*, and *Ligulidæ* the number of longitudinal trunks is increased to from 10 to 24, which anastomose in a definite way. A contractile terminal vesicle, into which all the longitudinal trunks enter, occurs only in the end of the oldest segment of the tapeworm; in all other segments, after successive detachments of the older segments, the longitudinal trunks open outward directly and independently; some of them, however, may close, and thus end blindly. We have an apparent exception to this rule in *Tænia cucumerina*, in which, as segments detach themselves behind, a new contractile terminal vesicle is always formed in the next segment. In many *Cestoda*, besides the terminal apertures of the water-vascular system, special secondary openings have been observed, generally in great numbers. These are canals, which proceed at right angles from the main canals and open outward through pores. These secondary exits are generally found only at the front end of the body, in the scolex (in *Triænophorus*, many *Tæniæ*, and *Tetrarhyncha*), less frequently in the proglottides also (*Bothriocephalus punctatus* and a few other forms).

The larger canals show a tendency towards the formation of islands in very many Platodes, and especially in the *Cestoda*. They then break up into a more or less complicated anastomosing network. It is probable that the numerous longitudinal trunks bound together by anastomoses in the above-named *Cestoda* have proceeded from a few (4) longitudinal trunks by the formation of islands.

XII. The Sexual Organs.

All Platodes, with the exception of the genera *Microstoma* and *Stenostoma* among the *Rhabdocœla* and of *Distoma hæmatobium* among the *Trematoda*, are hermaphrodite. The male sexual products, however, almost universally develop before the female—a phenomenon which has received the name of protandrous hermaphroditism. Both male and female sexual apparatus consist (1) of places of formation of the sexual products which are imbedded in the body parenchyma (**ovaries** and **testes**), (2) of special canals, **efferent ducts**, which conduct the sexual products away from the places where they were formed to (3) the outer **copulatory apparatus**. We will describe these three parts in succession.

A. The Places of Formation of the Sexual Products.

1. **The Female Germ Glands.**—We meet with these in the Platodes in two forms. First, and this is the simpler and no doubt also the older condition, as simple **ovaries**, in which the egg germs ripen into eggs, in whose protoplasm particles of deutoplasm or nutritive yolk occur. Secondly, and this is the derived condition, in the double form of **germaria** and **vitellaria**. The germaria yield the egg germs, *i.e.* the young egg cells. The vitellaria, however, have undertaken the work of supplying these egg cells with the nutritive yolk which is necessary for their further development. Comparative research has shown that the vitellaria are not newly formed accessory glands of the female sexual apparatus, but that they are metamorphosed ovaries or portions of ovaries adapted to a special function. It need not be pointed out that the germaria are ovaries.

In the *Polyclada* there are only ovaries and no vitellaria. The ovaries (Fig. 24, *D*, p. 29) are roundish bodies whose structure exactly corresponds with that of the female gonades of the higher *Cnidaria*. They lie in great numbers (Fig. 111, *o*) on and between the intestinal branches or gastro-canals in the lateral parts of the body.

In the *Triclada*, besides a few eggs in the discharged egg cocoons, there are extraordinarily numerous yolk cells, which serve to nourish the former. Light is thrown on this phenomenon by the fact that in certain *Polyclada* and *Mollusca* several eggs may be deposited in one cocoon, of which, however, only some develop; the others sooner or later become disorganised and serve as food for the former. Thus perhaps the yolk cells in the *Triclada* cocoon may be considered as modified egg cells, which develop no further, but serve as food for the few fertilised egg cells which do develop. Division of labour, therefore, has stepped in among the germ-preparing organs, the ovaries; some yield eggs capable of fertilisation and development; others yield modified egg cells laden with yolk, which serve as food for the above, and are no longer capable of fertilisation and development. The first are the germaria (Fig. 112, *ks*), the second the vitellaria (*ds*). These two are homologous structures, and in a young condition look quite alike. In consequence of the large number of yolk cells which are given to the eggs, the vitellaria are far more numerous than the germaria, of which only 2 remain; but as these have only to yield eggs without yolk, they are quite sufficient in number. They generally lie at the anterior end of the body, whilst the vitellaria always occur in the lateral parts of the body between the intestinal branches.

In the *Rhabdocœlidæ* the germ-preparing organs are considerably reduced in number, but on the other hand are, in relation to the body, much larger than the single ovaries of the *Polyclada.* Many forms possess ovaries only. The *Acœla*, and the *Macrostomidæ* among the *Rhabdocœla*, have 2 lateral ovaries, the *Microstomidæ* only 1 ovary. In many *Rhabdocœlidæ* so-called **germ-vitellaria** attain development, one often clearly separated portion of the ovary yielding only egg germs, the other only yolk.

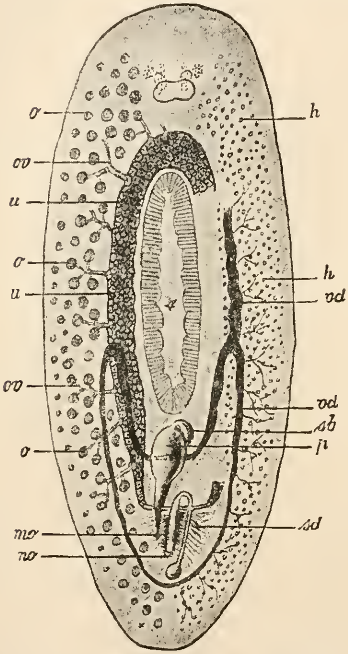

FIG. 111.—**Sexual organs of a Polyclad (Leptoplana).** To the left only the female, to the right only the male organs are depicted. *o*, Ovaries; *ov*, oviduct; *u*, uterus; *h*, testes; *vd*, vasa deferentia; *sb*, seminal vesicle; *p*, penis; *sd*, shell gland; *mo*, male sexual aperture; *wo*, female aperture.

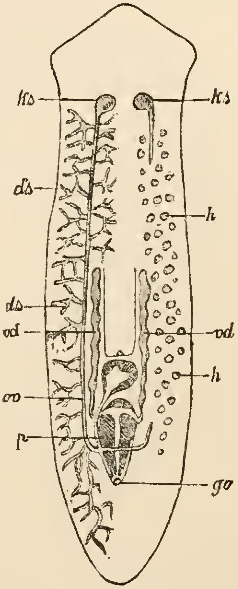

FIG. 112.—**Sexual organs of a fresh-water Planarian (Triclad).** *ks*, Germaria; *ds*, vitellaria; *h*, testes; *ov*, oviduct; *vd*, vasa deferentia; *p*, penis; *go*, common external genital aperture.

One single germ-vitellarium is found in the *Prorhynchidæ. Proxenetes* among the *Mesostomidæ*, *Schultzia* among the *Vorticidæ*, and *Cylindrostoma* among the *Plagiostomidæ* possess two.

In the greater number of *Rhabdocœla* and *Alloiocœla*, however, there is a complete separation into germaria and vitellaria. The germaria are mostly small and round, the vitellaria (*ds*) are large, often lobate, branched or reticulate. The vitellaria are generally double; where they are single reticulate branched masses, their originally double condition can be recognised by the duplication of their efferent ducts. The germarium is either double or single.

One germarium is found in most *Mesostomidæ*, *Gyrator* among the *Proboscidea*, most *Vorticidæ*, and *Solenopharynx*. Two are found in *Promesostoma*, most *Proboscidea*, *Provortex* and *Graffilla* among the *Vorticidæ*, and the *Alloiocœla*.

Separate germaria and vitellaria are found in all *Trematoda* and *Cestoda*. The germaria (Figs. 114 and 115, *ks*) are either simply round, or lobed, or branched. The vitellaria (*ds*) are mostly (excepting in the *Tæniæ*) very extensive, and branched in a reticulate manner, or else broken up into a large number of small globular bodies or saccules.

The *Trematoda* possess a median germarium and 2 lateral vitellaria, the *Cestoda* 2 germaria and either 2 lateral vitellaria or a small posterior vitellarium (*Tæniæ*).

II. **The male germ elements** or **testes** are present in the *Polyclada* (Fig. 111, *h*) in greater numbers than the ovaries. They always lie in the lateral parts of the body between and under the intestinal branches. The same holds good of the numerous testes of the *Triclada* (Fig. 112, *h*). In *Gunda segmentata* the testes lie on each side in a single longitudinal row in the dissepiments which separate the consecutive intestinal branches. They thus repeat themselves in the body just as regularly as do the intestinal branches, dissepiments, transverse commissures of the nervous system, and the external apertures of the water-vascular system. In the *Rhabdocœlidæ* there are either 2 testes (Fig. 113, *h*, *Rhabdocœla*), or the testes are broken up into numerous lobes or vesicles, which are scattered in the parenchyma (*Acœla*, *Alloiocœla*). Nearly all *Trematoda* (Fig. 114, *h*) possess 2 round, or lobed, or branched testes, while in the *Cestoda* (Fig. 115, *h*) there are numerous scattered testicle vesicles.

B. The Efferent Ducts of the Sexual Products.

The Female Ducts.—The female sexual glands are produced into tubular ducts, which collect the sexual products and carry them to the exterior. The ducts are either egg ducts (oviducts) when they proceed from the ovaries or germaria, or yolk ducts (vitello-ducts) when they carry out material formed in the vitellaria. The anatomy of this part is so varied that we can only select the most important points.

In the *Polyclada* (Fig. 111) numerous oviducts (*ov*) proceed from the numerous ovaries. These ducts frequently unite to form larger ducts, which again enter more spacious tubes, generally running in the longitudinal direction on both sides of the middle line. Numerous eggs collect in these tubes, which are called **egg receptacles** or uterus tubes (*u*). As they enter the female copulatory apparatus they unite in an unpaired terminal portion, the **egg passage,** into which the thread-like efferent ducts of the numerous glands (*sd*) which are imbedded in the surrounding parenchyma open. The glands whose hardening secretions yield the egg shell which covers the egg or eggs are collectively known as the **shell glands.** They occur almost universally in the Platodes.

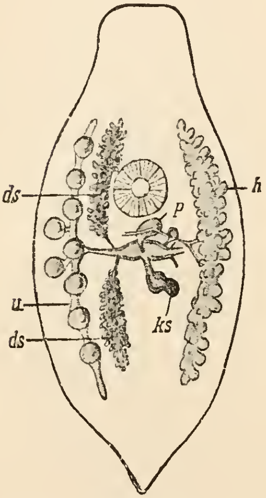

Fig. 113.—**Sexual organs of a Rhabdocœle (Mesostoma Ehrenbergii).** To the left the testis is omitted; to the right the vitellaria and the uterus are left out. *h*, Testis; *ds*, vitellaria; *u*, uterus; *p*, penis; *ks*, germarium.

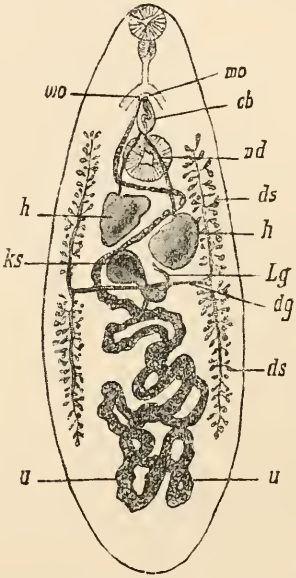

Fig. 114.—**Sexual organs of a Trematode (Distoma),** after **Leuckart.** *h*, Testes; *ks*, germarium; *u*, uterus; *ds*, vitellarium; *dg*, yolk or vitelloduct; *vd*, vasa deferentia; *Lg*, Laurer's canal; *cb*, cirrus pouch; *mo*, male, *wo*, female sexual aperture.

In the *Triclada* (Fig. 112) there are 2 lateral longitudinal oviducts (*ov*), which conduct the eggs from the 2 germaria in the front of the body backwards to the copulatory apparatus. Apertures are found on. the way, through which the vitellaria empty their products into them. Before passing out into the copulatory apparatus they unite to form a short unpaired egg passage, into which the efferent ducts of the shell glands open.

In the *Rhabdocœlidæ* (Fig. 113) the female sexual glands are generally placed with their ends directly on the outer copulatory apparatus, and open into it. There is often a union of the vitellaria and the germaria before their exit into a common terminal portion. The shell glands open either into the outer copulatory apparatus, or into a special fold of the same into which eggs and yolk are conducted, and which will here be called the uterus. In the *Acœla* and *Alloiocœla* no definite connection between the germ glands and the copulatory apparatus can be demonstrated. The sexual products here make their way through the parenchyma to the copulatory apparatus.

In the *Trematoda* (Fig. 114) an oviduct proceeding from the ovarium is found, then two yolk ducts (*dg*) which collect the yolk from the two lateral vitellaria. The oviduct and the yolk ducts together enter an unpaired canal which we shall call egg passage. This passage falls into 2 parts—one small part at the beginning, the **ootype**, into which the 3 ducts mentioned enter, and a long, generally coiled portion, the **uterus** (*u*), leading from the ootype to the female genital aperture. The ootype receives the efferent ducts of the shell glands. Fertilisation takes place here, and also the union of the yolk with the egg; and here a shell is formed round the fertilised egg. The ootype has an exit either in the dorsal or the ventral surface of the body through one more canal, **Laurer's canal** (*Lg*), through which, probably, in copulation, the sperm reaches the ootype from outside. The fertilised eggs pass from the ootype into the uterus, where they often collect in enormous numbers, at least in the *Distomidæ*. The uterus in these animals is consequently very long, and runs to the female copulatory apparatus in numerous coils, which in the adult often fill the greater part of the body.

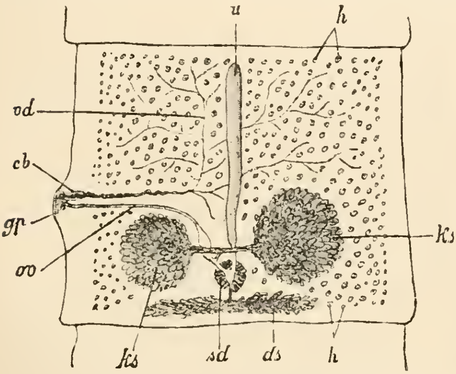

Fig. 115.—**Sexual organs of Tænia saginata (medio-canellata), after Sommer.** *h*, Testes; *vd*, vasa deferentia; *cb*, cirrus pouch; *gp*, genital pore; *ov*, oviduct; *ks*, germaria; *sd*, shell glands; *ds*, vitellarium; *u*, uterus.

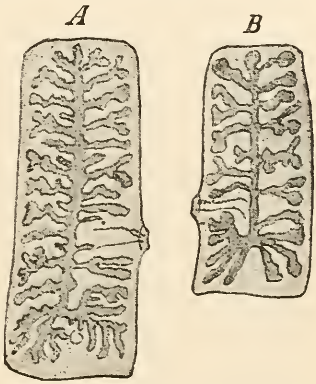

Fig. 116.—**Fully ripe proglottides (segments).** *A*, **Of Tænia saginata**; *B*, **of Tænia solium.** The dendriform figure represents the uterus.

The *Cestoda* (Fig. 115) are closely allied to the *Trematoda*, especially in forms in which, as in *Bothriocephalus*, the sexual apertures lie on one of the surfaces, and in which there are 2 lateral vitellaria. The collecting passages of the vitellaria unite in such forms into

2 yolk ducts, which, as well as 2 oviducts, enter the ootype by a common terminal piece, into which the efferent ducts of the shell glands open. From the ootype a canal proceeds to the copulatory apparatus (*ov*) on one side, and on the other side arises a widened uterus filled with eggs (Fig. 115, *u*; Fig. 116) running in coils, or provided with lateral sacs; this uterus often reaches the exterior by a special aperture which recalls Laurer's canal in the *Trematoda*. Where there is only one vitellarium, only one yolk duct naturally enters the ootype (as in Fig. 115).

II. **Male ducts.**—In the *Polyclada* numerous very fine canalicules enter the larger **semen ducts, vasa deferentia** (Fig. 111, *vd*), in which the spermatozoa collect, and these canals again have their exit in the male copulatory apparatus (*p*). The fine canals correspond to the oviducts, the wider ones to the uterus of the female sexual apparatus. In the *Triclada* there are 2 lateral vasa deferentia (Fig. 112, *vd*), into which some at least of the testes empty their contents direct, while the manner in which the testes which are at a greater distance from the vasa deferentia empty themselves is not yet fully understood.

In the *Rhabdocœla* (Fig. 113) the 2 testes are often continued without any sharp demarcation into 2 semen ducts which enter the male copulatory apparatus either separately or by means of a common terminal portion. In the *Acœla* and most *Alloiocœla* special ducts are wanting; the spermatozoa reach the copulatory apparatus through the parenchyma. Only in the *Monotidæ* among the *Alloiocœla* the transmission takes place by means of special ciliated vasa deferentia. The two testes of the *Trematoda* (Fig. 114) send out two semen ducts (*vd*) which unite into one common duct. In the *Cestoda* also (Fig. 115) many of the numerous canalicules proceeding from the testicle vesicle enter a common vas deferens leading to the male copulatory apparatus.

C. The Copulatory Apparatus.

There is wonderful variety in the structure and position of the copulatory apparatus in the Platodes. Nearly related species often differ greatly in this point.

I. **The male copulatory apparatus** is always more complicated in structure than the female. It consists in the simplest cases of a muscular pouch which projects from the surface into the parenchyma, and into whose blind end, which is directed inwards, the semen duct, or ducts, enter. It is found in this form in certain *Rhabdocœlidæ*. In most *Turbellaria*, however, it becomes complicated, and then we can generally distinguish the following distinct portions: (1) a **penis sheath** or **penis pouch**, (2) the actual **penis**, (3) a **seminal vesicle**, and (4) a **granular gland.** The penis and penis sheath show a structure which is on the whole like the structure of the pharyngeal apparatus described above. The penis is, in fact, a muscular circular fold which projects into the penis sheath from its wall in a manner similar to that in which the pharynx projects into the pharyngeal pouch. As the pharynx is protruded out of the pharyngeal pouch through the mouth, so is the penis protruded through the sexual aperture. During copulation the wall of the penis sheath also is pushed out or evaginated. The penis sheath is occasionally double, or there are several sheaths, each of which is related to the one outside it as the penis is to the penis sheath, and the whole apparatus may be telescopically extended and protruded. The penis is sometimes conical, sometimes cylindrical, sometimes bent, either naked or armed in various ways. Its free end is often a hard chitinous tube. Between the penis on the one side and the terminal portion of the semen duct on the other, there is a vesicular expansion with muscular wall, the **seminal vesicle** (Fig. 111, *sb*), in which the semen collects, and which, by its contraction during copulation, causes the ejection of the semen through the penis canal (ductus ejaculatorius). In nearly all *Turbellaria* there is, in connection with the male copulatory apparatus, a **granular gland**, the structure of which differs greatly in details. It forms a finely granular secretion, which mixes with the semen.

The male copulatory apparatus of the *Trematoda* (Fig. 114, *cb*) and that of the *Cestoda* (Fig. 115, *cb*) are very similar in structure.

In mechanism it corresponds with a *Tetrarhynchus* proboscis. There is a cylindrical or club-shaped penis sheath. Into the inner blind end of this penis sheath enters the unpaired terminal portion of the vas deferens. On entering the penis sheath it generally expands into a seminal vesicle, and then runs as a coiled thin tube through the penis sheath to emerge at the sheath's outer end through the male genital aperture. This tube, which is often furnished internally with barbed hooks or covered with an elastic cuticle, is forced out as an actual penis by the contraction of the penis sheath. The space between the penis and the penis sheath is filled with loose connective tissue. The penis and penis sheath are generally called **cirrus** and **cirrus pouch** in the *Trematoda* and *Cestoda*. Glands connected with the copulatory apparatus have also been observed.

II. **The female copulatory apparatus** very often, in many *Turbellaria* and in all *Trematoda* and *Cestoda*, consists of a simple tube of varying length, the **vagina**, which connects the egg passage or the ootype with the female sexual apparatus. This tube often serves merely as a place for depositing the eggs, not for copulation, *i.e.* it does not receive the penis. This is at least often the case with those *Polyclada* which have more than one copulatory apparatus, but only one female genital aperture.

In very many *Turbellaria*, however, the vagina is differentiated into a strong muscular organ, often provided with a hard cuticle, the **bursa copulatrix**, which is adapted for the reception of the penis during copulation. This may be developed independently as an accessory organ of the female copulatory apparatus. There is in many forms another broad, round, or pear-shaped accessory organ, the **receptaculum seminis**, a reservoir in which the semen is preserved after copulation.

In the *Trematoda*, many *Cestoda*, and in *Trigonoporus* among the *Polyclada*, the ootype, or the uterus, or the egg passage, is connected with the exterior by another special passage, Laurer's canal, already mentioned. The physiological signification of this canal is not yet certainly understood.

D. The Position and Number of the Copulatory Apparati and the Sexual Apertures.

It may be considered the rule that one male and one female copulatory apparatus are present, and that each opens externally by its own special aperture somewhere in the middle line on the ventral side. The two sexual apertures are generally very near each other, and in many forms—most *Trematoda*, *Cestoda*, and *Triclada*, and in many *Polyclada* and *Rhabdocœlidæ*—come to lie in the base of a more or less deep depression of the outer skin—**atrium genitale**—so that only one common outer sexual aperture is present.

In this point there is great variety in details, and many often striking deviations. In the *Polyclada* the sexual apertures always lie behind the mouth, in the *Cotylea*, in particular, between the sucker and the mouth. The male aperture always lies in front of the female. *Stylochus* and *Stylochoplana* have a common external sexual aperture. In *Anonymus* there are several copulatory apparati and sexual apertures in 2 lateral longitudinal rows. Many *Pseudoceridæ* possess 2 male copulatory apparati. The female copulatory apparatus and its aperture always remain single. In *Stylostomum* there is one common external aperture for the pharynx and the penis.

In the *Triclada* the common sexual aperture lies behind the mouth, the male copulatory apparatus in front of the female.

In the *Rhabdocœlidæ* the arrangements are extraordinarily varied. There are sometimes two separate apertures, sometimes an atrium genitale, and thus a common external sexual aperture. Sometimes the male aperture lies in front of the female, and sometimes the reverse is the case. In *Prorhynchus* the male copulatory apparatus opens in the mouth.

The genital apertures of the *Trematoda*, which either enter a common shallow atrium genitale or are very near together, generally lie at the anterior end of the body; in the *Distomidæ*, between the mouth and ventral sucker. Less frequently they lie at the posterior end of the body (*e.g. Gasterostomum*, *Opisthotrema*), or asymmetrically to the left near the anterior edge of the body (*e.g.* in *Tristomum*).

In the *Cestoda* there is generally a common external genital pore, or else the genital apertures are very near each other. The porus genitalis or the two genital apertures of each proglottis either lie at the edge (*Tetraphyllidæ*, *Tetrarhynchidæ*, most of the *Tæniadæ*, *Triænophorus*), or on one of the flat surfaces, which is therefore the ventral side (*Ligula*, *Bothriocephalus*, *Schistocephalus*, a few *Tæniæ*). In *Amphilina* they lie at the posterior end of the body.

Copulation is generally mutual, both the copulating individuals acting as male and as female. Self-fertilisation, however, also seems to take place, *e.g.* in *Cestoda*, and perhaps also in a few *Trematoda* and *Turbellaria*.

Development.—Like the atrium genitale, which is only a pit-like depression of the outer skin, so the male and female copulatory apparati arise, at least according to investigations made in the *Polyclada*, by folds from the exterior. The portion of the female genital organs which arises from invagination apparently reaches to the egg passage or ootype, so that not only the glands which open into the male genital organs, but the shell glands also of the female genital organs must be considered as modified dermal glands.

XIII. Asexual Reproduction and its Origin—The Organisation of the Cestoda.

Many Platodes, and especially the *Turbellaria*, show a marked **capacity for regeneration.** The body can not only re-form parts torn off, but broken off pieces of various sizes can become regenerated into new animals. Such a capacity of regeneration is very widespread, chiefly among lower stationary animals. In the *Cœlenterata* it is almost universal. The great advantage of this capacity for the preservation of the individual and of the race is evident. For attached animals, or very long or delicate soft-bodied animals, who are more exposed than others to mutilation and injuries to the body from enemies, etc., it is of very great importance. We can perhaps trace back to it the power of asexual reproduction by fission and gemmation which occurs in the *Metazoa*. We speak of such a method of reproduction when an animal form shows the peculiarity of falling into 2 or more pieces, apparently spontaneously, *i.e.* from causes unknown to us, these pieces becoming regenerated into organisms similar to the common mother animal ; or when, from unknown causes, a smaller or larger piece of the body regularly detaches itself, the body thus reduced again replacing the lost portion, while the detached part becomes regenerated into a complete animal.

Thus *e.g. Lumbriculus*, one of the worms belonging to the *Oligochæta*, falls spontaneously, or apparently spontaneously, into 2 or more pieces, each of which can become regenerated into a whole animal. Certain marine star-fish throw off one or more arms apparently spontaneously, which they soon replace by regeneration. As if this were not enough, each detached arm can again be regenerated into a complete star-fish.

This conjectural origin of asexual reproduction is, however, almost always unrecognisable ; because different parts of an individual develop into whole individuals before they have fully separated, or an animal replaces a part by regeneration before this part has completely detached itself. **Temporary animal stocks** thus arise. If the parts do not detach themselves typical animal stocks arise, which by division of labour between the portions which are being regenerated into whole individuals (*i.e.* between the individuals which have arisen by gemmation), and by the development of a form and organisation in each adapted for some special function, may become **polymorphous animal stocks.**

The reproduction and life-history of the *Acraspede Medusa*, *e.g.* of *Aurelia*, is specially suitable for the elucidation of the above view. We know that from the fertilised egg of this *Medusa*, under certain circumstances, another *Medusa* may proceed, without any attached stage multiplying asexually. Generally, however, the larva developed from the fertilised egg attaches itself and becomes a coral-like animal, the Scyphula, and later develops into an attached young

Medusa, the Scyphistoma. When this Scyphistoma has developed to a certain stage, in one case the larger portion of the body tears itself from the stem as a free-swimming *Medusa*. The remaining stem can, however, become regenerated into a complete attached *Medusa* (monodisc strobila), and the whole process may be repeated. We thus have here multiplication by detachment and subsequent regeneration. The detached piece has indeed so little to regenerate in it that the regenerative process may be described as cicatrisation.

Or again the stem of the Scyphistoma becomes regenerated into a new Scyphistoma before the first *Medusa* has detached itself, and when this regenerative process continues without the *Medusæ* at once fully detaching themselves we have a polydisc strobila. We call the whole process strobilation, and it has been described as asexual multiplication by axial budding. The polydisc strobila is a temporary animal stock.

What has here been said helps us to understand the

Organisation of the Cestoda Body.

In the body of the large majority of *Cestoda* the **scolex** (Fig. 117) is distinguishable from a row of subsequent **segments or proglottides** (Fig. 110, *E*, p. 153; Figs. 115, 116). The small pear or cone-shaped scolex itself consists of the **head** and **neck**. The former carries the organs of adhesion (suckers, hooks, proboscides), by means of which it attaches itself to the intestinal wall of the host. In it lie the single commissures between the longitudinal trunks of the nervous system which may be regarded as brain commissures. It therefore corresponds with the anterior end of the *Trematoda* body. The thinner neck portion of the scolex is followed by the flattened segments, which are small at first but increase in size posteriorly. The neck portion of the scolex constantly produces new segments, which push back those already existing. The oldest and largest segment of the whole chain is therefore the hindmost. In the segments the genital organs develop; indeed, the whole hermaphrodite genital apparatus of each segment answers to the whole genital apparatus of a *Trematode*. The male genital organs are first developed in each segment, then the female; then follows fertilisation, and finally the segment is little else than a case which, besides the remains of the genital organs, is almost exclusively occupied by the extended uterus containing thousands of fertilised eggs. The row of segments from the head to the last segment represents the row of consecutive stages of development of the genital organs. The last segments from time to time detach themselves singly, or several together, and reach the exterior with the excrement of the host.

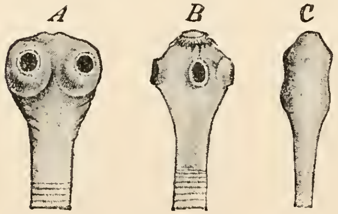

FIG. 117.—Three heads of Tapeworms (scolices). *A*, Of Tænia saginata; *B*, of Tænia solium; *C*, of Bothriocephalus latus.

On comparing the head and the segments we find that the head has no genital organs, and none of the segments have the organs of adhesion and the brain commissures; or, when we compare the head and proglottis with a *Trematode*, we find that the head has not the trunk, and the proglottis not the head, of the *Trematode* body. The head and one proglottis together, however, answer to the head and trunk, and thus to the whole body of a *Trematode*, apart from the fact that an intestinal canal is altogether wanting in the *Cestoda*.

We, however, know forms whose body during life consists only of head and trunk, which is not clearly divided into a scolex and a proglottis. Such forms are *Amphilina*, *Caryophyllæus*, and *Archigetes*. These may be regarded either as intestineless *Trematoda*, or unsegmented *Cestoda*. They are, in any case, transition forms between the *Trematoda* and *Cestoda*. The relation existing between them and the segmented *Cestoda* is somewhat similar to that between the *Acraspeda* which are attached throughout life (*e.g. Lucernaria*), and the polydisc strobila of *Aurelia*.

A segmented tapeworm must in fact be considered as a strobila. The young, still unsegmented tapeworm, which attaches itself to the intestinal wall, *i.e.* the scolex, answers to the young stage of one of the unsegmented *Cestoda* mentioned above (*Amphilina*, *Caryophyllæus*, or *Archigetes*), in which the genital apparatus is not yet developed in the slightly developed trunk, the future neck. Now follows the incomplete constriction of that part of the body of the scolex (the trunk or the first proglottis) in which later the genital organs develop. Regeneration of the constricted part then takes place; this part is again constricted and again regenerates, and so on. The single parts remain connected for a longer or shorter time, and form the segments of the tapeworm chain or strobila. Finally, like the oldest *Medusa* discs of a polydisc strobila of *Aurelia*, the oldest segments of the tapeworm strobila detach themselves. The points in which the process differs in the two groups are essentially the following. The *Medusæ* which detach themselves from a polydisc strobila develop further, and their sexual organs attain development only after detachment. The segments of the *Cestoda* which detach themselves, however, are already more than mature (sexually); they have performed their function, the production of fertilised eggs, and they make no attempt to regenerate the part which is wanting to make them complete Platodes, *i.e.* the head. In the *Medusa* strobila, further, that part of the body by which it is attached, viz. the apex of the exumbrella, is an insignificant part of the body both physiologically and anatomically, while the part by which the tapeworm is attached contains at least the principal part of the central nervous system.

It does not seem difficult, in the case of the *Tapeworm*, to trace back strobilation to the phenomenon of regeneration. Proceeding from forms, like *Amphilina*, capable of regeneration, we can understand that by the peristaltic movements of the intestinal canal in which the animals lived parasitically, and by the outward movement of the excrement, the trunk, with the genital organs it contains, would be torn off and ejected, the head which remained being, however, able to produce a new trunk by regeneration. This process—the tearing off of the trunk with the eggs, the continued attachment of the head, and regeneration—must have been of the greatest use to these parasitic forms. By the tearing off of the trunk and its ejection the greater dispersal of the eggs was secured, and the probability of the infection of new hosts or intermediate hosts thus increased. The attached head could keep its ground in the already attained favourable refuge for the parasite, and easily regenerate a new trunk and new genital organs. The strobila consisting of many segments, however, offered the immense advantage that many segments could be benefited by the favourable nutritive conditions of parasitism, and could develop the genital organs; on the other hand, by the periodical tearing off of the trunk of an unsegmented *Tænia*, not only a longer time must pass before a new sexually ripe trunk would form, but the favourable conditions of nutrition would be much less utilised.

There are *Tæniæ* with only very few segments (*Tænia Echinococcus*, with 3 to 4 proglottides); others possess several hundreds.

In a few *Tæniæ*, such as *Ligula* and *Triænophorus*, the outer segmentation is more or less indistinct; internally, however, we find the same repetition of the genital organs as in the typically segmented tapeworms, from which these forms must without doubt be derived.

In freshwater *Triclada*, multiplication by fission has been observed.

Among the *Rhabdocœla*, in the genera *Microstoma* and *Stenostoma*, we find interesting processes of reproduction by axial budding. They can be best investigated in *M. lineare*. In the posterior end of the body of an individual a double transverse partition wall forms between the intestine and the skin. Immediately behind this the organs characteristic of the head portion of the *Microstoma*,—the pharynx and the brain,—with the nerve commissure surrounding the pharynx, form. The two septa subsequently move somewhat apart. An annular constriction of the body takes place between them, and the intestine finally also becomes constricted. Only then does the spontaneous separation of the two pieces occur. Long before this separation occurs, however, new phenomena have appeared in both pieces. In the first place the posterior piece grows to the same size as the anterior. Then in the posterior part of each a head portion again forms. The posterior parts of each principal piece thus marked off then grow to the size of the two parts lying in front of them. The whole body now consists of 4 pieces of equal size. This process is repeated twice in the same way, till 16 pieces are formed, *i.e.* till the worm stock consists of 16 individuals, the one most to the front possessing the original pharynx, the original brain, etc. Then follows generally the spontaneous separation of the individuals.

Reproduction by gemmation occurs further in the young stage of *Tænia* called the Finn, and especially in those finns which are known as *Cœnurus* and *Echinococcus*. This will be described later on.

XIV. Ontogeny of the Polyclada.

As a short illustration of the development of the Platodes from the fertilised egg, we choose the *Turbellaria* (*Polycladidæ*). [The ontogeny of the *Rhabdocœla* is almost unknown, and the development of the *Triclada* seems to us to be markedly cœnogenetic. The eggs of these latter animals develop at the expense of the numerous yolk cells in the midst of which they lie imbedded within the egg cocoon, and it might with justice be said that the eggs and embryos of the *Triclada* live parasitically on these yolk cells, which is not the case in the *Polyclada.*]

We have already (Fig. 94, p. 125) described and illustrated the first stages of segmentation. The 4 micromeres which are first separated by constriction yield the whole ectoderm; the next 4 or twice 4 in like manner produced form a large part of the later mesoderm. The descendants of the 4 ectoderm micromeres grow round the whole germ by repeatedly dividing, thus enclosing not only the 4 macromeres, but also the 4 or 8 mesoderm micromeres. They thus form at last a continuous layer of epithelial cells round the whole germ, which is only broken through at the vegetative pole by a longitudinal slit corresponding with the ventral medium line of the embryo. This longitudinal slit is defined as the blastopore; it soon completely closes. The germ is now at the stage of a bilaterally symmetrical planula, in which there is already a formation of mesoderm between the endodermal rudiments (the 4 macromeres, which meantime by division of one of them have increased in number to 5) and the ectoderm.

The 4 or 8 mesoderm micromeres soon increase in number by fission, and thus form either a ring of mesoderm cells or 4 masses of mesoderm cells (2 anterior and 2 posterior). The macromeres, now surrounded on all sides, continue to give off by constriction micromeres, which again increase by fission and yield the intestinal epithelium. The yolk-containing macromeres finally become disintegrated, and the yolk is used up by the intestinal cells. Near the original blastopore a depression of the ectoderm occurs, the stomodæum, as the first beginning of the pharyngeal apparatus. The germ is now, apart from the fact that it is bilaterally symmetrical, at the stage of a *Scyphula* or a young *Ctenophoran* larva.

The mesoderm cells extend more and more between the endoderm and the ectoderm; the sensory organs first appear in the ectoderm, on the side opposite the stomodæum, near the original animal pole, but shifted somewhat along the median plane, so that now anterior and posterior ends can be clearly distinguished. These sensory organs take the form of 2 or 3 eyes, and of cells which carry tufts of long hairs. In connection with these sensory organs, which in the case of eyes soon sink down below the ectoderm and become mesodermal, the paired cerebral rudiments arise as products of the ectoderm, and these also soon sink under the surface and become mesodermal. The two rudiments become secondarily connected by transverse bridges. The principal nerve trunks seem to arise as outgrowths of the cerebral rudiments which form the so-called **neural plate.**

The ectodermal body epithelium becomes provided with cilia at an early stage. In the centre of the endoderm the enteric cavity arises in consequence of the increasing absorption of the yolk by the endoderm cells, which arrange themselves peripherally like an epithelium. Into the base of this cavity the stomadæum soon breaks. The enteric aperture is thus formed. The stomodæum changes in the following way into the definite pharyngeal apparatus. A circular invagination forms in it, the first beginning of the pharyngeal pouch. This is surrounded by a collection of mesoderm cells. Into the pharyngeal pouch the pharynx itself grows as a circular fold, consisting of mesoderm cells and a covering of epithelium. The body, which till now has been tolerably round, begins to flatten; the surface in which the mouth lies can as the ventral surface be distinguished from the dorsal surface under which lie the eyes and brain. The mesoderm cells everywhere spread out between the intestine and the body epithelium, and form a continuous mass, which is thicker at the ventral side. Those layers of mesoderm which lie close under the epithelium yield the dermal musculature; the deeper mesoderm cells yield the body parenchyma, and most probably also the germ-preparing organs of the genital apparatus.

In a series of *Polyclada* whose embryos leave the egg shell very early as free-swimming **Müller's larvæ** (Fig. 118), a ring of strong and long cilia which encircles the body arises directly in front of the mouth; this is the so-called **preoral ciliated ring**, running out round 4 or 8 processes of the body, one of which lies immediately before the mouth and one in the middle line of the back, while the other 2 or 6 lie laterally in pairs. These processes, with their strong cilia, are drawn in and reabsorbed when the free-swimming larvæ sink to the bottom and begin the creeping manner of life.

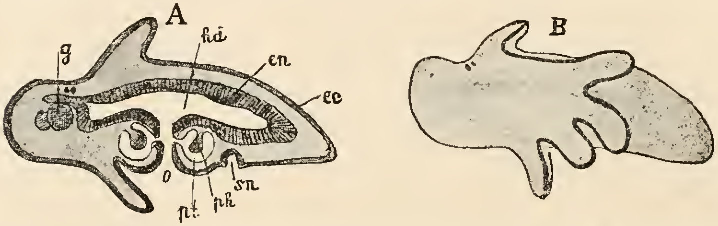

FIG. 118.—**Müller's Polyclad larva (of Thysanozoon or Yungia).** *A*, Median longitudinal section. *g*, Brain; *hd*, main intestine; *en*, endoderm; *ec*, ectoderm; *sn*, sucker; *ph*, pharynx; *pt*, pharyngeal pouch; *o*, mouth. *B*, The same from the side. The black line indicates the course of the preoral ciliated ring.

The differentiation of the originally single enteron into main intestine and gastro-canals follows in consequence of the growth of mesodermal septa from the periphery more or less far inwards.

The position of the mouth and pharynx on the ventral surface in the adult animal is determined by the relative growths of the anterior and posterior halves. If they grow equally, these organs lie centrally; if the anterior half grows the more strongly, they lie posteriorly; if the posterior grows the more, then they lie anteriorly.

XV. The Life-history of the Trematoda.

Whereas from the fertilised eggs of the ectoparasitic or monogenetic *Trematoda* other *Trematoda* develop direct without their young being assigned to another animal or host than that occupied by the adult, the development and life-history of the endoparasitic or digenetic *Trematoda* is remarkably complicated. We choose as an example the tolerably complicated **life-history of the fluke**, *Distoma hepaticum* (Fig. 119), which is parasitic in the liver of the sheep, causing the "sheep rot." The eggs of the fluke leave the liver of the host by the bile ducts, pass into the intestine, and are ejected with the excrement. They only develop when they meet with water. In this case there develops in the egg shell (*A*) a ciliated embryo, which leaves the egg shell and swims about freely (*B*). It is club-shaped; at the thicker anterior end it has a small median prominence, behind this an X-shaped eye spot, and under this a ganglion, and further a granulated mass which is considered to be the intestinal rudiment. We can also recognise 2 ciliated cells of the excretory system. The greater mass of the body, however, is formed of germ cells, which are considered to be parthenogenetic eggs, possessing the capacity of developing without being fertilised. These germ cells divide (furrow) early, and become cell spheres.

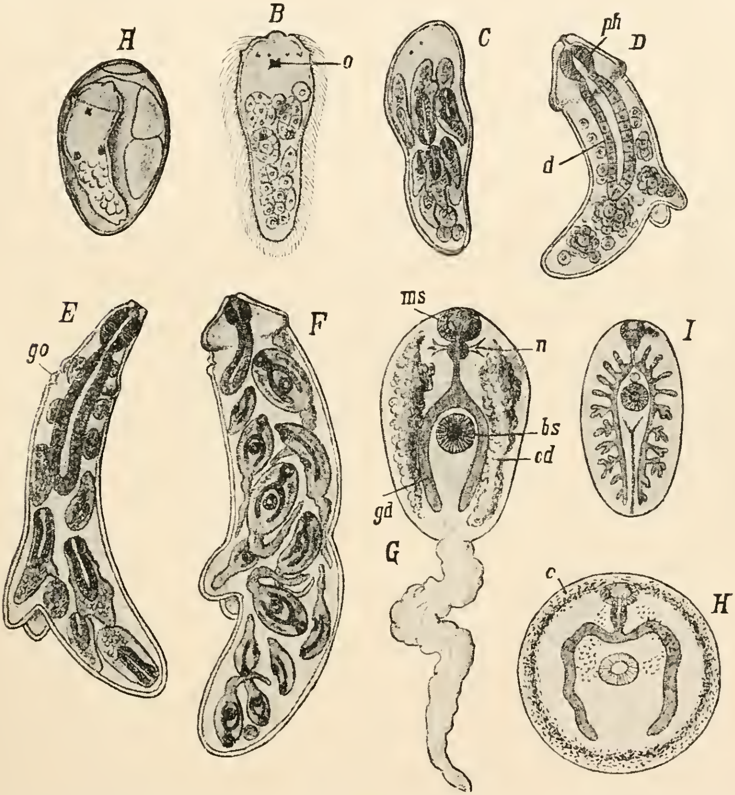

Fig. 119.—**Life-history of Distoma hepaticum**, after **Leuckart**. *A*, **Egg with embryo.** *B*, **Free-swimming ciliated embryo**; *o*, eye spot. *C*, **Sporocyst.** *D*, *E*, and *F*, **Rediæ**; *ph*, pharynx; *go*, birth aperture; *d*, intestine. *G*, **Cercaria**; *ms*, oral sucker; *n*, nerve ganglia; *bs*, ventral sucker; *gd*, forked branches of the intestine; *cd*, glands, whose secretion yields the cysts. *H*, **Encysted young Distoma**; *c*, cyst. *I*, **Young Distoma in the sheep's intestine.**

The embryos must meet with a water-snail, *Limnæus truncatulus*, and penetrate into its respiratory cavity in order to develop further. They here lose the covering of cilia; the eyes, the ganglion, and the granulated mass become disorganised. Their bodies represent a pouch, containing in its interior a certain number of cell spheres which have developed out of the germ cells or parthenogenetic eggs. Instead therefore of the young animals, which are called *Sporocysts* (*C*), developing further into new *Distoma*, they not only remain at a low stage of development, but they even suffer a considerable degeneration. It seems as if early reproduction were the only function of this *Sporocyst.* The cell spheres which they contain actually develop again into new germs, which leave the *Sporocyst's* body as *Rediæ* (*D, E*), the *Sporocyst* finally disintegrating, and thus never developing into a fluke. The *Rediæ* which have become free, being developed out of the parthenogenetic eggs of the *Sporocysts*, reach a higher stage of development than their mother. They have at the front end of their body a sucker-like formation, and also a pharynx, a simple intestinal tube, and a birth aperture behind two blunt processes. Here also we find numerous germ cells between the intestine and the body wall; these begin early to develop, *i.e.* to divide. The *Rediæ* in fact, like the *Sporocysts*, do not grow into flukes; they first creep about in the respiratory cavity of their host, *Limnæus truncatulus*, and then penetrate into its liver. The germs which develop in them again become *Rediæ*, which pass out by the birth aperture and are parasitic in the liver with their parents. This second generation of *Rediæ* (*F*) again reproduces itself parthenogenetically. From their germs, however, at a warm time of year are developed, not *Rediæ* again, but larvæ which are called *Cercariæ* (*G*). These *Cercariæ* already show the structure of a young *Distoma*; they are flat, have oral and ventral suckers, a pharynx and a forked intestine, a double ganglion joined by a transverse commissure in front of and above the pharynx, both the principal branches of the excretory system, and besides these — and this is characteristic of the *Cercariæ* — a movable caudal appendage. The *Cercariæ* leave the mother body, *i.e.* the *Rediæ*, by the birth aperture, forsake their host, and reach the water, in which they swim about for a time by means of their tail. They then settle upon grasses or plants growing in water in flooded meadows, lose their tail and become encysted by the help of the secretion contained in two very large glands which lie laterally in the body. In this encysted condition (*H*) they can remain a long time, and can withstand desiccation. They reach the sheep's intestine if occasion offers in the fodder, and there presumably the cyst is dissolved and the young *Distoma* enters the liver through the bile ducts. Such a young *Distoma*, with the first branchings of the intestine, is depicted in Fig. 119, *I*.

The life-history of other endoparasitic *Trematoda* runs, as far as we know, the same course. The free-swimming *Cercaria*, however, often enters into a second intermediate host, in which it becomes encysted and loses its tail. This second host is generally an invertebrate animal. The encysted *Cercaria* enters the body of the final host (generally a vertebrate animal) when the second intermediate host is eaten by the latter.

Several different generations, therefore, follow each other in a regular manner in the endoparasitic *Trematoda.* The generation which multiplies by fertilised eggs always reaches the full degree of organisation of the *Trematoda*; the following generation, which reproduces itself parthenogenetically and lives in other hosts, never reaches that degree of organisation; they are ripe extraordinarily early, and perish after they have produced another generation, which also remains at an early embryonic stage. The different generations are known as *Sporocysts*, *Rediæ*, and *Distoma* generations. The regular alternation of such generations is called **Heterogeny.**

XVI. The Life-history of the Cestoda.

From the fertilised eggs of the *Cestoda* there proceed, generally while they still lie in their egg shells in the uterus, embryos which, since they are provided with 6 hooks, are called the 6-hooked embryos. The fate of this embryo, which only in *Bothriocephalus* is ciliated and swims about freely in water, is very different in different *Cestoda.* In *Tænia cucumerina*, which is parasitic in the intestine of the dog, it enters the body of the dog louse, *Trichodectes canis.* It here gets rid of the egg shell and reaches the body cavity, where it develops into a small worm, at one end of which the head develops with its rostellum and its 4 suckers, while at the other the pore of the excretory system can be made out. The head is somewhat sunk into the body. The body is filled with numerous calcareous granules. We have here simply an unsegmented, not yet sexually developed, tapeworm, which may be compared with a young *Amphilina*, or *Caryophyllæus*, or *Archigetes.* Through the dog's habit of licking and cleaning itself, the present host of this young form, which we may simply call scolex, is liable to be swallowed. While the louse is digested, the scolex withstands digestion, the calcareous granules neutralising the acid juices of the stomach. It fastens itself to the intestinal wall, and begins to produce, by terminal budding or strobilation, the chain of proglottides in which the genital organs develop.

In this simple case we have one and the same individual, from the egg to the strobilising intestinal scolex. The 6-hooked embryo, the scolex in the body cavity of the louse, and the strobilising scolex in the intestine of the dog, are the same individual in various stages of development and in various habitats. In most of the *Cestoda*, in consequence of peculiar complications in the development, this is by no means so clear. In a series of *Cestoda*, to which *Tænia solium* and *T. saginata* belong, the 6-hooked embryo in the tissues of its host changes, by the accumulation of fluid internally, into a vesicle surrounded occasionally by a special capsule or cyst formed out of those tissues. From the wall of this vesicle, which is called **Finn** or **Cysticercus,** there arises, at the base of an invaginated hollow cone, a tapeworm head with suckers, rostellum, etc. (Fig. 120). While most investigators regard this process as one of gemmation, we hold it to be simply one of growth and differentiation. The head with the vesicle is, according to our opinion, a young sexless *Cestode* answering to the scolex of *Tænia cucumerina* in the body cavity of the louse, only in this case the trunk or proscolex becomes extended into a large vesicle by the accumulation of fluid before the head of the tapeworm with its suckers, etc., forms. The development of this vesicle ought to be regarded as a special adaptation for the protection of the head. If such a *Cysticercus* reaches, with the tissue of its host, the intestine of a new host, not only the cyst, but the whole vesicle dissolves, while the head and rudimentary neck which are evaginated resist digestion because of the calcareous bodies they contain. In other words, the young, sexless, unsegmented tapeworm loses its vesicular trunk. The scolex fastens itself, by means of its organs of adhesion, to the intestinal wall, and at once regenerates the lost portion of the body in the form of the first proglottis, which in the developed tapeworm chain at length becomes the last and oldest, and new segments follow this one.


Fig. 120.—**Cysticercus cellulosæ. Finn of Tænia solium,** cut in half. The scolex, which is invaginated into the vesicle, is seen with its suckers and rostellum. After **Leuckart.**

The vesicle of the *Cysticercus* of different tapeworms varies in size according to the amount of fluid contained. It is sometimes a large sphere, sometimes merely a small swelling at the posterior end of the worm-like *Cysticercus.*

In a few tapeworms development is complicated by the occurrence of an alternation of generations, the young unsegmented form in the intermediate host, the finn, multiplying asexually by gemmation. On the wall of the finn there thus arise, not only one rudimentary head, but several, indeed very many heads. Such a finn is called a **Cœnurus.** It occurs in *Tænia cœnurus.* In the finn known as *Echinococcus* (of *Tænia Echinococcus* of the dog) there arise internally in the vesicular body by invagination of the wall numerous daughter vesicles, and even two generations of such vesicles, on whose walls several heads form.

We must further remark here that asexual scolices living free in water have been observed.

The Influence of Parasitism on the Structure and Development of Animals.

In the race of the Platodes, for the first time among the Metazoa, the parasitic manner of life is met with as a very widely spread phenomenon. Of the three classes which form this race, the two classes of the *Trematoda* and the *Cestoda* consist entirely of parasitic forms, while most of the *Turbellaria* live freely. The transition from the free life to the parasitic brings with it such far-reaching changes in the conditions of existence that the original organisation, development, and life-history of the animals must necessarily be strongly influenced by it. This influence can be stated in a way which suits all cases in the animal kingdom where, in a naturally demarcated animal group, parasitic forms appear side by side with free-living forms. Similar variations in the conditions of existence have as a consequence similar variations in structure and development.

We can, apart from fine shades of difference in manner of life, distinguish two principal groups of parasites: (1) the **Ectoparasites,** which are parasitic on the outer surface of other animals, and (2) **Endoparasites,** which are parasitic in the intestine or other inner organs. The ectoparasites in many ways form the transition from non-parasitic to endoparasitic animals, for they still retain relations to the outer world which the latter have entirely given up.

Parasitic life is the most convenient manner of life for the attainment of food. Parasites feed at the expense of the juices or tissues of their hosts, which are abundantly within their reach. Once on or in the host's body, it is of the greatest utility for them to retain the position they have gained. Hence the numerous and varied adaptations for the attachment of the body. In the *Trematoda* and *Cestoda* we find suckers, hooks, and protrusible proboscides armed with barbed hooks and other organs of adhesion. Many parasites possess a sucking apparatus to suck the juices of the host. *Trematoda* suck with the oral sucker and pharynx the mucus on the surface of the body, or the food pulp in the intestine, etc.

The ectoparasitic *Trematoda* possess a well-developed alimentary canal, which is often even richly branched; in the endoparasitic forms, which are supplied with food already partly dissolved, the work of digestion is facilitated. The intestine in endoparasitic *Trematoda* is reduced to two main branches or to a simple cæcum; in the *Sporocyst* generation, which multiplies parthenogenetically, it has become quite rudimentary. Here feeding takes place simply by the diffusion of the juices of the host through the outer skin of the parasite. The same is the case in the *Cestoda*, which have entirely lost their alimentary canal. We may therefore state that progressive accentuation of parasitism is accompanied by progressive reduction of the gastro-canal system, ending in its entire disappearance.

The capacity of active locomotion is generally of very little use to endoparasites. We accordingly find in them that those parts which serve for locomotion, locomotive organs and musculature, are more or less reduced. On the other hand many ectoparasites (not indeed exactly Platodes) possess a well-developed capacity of locomotion, which is of great importance to them, chiefly for the object of infecting new hosts (*e.g.* the flea). Very many ectoparasites can, in fact, live a free life for a time. The locomotory system and its musculature are therefore generally less degenerated in them than in endoparasites.

In consequence of the very limited locomotion of endoparasites the power of directing themselves by special sensory organs is unnecessary, at least while parasitism lasts. The ectoparasitic *Trematoda* already are far more sparingly supplied with sensory organs than the free-living *Platodes.* They still possess eyes, although of a very simple sort. The endoparasitic *Trematoda* have lost even these sensory organs, which occur only temporarily in the freely moving young stages of the ciliated larvæ and the *Cercariæ.* In the *Cestoda* special sensory organs are altogether wanting.

The degree of development of the nervous system depends (1) on that of the musculature, and (2) on that of the sensory organs. We thus understand the gradual simplification of the nervous system, especially the sensory portion, from the ectoparasitic *Trematoda* to the endoparasitic, and finally to the *Cestoda.* On account, however, of the strong development of the musculature of the organs of adhesion the nervous system in relation with them is more or less strongly developed. Compare the strong development of the nervous system in the head of the *Cestoda* with its great reduction in the segments.

Parasites seem to have a very slightly developed need for respiration. Judging from what we find in other divisions of the animal kingdom, the respiratory organs very often become degenerated, especially in endoparasites. The parasitic Platodes have no covering of cilia.

The excretory system in the Platode parasites is developed at least as strongly as in the free-living forms.

The genital organs also are as strongly developed, indeed even more strongly developed, in the former than in the latter. Ripe *Distoma* or ripe segments of *Cestoda* consist almost exclusively of the genital apparatus and the genital products. But to this we shall return.

We therefore see that with increasing accentuation of the parasitic mode of life there is a proportional reduction of the sensory organs of the nervous systems, of the special digestive system, of the locomotory organs, and also of the respiratory organs, and thus a degeneration of all the organs except the genital and the excretory organs and the organs for adhesion and sucking.

The influence of the parasitic mode of life on the development, and generally on the whole life-history of the parasite, is not less striking.

If the parasite were to remain during life and in all stages of development parasitic on or in the same host, it would perish when the latter died, and the whole race to which it belongs would soon also perish. There must therefore be some provision or other for the infection of new hosts. This infection takes place in the simplest way in most ectoparasites. Many of these retain during youth their free mode of life, so that they can themselves seek out their hosts. Others retain throughout their power of free locomotion, and vividly recall in their mode of life the beasts of prey.

In the ectoparasitic *Trematoda* very little is known about the manner of infection of new hosts, but we do know—and this is very important—that the course of their development is direct and without intermediate hosts belonging to animal groups different from that of the final host. In the endoparasites the life-history is, as we have seen, more complicated. But here also originally free-living young forms must have provided for the spread of the individuals and the infection of new hosts, and thus for the preservation of the race. The observation of free scolices gives countenance to the presumption that originally a free-living young form, a scolex, developed from the fertilised egg, and in some way or other again found its way into the body of the final host. Most parasites are specialists, *i.e.* they thrive only in the bodies of one or of a few definite animal species. It is certain, however, that of their eggs or young forms only very few on the average reach the bodies of true hosts ; many perish without reaching any host, many find their way to the wrong place, go astray in the body of a host other than the usual one and there perish, or they may for a time hold their ground and also, as experience shows, develop somewhat further, never, or very seldom at any rate, attaining full development. This perhaps throws light on the origin of development by means of intermediate hosts. Carnivorous animals devour certain animals as their favourite food ; the latter are themselves carnivorous or herbivorous. If the eggs or young of a parasite accidentally reach the body of an animal which is the favourite food of its proper host, and if they could there remain alive for a longer or shorter time, the probability of their reaching in their new (intermediate) host the intestine of their proper host would be greatly increased. This or some similar advantageous manner of being smuggled into the body of the proper host might become established as that most advantageous for the preservation of the race, and would finally become the normal mode of infection.

In the systematic review the intermediate hosts of several *Trematoda* and *Cestoda* are given, as well as the final hosts. The biological relations between the host and the intermediate host can easily be recognised, especially in the case of the *Cestoda.*

Occasionally there are two intermediate hosts in the normal course of life. Free-living young forms, *e.g.* the ciliated larvæ of the *Trematoda*, often effect the transition of the parasite from host to intermediate host, or, as the *Cercariæ,* from intermediate host to definitive host.

In the *Cestoda* it is possible for parasitism to thrive to such an extent by the passive transmission of various stages of the parasite from host to host that the animals never lead a free life. The degenerating influence of the parasitic mode of life has here told upon all stages of development.

However refined the artifices for infecting new hosts may be, the result of the process must always to an extraordinary extent depend upon chance. It is a chance when the egg or the embryo of the *Distoma hepaticum* reaches the water, a chance when it meets a *Limnæus truncatulus*, a chance when the encysted *Cercaria*, with the plant on which it lies, is eaten by a sheep. Thousands and thousands of eggs thus miss their aim. There is therefore another way of providing for the maintenance of the race in parasites, viz. their extraordinary fruitfulness and their highly developed capacity of reproduction. This capacity is very easy for them, because the conditions of existence in which they find themselves are the most favourable possible. A *Distoma*, indeed a single proglottis of a *Tænia*, is capable of producing thousands, or even hundreds of thousands, of eggs and embryos. And if of all these eggs but 1 or 2 on the average reach their aim, the maintenance of the race is provided for. Propagation by gemmation comes to the assistance of sexual propagation by fertilised eggs in the segmented tapeworms and in the young forms known under the names of *Echinococcus* and *Cœnurus.*

In those cases also, in the *Trematoda*, where generations living in the so-called intermediate host are not surrounded by conditions so favourable that they can develop into adult *Trematoda* with male and female organs, they still possess the capacity, in spite of their reduced condition, of producing at an early stage a sort of egg, the germ cells; these dispense with fertilisation and nevertheless develop (parthenogenetic reproduction of the *Sporocysts* and *Rediæ*).

When we consider the degenerated condition of the *Sporocysts* there is some justification for assuming that the *Dicyemidæ* and *Orthonectidæ* (*cf.* p. 60), which are very similar to these *Sporocysts*, are degenerated *Trematoda* from whose life-history the typical *Trematode* generation has completely disappeared.

Strobilation and Segmentation.

We have seen that the bodies of most *Cestoda* are segmented, and we have shown this segmentation to be the result of an axial budding or strobilation. The whole segmented body is thus an animal stock. In a few *Turbellaria*, especially in *Gunda*, segmentation also occurs, but in quite another way; this is the regular paired arrangement of the organs which in the *Polyclada* and *Triclada* are generally present in considerable numbers. There is a repetition at regular intervals of the transverse commissures of the nervous system (the ladder nervous system), the male and female sexual glands, the lateral intestinal branches, the dissepiments lying between them, and the external apertures of the water-vascular system. Such a **segmented** body represents a simple *Platode* individual, not a *Platode* stock; it does not arise by budding. Strobilation and segmentation are therefore to be clearly kept apart.

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CHAPTER IV

THE ORGANISATION AND DEVELOPMENT OF THE WORMS (VERMES)

THE race of the worms is, even after the exclusion of the *Platodes*, which till now have been included in it, by no means a natural, well-demarcated division of the animal kingdom; now, as heretofore, it is like a lumber room, to which all those groups are relegated which cannot be placed elsewhere. It is therefore difficult to characterise the race of the worms in other than negative terms. All worms are **bilaterally symmetrical animals**; their detailed structure, however, is most varied. They are raised above the *Cœlenterata* and *Platodes* by the **possession of an anus, and of a blood-vascular system** which undertakes physiologically one of the functions of the gastro-canal system of these animals. Where these systems are wanting a secondary degeneration has perhaps taken place. **The mouth lies at the extreme anterior end of the body,** originally always on the ventral side. A **body cavity** is either wanting, or is developed in varying degrees. Under the outer body epithelium there is found in all unshelled forms a generally strong muscular layer (**dermo-muscular tube**). The **nervous system** is developed in very different ways. The only constant point is the presence of a nerve centre placed above the œsophagus (**brain, supra-œsophageal ganglion**). There is also generally a nerve ring surrounding the œsophagus, the **œsophageal ring**, from which longitudinal trunks run backwards in varying number, position, and arrangement. All these portions — brain, œsophageal ring, and longitudinal nerves—belong to the central nervous system. **Excretory organs (nephridia)** are found in all divisions, but under the most different conditions. They often perform the function of conducting the sexual products out of the body. **Segmented body appendages** (extremities) are as completely wanting as is a specialised muscular organ of locomotion placed on the ventral side (foot). A strictly localised central organ of the blood-vascular system (**heart**) has been observed only in the *Brachiopoda*.

VOL. I N

THE FOURTH RACE OR PHYLUM OF THE ANIMAL KINGDOM.

VERMES.

Systematic Review.

CLASS I. **Nemertina (Rhyncocœla).**

Body ciliated, externally unsegmented, elongated, generally somewhat flattened dorso-ventrally. Without distinct body cavity, intestine straight, mostly with lateral diverticula, anus at the posterior end of the body. Above the intestine a proboscidal apparatus, generally emerging in front of and above the mouth. The central nervous system consists of a brain lying between the proboscis and the œsophagus, and of two lateral longitudinal trunks. Blood-vascular and excretory systems present. Sexes separate. By regular repetition of the inner organs (lateral intestinal diverticula, circular commissures of the longitudinal nerves, sexual glands) a sort of inner segmentation often arises (Pseudometamerism). Almost exclusively marine.

Order 1. **Palæonemertina.**

Head without deep lateral longitudinal furrows. Proboscis without stylets. Mouth behind the brain. *Carinella*, *Polia*.

Order 2. **Schizonemertina.**

On each side of the head a deep longitudinal groove. Proboscis without stylets. Mouth behind the brain. *Lineus*, *Borlasia*, *Cerebratulus*, *Langia*.

Order 3. **Hoplonemertina.**

Head without deep lateral longitudinal grooves. Proboscis armed with one stylet or several. Mouth generally in front of the brain. *Amphiporus*, *Drepanophorus*, *Tetrastemma*, *Nemertes*.

Order 4. **Malacobdellina**

Head without lateral longitudinal grooves. Proboscis without stylets. One sucking disc at the posterior end of the body. *Malacobdella*. Parasitic in marine mussels.

CLASS II. **Nemathelmia.**

Body cylindrical, spindle-shaped, or thread-like, unsegmented, covered with a thick cuticle. Body cavity generally spacious. Intestine straight or wanting. Anus at the posterior end of the body. Neither blood-vascular nor excretory system comparable with those of any other worms. Sexes usually separate. Nervous system an œsophageal ring, a medio-dorsal, and a medio-ventral longitudinal trunk. An inner metamerism is wanting, but the circular commissures of the longitudinal nerves may repeat themselves in the Nematoda with tolerable regularity. Mostly parasitic.

Order 1. **Nematoda.**

With intestinal canal, without proboscis. Family *Enoplidæ*, mostly free-living in the sea, less frequently in fresh water or on land, without œsophageal bulb, often with eyes. Family *Anguillulidæ*, small, partly parasitic, partly free-living animals, with double œsophageal bulb, without eyes. *Tylenchus scandens*, in grains of wheat. *Anguillula aceti*, in paste, fermenting vinegar, etc. *Rhabditis nigrovenosa*, in damp muddy earth. Sexes separate. The females are viviparous, and produce only a few young (4 at most), which, after being hatched, find their way into the lungs of frogs and toads, and there develop into mature hermaphrodite animals (*Ascaris nigrovenosa*), from whose fertilised eggs the free-living *Rhabditis* generation again arises. The life-history thus exhibits a sort of heterogeny. *Sphærularia bombi*, the *Rhabditis*-like young form lives in the earth. The fertilised females find their way into the female humble bee, where they are parasitic in the body cavity or in the intestine. The uterus, which is filled with embryos, soon begins to hang out from the female genital aperture, and becomes a large pouch, to which the worm-body finally forms merely a small insignificant appendage. *Mermithidæ*, without anus. The young are parasitic in the body cavity of *Insects*; they make their way out into damp earth, where they become sexually mature and reproduce themselves; *Mermis nigrescens.*

Filariidæ: Filaria medinensis (medina worm), may have a breadth of 0·5–2 mm. and length of nearly a metre; in the subcutaneous connective tissue of man, in warm regions of the Old World. The young in small *Crustacea* (*Cyclopidæ*). *Trichotrachelidæ: Trichocephalus dispar*, with swollen hinder body, in the human cæcum.

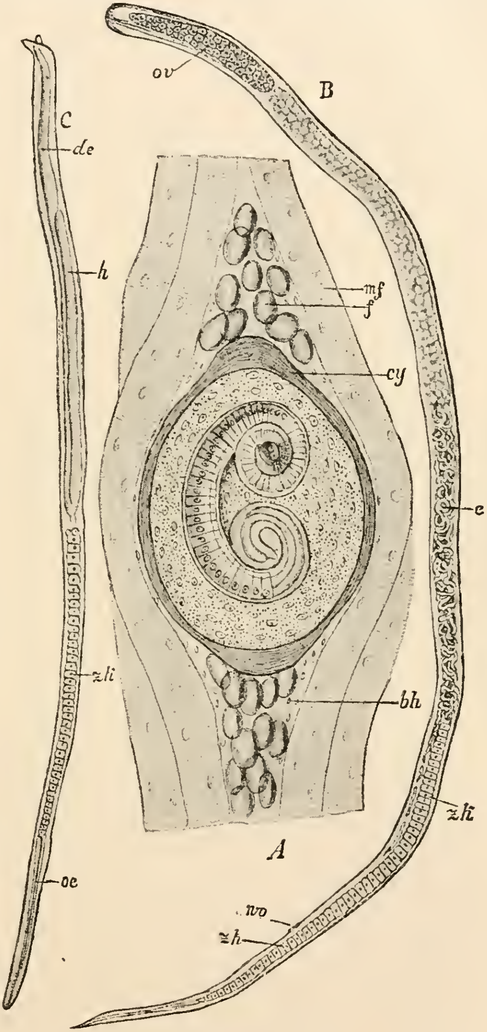


Fig. 121.—**Trichina spiralis** (after **Claus**). *A*, **Encysted muscle Trichina**; *mf*, unaltered muscle fibres; *f*, fat globules; *cy*, cyst; *bh*, envelope of connective tissue. *B*, **Female intestinal Trichina**; *ov*, ovary; *e*, embryos; *zk*, cell bodies (in the post œsophageal division of the intestine); *wo*, female aperture. *C*, **Male intestinal Trichina**; *œ*, œsophagus; *h*, testis; *de*, ductus ejaculatorius.

Trichina spiralis (Fig. 121) lives sexually mature as the so-called intestinal *Trichina* in the small intestine of man and in that of many mammals; is viviparous; the female (*B*) is ca. 3 mm., the male (*C*) half as long. The young bore their way into the intestinal wall, pass from here through the body cavity, or with the blood in the veins into the musculature, penetrate the muscle fibres, and there surround themselves with a cyst or capsule which afterwards becomes calcareous (*A*). Encysted muscle *Trichinæ* cause trichinosis. Men become infected by eating trichinous pork which is uncooked or not sufficiently cooked. Pigs are much exposed to infection on account of their omnivorous habits. The principal carriers of *Trichina*, however, are rats which happen to eat the dead bodies of infected animals, and so secure the continued existence of the parasites.

Strongylidæ: Dochmius (*Anchylostoma*) *duodenalis*, with strong oral capsule armed with teeth. Female as long as 2 cm., male half as long. In the human small intestine (Egypt, Brazil, India, the Antilles, Switzerland, Italy, Belgium). Chiefly among labourers in pits, mines, or tunnels. Causes the so-called miner's anæmia. *Eustrongylus gigas*, female 30-100 cm. long. In the pelvis of the kidneys of the dog and other mammals. *Ascaridæ: Ascaris lumbricoides*, male up to 25 cm., female to 40 cm. in length. In the human small intestine. *Oxyuris vermicularis*, female up to 1 cm. in length, male half as long. In the human large intestine. Specially common in children.

The *Gordiidæ* hold an isolated position among the *Nematoda* on account of peculiarities of inner organisation which will be spoken of in the anatomical portion. The mouth in adult animals is closed, and the intestine partly degenerated. *Gordius aquaticus*, in the adult sexually mature condition free in fresh water. The embryos find their way into insect larvæ, where they become encysted. If these larvæ are devoured by preying insects which live in water, the embryos develop in the body cavities of these new hosts, escaping into the water as sexual maturity approaches. 30-90 cm. long, 1 mm. thick.

Order 2. **Acanthocephala** (Fig. 172, p. 258).

Mouth and intestine wanting. At the anterior end a protrusible proboscis armed with hooks. Entirely parasitic. *Echinorhynchus: E. gigas*, in the small intestine of the pig. Larvæ in cockchafer grubs.

Class III. **Annulata (Segmented Worms)**.

Body elongated, cylindrical, or more or less flattened dorso-ventrally. Skin soft, or with more or less hard and rough chitinoid cuticle. Marked metamerism or segmentation of the inner organs; generally also outwardly visible. The body cavity, with the exception of *Hirudinea* and *Myzostomidæ*, well developed. The blood-vascular system generally well developed, seldom quite degenerated. The intestinal canal runs mostly in a direct line from the mouth to the terminal anus. The nervous system consists of a brain, an œsophageal ring, and a usually distinctly segmented chain of ventral ganglia. The excretory system (wanting in *Myzostoma*) consists of segmentally arranged paired nephridia. Nephridia often perform the function of conducting the sexual products to the exterior.

Order 1. **Hirudinea = Discophora (Leeches)**.

Body externally ringed. A definite number of consecutive rings correspond with an internal segment. Round the mouth an oral sucker, at the hinder end of the body under the anus a ventral sucker. Skin soft. Setæ wanting. Intestine mostly with paired lateral diverticula. Body cavity degenerated and communicating with the well-developed blood-vascular system. Numerous pairs of nephridia segmentally arranged (looped canals), which are not used for conducting the sexual products to the exterior. Hermaphrodite: testes in several pairs, segmentally arranged, with special efferent ducts ending in a single median external aperture. A pair of germaria placed in front of the testes; female aperture behind the male; both in the anterior end of the body. Parasites or carnivorous; fresh water, in the sea, or on land.

Sub-Order 1. **Rhynchobdellidæ.**

With cylindrical tubular pharynx lying free in the pharyngeal pouch, and protrusible through the mouth. *Clepsine*, *Pontobdella*, *Branchellion* (with gill-like appendages on the back). The two latter in the sea, parasitic on sharks.

Sub-Order 2. **Gnathobdellidæ.**

The pharynx is a muscular thickening of the œsophageal wall, which projects into the lumen in the shape of 3 plates or ridges occasionally toothed.

Hirudo medicinalis (the ordinary leech), *Hæmopis Aulastomum* (horse-leech), *Nephelis*. Some *Hirudinidæ* live on land. The remaining *Gnathobdellidæ* are fresh-water forms.

Order 2. **Chætopoda.**

The external segmentation of the body mostly corresponds with an inner segmentation. In special segmentally arranged glandular saccules of the outer integument (setigerous glands) arise setæ, which project freely above the skin. Body cavity well developed, separated from the blood-vascular system. The sexual products develop in special regions of the epithelial lining (endothelium) of the body cavity, into which they generally soon fall, and escape thence through more or less strongly modified nephridia (vasa deferentia, oviducts, genital pouches, segmental organs). The following division is artificial, and is only retained from practical considerations.

Sub-Order 1. **Oligochæta.**

The setigerous glands do not open on special blunt processes of the body (parapodia); outer appendages (antennæ, feelers, feeler-cirri, cirri, gills, etc.) are wanting. Hermaphrodite. Direct development. In fresh water or on land. Fam. *Aphanoneura: Æolosoma*. Fam. *Naidomorpha: Nais, Dero, Stylaria*. Fam. *Chætogastridæ: Chætogaster*. Fam. *Discodrilidæ* (posterior end of body modified into a sucker; parasitic on *Crustacea*): *Branchiobdella*. Fam. *Enchytræidæ: Pachydrilus, Enchytræus, Anachæta*. Fam. *Tubificidæ: Tubifex, Psammoryctes, Clitellio, Limnodrilus*. Fam. *Phreoryctidæ: Phreoryctes*. Fam. *Lumbriculidæ: Lumbriculus, Rhynchelmis, Stylodrilus*. Fam. *Criodrilidæ: Criodrilus*. Fam. *Lumbricidæ: Allurus, Dendrobæna, Allolobophora, Lumbricus* (earth-worm). And the related forms *Urochæta, Eudrilus, Acanthodrilus, Perichæta, Pleurochæta, Moniligaster*.

An uncertain position within the *Chætopoda* is taken by the so-called *Archiannelida* (*Polygordius, Protodrilus, Ctenodrilus, Histriobdella*) and *Saccocirrus*—forms whose organisation exhibits simple embryonic characteristics.

Between the *Oligochæta* and the *Polychæta* stand the families of the *Capitellidæ* (*Capitella, Notomastus, Dasybranchus*), and *Opheliacea* (*Ophelia, Travisia, Polyophthalmus*). The first have no blood-vessels. In both the parapodia are much reduced. Gills may be present or absent. Head not distinctly separated.

Sub-Order 2. **Polychæta.**

The setæ stand on very strongly developed segmentally arranged elevations or parapodia. On the head, antennæ or feeler-cirri; on the trunk segments, cirri, gills, or other appendages, which generally stand on the parapodia. Sexes mostly separate. Development with metamorphosis. Marine.

A. **Sedentaria = Capitibranchiata** (Tubicolous worms).—Pharynx (proboscis) mostly non-protrusible; without jaws. Eyes wanting, or small but numerous in the head. Parapodia slightly developed, the upper with hair-like setæ; the lower are transverse swellings with hooked setæ. Gills chiefly on the anterior segments, or limited to the head. Live in various kinds of tubes. Fam. *Cirratulidœ: Cirratulus.* Fam. *Arenicolidœ: Arenicola.* Fam. *Spionidœ: Spio.* Fam. *Arieiidœ: Arieia.* Fam. *Chlorhœmidœ: Siphonostoma.* Fam. *Terebellidœ: Lanice* (Terebella), *Polymnia, Amphitrite.* Fam. *Serpulidœ: Serpula, Sabella, Spirographis, Myxicola, Protula.* Fam. *Hermellidœ: Sabellaria* (Fig. 147, p. 221). Fam. *Sternaspidœ: Sternaspis.*

B. **Errantia = Dorsobranchiata** (carnivorous Annelids).—Pharynx protrusible, mostly with jaws; head distinct, mostly with a few large eyes. Parapodia well developed. Gills generally on the dorsal parapodia. Free-swimming or creeping animals, many of which live, at any rate at certain times, in tubes of their own making. Fam. *Aphroditea: Aphrodite, Hermione, Polynoe.* Fam. *Amphinomidœ: Amphinome, Euphrosyne, Notopygos.* Fam. *Eunieidœ: Diopatra, Eunice* (Fig. 124, p. 188), *Halla.* Fam. *Nereidœ: Nereis, Nephthys.* Fam. *Glyceridœ: Glycera.* Fam. *Syllidœ: Haplosyllis, Syllis, Exogone, Autolytus, Myrianida.* Fam. *Hesionidœ: Hesione.* Fam. *Phyllodoeidœ: Phyllodoce.* Fam. *Alciopidœ: Alciope, Asterope.* Fam. *Tomopteridœ: Tomopteris.*

Sub-Order 3. **Echiuridæ.**

Body tubular, in adult condition unsegmented or indistinctly segmented, without parapodia, without cirri, without gills. In front, on the ventral side, 2 hooked setæ. In the terminal portion of the much-coiled intestine 2 anal glands enter (modified nephridia of the anal region), which may be considered as excretory organs. There are besides 2 or 3 pairs of nephridia, or only one nephridium. Anterior end of the body over the mouth produced into a long variously shaped mobile prostomium (cephalic lobe) with ventral furrow. With blood-vascular system. Sexes separate. Development with metamorphosis. Marine animals with unknown mode of life. *Echiurus* (Fig. 148, p. 223), *Thalassema, Bonellia.* The diminutive *Turbellaria*-like ciliated males of this last species live parasitically in the females.

Order 3. **Myzostomidæ.**

Body flat, disc-shaped, externally unsegmented. Margin of the body with cirrus- or wart-like processes. On the ventral side, in two longitudinal rows, 5 pairs of parapodia, with hooks and supporting rod. In addition to the parapodia, on each side 4 suckers. Pharynx as in the *Rhynchobdellidœ* among the *Hirudinea.* Intestine with branched lateral diverticula. Body cavity reduced. Circulatory, excretory, and respiratory organs wanting. The nervous system consists of the œsophageal ring, and of a ventral chord fused into a ventral ganglionic mass. The brain is reduced. Hermaphrodites. The oviducts and the intestine together enter a cloaca. The seminal ducts have two separate external apertures on the ventral side. Besides hermaphrodite individuals, there are, in certain species, small males (complementary males). Parasitic on *Crinoids* (Fig. 175, p. 262).

CLASS IV. **Prosopygia.**

Body naked or shelled, varying greatly in form. Round the mouth a circle of ciliated tenacles, which are often inserted on a common horseshoe-shaped tentacle-carrier (lophophore), which may itself be produced into arms on each side. Without parapodia, and mostly without setæ. The anus is nearly always placed far to the front. The intestine runs backwards, but bends forwards again in a loop. Body unsegmented, or quite indistinctly segmented. Blood-vascular system wanting, or developed in varying degrees. Number of nephridia reduced (at the most 2 pairs); they occasionally serve as ducts for the transmission of the sexual products, and emerge to the front not far from the anus. Sexes separate. Only *Phoronis* is hermaphrodite. Live in the sea ; only a few forms in fresh water.

Order 1. **Sipunculacea.**

Body elongated, tubular, naked. The front part of the body, which is mostly thinner, can be invaginated like a proboscis into the larger and longer hinder part (trunk) by means of special retractors. Body cavity very spacious. Blood-vascular system (?) much reduced or wanting. The central nervous system consists of brain, œsophageal ring, and median ventral longitudinal trunk. Segmentation is perhaps denoted by nerve rings, which are regularly repeated. Live in mud or lurk in holes ; marine.

Sub-Order 1. **Sipunculidæ.**

Anus dorsal and anterior, on the boundary between the proboscis and the trunk. Mouth surrounded by tentacles. Usually 2 typical nephridia, opening externally in the neighbourhood of the anus ; also serving as efferent ducts for the sexual products. The vascular system consists principally of 2 tentacle vessels, which accompany the fore-gut. *Sipunculus* (Fig. 138, p. 208), *Phascolosoma.*

Sub-Order 2. **Priapulidæ.**

Anus dorsal at the posterior end. No tentacles around the mouth. No blood-vascular system. No nephridia. Two anal glands which emerge close to the anus and function in the young as excretory organs and in adults as genital organs. *Priapulus* (at the posterior end a tuft of appendages which probably function as gills), *Halycryptus* (without this caudal appendage).

Order 2. **Phoronidæ.**

Body vermiform, in an attached chitinous tube. Numerous tentacles stand on a horseshoe-shaped base around the mouth. Anus quite to the front, towards the dorsal side, near the mouth. Around the mouth a nerve ring (œsophageal ring). Two nephridia emerging to the front, serving at the same time as ducts for the transmission of the sexual products. A simple blood-vascular system present. Hermaphrodites. Single species : *Phoronis.*

Order 3. **Bryozoa.**

Small animals. Anus towards the dorsal side, near the mouth. A cerebral ganglion between mouth and anus. Nephridia, when present, in one pair of embryonic type, emerging near the mouth and not acting as ducts for the transmission of the sexual products. Numerous tentacles on a base, which is often horseshoe-shaped, around the mouth. Form, mostly by gemmation, variously shaped attached stocks.

Sub-Order 1. **Pterobranchia.**

Tentacle-carrier lengthened out on each side into a long arm-like process directed dorsally and posteriorly, and carrying the little tentacles in two longitudinal rows along its whole length. Intestine limited to the swollen anterior part of the body, which is prolonged backwards like a stalk. Body cavity little developed. Colonial, in tubes which raise themselves on a common creeping stem. *Rhabdopleura*, *Cephalodiscus* is a related form.

Sub-Order 2. **Ectoprocta**.

Anal opening outside of the tentacle carrier. Tentacle carrier not produced. Anterior body naked, posterior body shelled. Without stalk. Anterior body so enveloped in a fold of the posterior body as to be either temporarily or permanently surrounded by a sheath (tentacle sheath) out of which it can be protruded. Body cavity tolerably spacious. Shell often calcareous. Colonial. *Phylactolæmata.* Tentacle carrier horseshoe-shaped. Inhabit fresh water. *Cristatella, Alcyonella, Fredericella, Lophopus* (Fig. 122), *Plumatella* (Fig. 139, p. 208). *Gymnolæmata.* Tentacle-carrier circular. Live, with the exception of *Paludicella*, in the sea. *Cellepora, Eschara, Bugula, Flustra, Alcyonidium, Hornera*, etc.

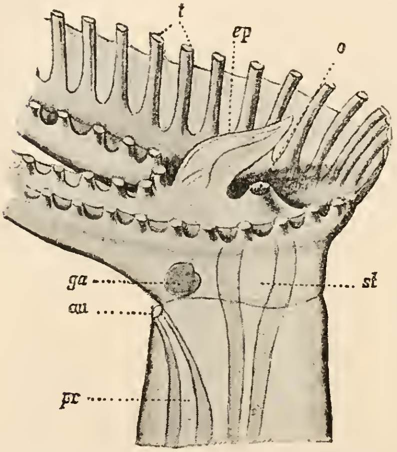


FIG. 122.—**Anterior body of Lophopus** (after **Allman**), from the right side. *t*, Tentacles cut off near the base; *o*, mouth; *ep*, epistome; *st*, fore-gut; *ga*, ganglion; *an*, anus; *pr*, hind-gut. The free ends of the tentacle-carrier are cut off.

Sub-Order 3. **Entoprocta**.

Anal opening inside the tentacle carrier. A tentacle sheath wanting. Body stalked. With one pair of nephridia. Body cavity reduced. *Pedicellina*, colonial. *Loxosoma*, living singly. Marine.

Order 4. **Brachiopoda** (Fig. 178, p. 269).

The dorsal and the ventral body walls form a fold directed to the front, so that the body is covered by dorsal and ventral mantle folds, which may coalesce behind and at the sides. The mantle folds secrete calcareous, and occasionally horny shell valves, a dorsal and a ventral. The ventral valve is generally the more concave. At the sides of the mouth are inserted the two long oral arms set with lateral cirri; these arms lie spirally rolled up in the mantle cavity, which is formed by the mantle folds, and are often supported by a special calcareous skeleton united to the dorsal valve. Anus wanting, or lies asymmetrically and anteriorly, to the right, near the mouth. In *Crania* only it lies quite behind, in the dorsal middle line. Central nervous system is an œsophageal ring with weakly developed brain and infra-œsophageal ganglionic swellings. One pair (less frequently two pairs) of nephridia, at the same time ducts for the transmission of the sexual products, open to the right and left of the mouth into the mantle cavity. Blood-vascular system probably present, with a heart placed above the intestine. The posterior end of the body is often prolonged into an attached stalk, which emerges either between the shell valves (*Lingula*), or through a hole in a posterior upward bulging of the larger ventral valve. In many cases the stalk is wanting, and the shell is fastened to the surface on which it rests direct by the ventral valve. Exclusively inhabitants of the sea. The larger proportion of the species and genera are fossil. The species *Lingula* has maintained itself since the Paleozoic epoch.

Sub-Order 1. **Testicardines.**

The shell valves are hinged together by interlocking processes. An anus is wanting. *Terebratula*, *Waldheimia*, *Thecidium* (attached by the larger shell valve). *Argiope*, *Rhynconella* (Fig. 125, p. 191), *Spirifer*.

Sub-Order 2. **Ecardines.**

Without hinge. Intestine with anus. *Crania*, *Lingula*.

Class V. **Rotatoria** (**Wheel Animalcule**, Fig. 123 ; Fig. 161, p. 245).

Small, mostly microscopic animals. Inner segmentation wanting. At the anterior end a variously shaped ciliated organ (wheel organ) ; posterior end prolonged in a frequently segmented appendage (foot-stalk). Cloacal aperture dorsal on the boundary of body and foot. A vascular system wanting. One pair of nephridia, of the embryonic type, with several inner ciliated cells, emerge with the anus and the oviduct into the cloaca. Sexes separate. The males small, with degenerated alimentary canal. Chiefly fresh-water animals. Forms living in attached tubes or envelopes: *Floscularia*, *Stephanoecros*, *Melicerta*, *Lacenularia*. In these the wheel organ is produced into lobes or tentacles. Free-living forms: *Notommata*, *Hydatina* (Fig. 161, p. 245), *Brachionus* (carapaced), *Asplancha*, *Seison* (parasitic on *Nebalia*).

We must place near the *Rotatoria* the peculiar species *Dinophilus* (Fig. 162, p. 246), which has the same appearance as certain annelid larvæ. Male and female are alike, or the male is smaller, without intestine. The whole ventral side of the body is ciliated. Besides this there are several ciliated rings lying one behind the other on the body. A wheel organ is wanting. Nephridia in segmental arrangement of the embryonic type.

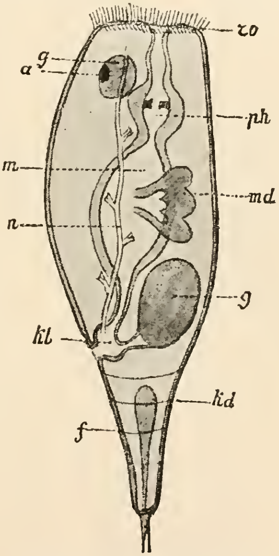


Fig. 123.—**Diagrammatic representation of the organisation of a Rotifer**, from the side. *ro*, Wheel organ ; *g*, brain ; *a*, eye ; *ph*, pharynx; *m*, stomach; *n*, nephridium; *md*, gastric gland ; *g*, genital gland ; *kl*, cloaca ; *kd*, cement gland of the foot (*f*).

Appendage to the Race of Vermes.

Class VI. **Chætognatha** (Fig. 152, p. 227).

Body cylindrical, elongated, with horizontal border of fins (lateral fins, caudal fin) round the posterior body. Head tolerably distinctly separated from the trunk. Body cavity spacious ; divided by partition walls into three consecutive parts—head cavity, trunk cavity, and tail cavity. Mouth surrounded by setæ (jaws). Intestine straight, anus ventral, at the commencement of the tail. The central nervous system consists of the brain, the œsophageal commissures, and a large ventral ganglion lying in the trunk. Without vascular system. Hermaphrodites—ovaria in the trunk cavity, testes in the caudal cavity. Paired efferent ducts (transformed nephridia ?) emerge to the right and left at the end of the trunk and of the tail. Live in the sea. *Sagitta*, *Spadella*.

Among the worms, generally near the *Rotatoria*, we place the little group of the **Gastrotricha.** Small animals with ciliated ventral surface; with pointed processes arranged in longitudinal rows on the dorsal surface. Posterior end running out into two lateral points. Intestine straight, the mouth followed by a muscular pharynx. Anus at the posterior end. Hermaphrodites. Nephridia insufficiently known. Blood-vascular system wanting. *Ichthydium*: principally inhabitants of fresh water. The **Echinodera**, which are often placed near the *Nematoda*, are minute marine animals without cilia, with ringed bodies; with setæ. Inner organisation not sufficiently known.

The phylogenetic relations of the worms are still a subject of much dispute. There are many different views. The *Nemertina* form a natural well-demarcated class which in many points of their organisation (nervous system, excretory system, absence of body cavity) recalls the *Turbellaria*, but they are raised above the *Platodes* by the possession of a blood-vascular system and an anus. The pseudo-metamerism of the Nemertian body is similar to that of certain *Turbellaria* (*Triclada*). The systematic position of the *Nemathelmia* is quite uncertain. Their ancestors were probably more highly developed worms, in whom adaptation to the parasitic mode of life has led to degeneration. Perhaps the *Gordiidæ* among the now living *Nematoda* are the nearest to the ancestral form. The *Annulata* form a large group extraordinarily rich in forms, in which the typical segmented condition of the body may be regarded as primitive. The *Myzostomidæ*, *Echiuridæ*, many simply organised *Chætopoda*, and in some respects the *Hirudinea*, are to be regarded as one-sidedly developed, partly simplified or degenerated forms. Opinions are very divided as to the racial history of the whole class. Many investigators, among whom we include ourselves, hold the segmentation (metamerism) of the *Annulate* body to be a continuation of the pseudo-metamerism of animals resembling the *Turbellaria* and the *Nemertina*. Others consider the *Annulate* body as a sort of animal stock, which has arisen by axial budding. They see in the *Rotatoria* the nearest approach to the unsegmented (not budding and not stock forming) racial form, while we, on the other hand, are inclined to consider the wheel animalculæ as simplified animals which attain sexual maturity at an earlier stage of development, so that they now no longer rise above the degree of organisation of a young *Annelid* larva. The class of the *Prosopygia* falls into a few natural orders to some extent sharply distinguished from each other; their organisation is in many respects quite comprehensible, if we refer it back to an old adaptation to a more or less attached mode of life, and bear in mind the degenerating action of shell, case, or tube formations on the bodies of segmented worms originally more highly developed. The systematic position of the *Chætognatha* also is very uncertain. They are, perhaps, best considered as *Annulata* with a small number (3) of segments. It has till now been impossible finally to decide the systematic position of *Gastrotricha* and *Echinodera*.

I. Form of Body and Outer Organisation.

The body of the *Nemertina* is elongated, ribbon-shaped, being more or less flattened dorso-ventrally; it is ciliated all over the surface, soft skinned, unsegmented, and without outer appendages. The mouth lies ventrally at or near the anterior end of the body, and in the form of a longitudinal slit. In front of it, and generally quite at the foremost end of the body, is the proboscidal aperture. Mouth and proboscidal aperture are united into a single external aperture only in *Amphiporus*, *Malacobdella*, and *Geonemertes palaensis*. On each side of the head there is often a strongly ciliated longitudinal furrow or lateral cleft. The anus is terminal. In the parasitic *Malacobdella* the posterior end forms, in front of and under the anus, a ventral sucker disc.

The body of the *Nemathelmia*, which is covered by a rough, frequently ringed cuticle, is elongated and spindle-shaped, without outer appendages, and with at the most small papillæ or small fringes at the anterior and posterior ends. Mouth and anus are, when present, terminal. The *Acanthocephala* possess at the anterior end a proboscis which can be withdrawn into a special sheath, and which is provided with hooks directed backwards; this serves for attachment to the intestinal wall of the host. The males have at the posterior end a protrusible copulatory organ, which, when protruded, is bell-shaped.

The various classes of the *Annulata* must be dealt with separately.

The body of the *Hirudinea* is long, and generally flattened dorso-ventrally; less frequently it is cylindrical (*Pontobdella*, *Piscicola*). Round the mouth there is a small oral sucker and posteriorly, always under the anus, a ventral sucker, which is usually larger than the oral. The body is divided by furrows into numerous consecutive rings; these do not, however, correspond in number with the inner segments. In all the *Hirudinea* the number of the latter corresponds with the number of the ganglia, and is 33. The number of rings to a segment in the central part of the body is typical for the various genera and species. Among the *Rhynchobdellidæ* it is 3 (*Branchellion*, *Clepsine*), or 6 (*Calliobdella*, *Ichthyobdella*, *Pontobdella*), or 12 (*Piscicola*); among the *Gnathobdellidæ* it is 5. In all *Hirudinea* the segments are shorter at both the anterior and posterior ends of the body, the number of rings in them being gradually reduced. Where the separate rings of the typical central segments are in any special way externally marked, the marks are repeated in regular succession throughout the body, *i.e.* when such marked rings have not disappeared in the shortening of the segments. These marks take the form of tactile papillæ, warts, protuberances, pigment spots, nephridial apertures, etc. The large protuberances on the integument of *Pontobdella* play a most important part in the dermal respiration. In *Branchellion*, on each side of each ring in the middle region of the body, there is an integumental appendage which functions as a gill. The appendages on the first ring of each segment swell at their bases and form contractile vesicles.

In the *Chætopoda* the outer segmentation generally answers to the inner. The former is most distinctly to be recognised by the arrangement of the setæ, which are repeated in strict accordance with the segments. The setæ generally stand in groups. Every segment, except the oral, carries typically on each side two bundles of setæ, one dorsal and the other ventral.

The shape, number, and arrangement of the setæ vary in details to an extraordinary degree, and are of the greatest significance for classification. Setæ are wanting only in a few *Chætopoda*, as in the *Enchytræidæ* (*Anachæta*) and in *Brachiobdella* among the *Oligochæta*, in the so-called *Archiannelida* (*Polygordius*, *Protodrilus*, etc.), and in the *Tomopteridæ*. In *Chætogaster* the dorsal rows of setæ are wanting; and in *Saccocirrus* also only one longitudinal row is found on each side. In the stationary *Polychæta* each ventral bundle of setæ is developed in the form of a transverse row of short hooks. The bundles can break up into their component parts, the setæ being arranged in *Perichæta* in a single row round the segment. The setæ may disappear in certain regions of the body. They are specially reduced in number in the *Echiuridæ* (see systematic review).

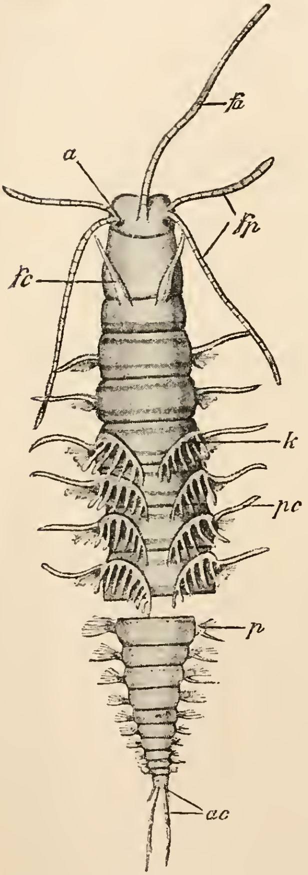


Fig. 124.—**Eunice limosa** (after **Ehlers**). Anterior and posterior ends of the body; dorsal side. *fa*, Unpaired feeler; *fp*, paired feelers; *a*, eyes; *fc*, feeler-cirri; *k*, gills; *pc*, dorsal parapodial cirri; *p*, parapodia; *ac*, anal cirri.

The bundles of setæ stand either simply in the integument, or on special elevations of the body wall, the so-called **parapodia** (Fig. 158, p. 237). The former is the case chiefly in the *Oligochæta* and *Echiuridæ*, the latter in most of the *Polychæta*. The parapodia are well developed as strong rowing and locomotory organs principally in the *Errantia*, while they are reduced in the *Sedentaria*, especially the ventral parapodia, which are for the most part insignificant ridges carrying hooks. In a few tube-worms (*e.g. Serpulidæ*) the parapodia are entirely obliterated, no doubt in adaptation to the tubicolous manner of life. They are also wanting in the *Archiannelida*. We do not always find separate ventral and dorsal parapodia; there is often on each side only one row of parapodia. We then, however, find in each parapodium a dorsal and a ventral branch. Whether the uniserial or the biserial arrangement is the original cannot yet be decided.

In the *Polychæta* the parapodia themselves again carry characteristic appendages (Fig. 124). These are the **cirri**, unsegmented or segmented filaments, one of which, in the simplest cases, occurs on each parapodium. We can thus distinguish dorsal and ventral cirri. The cirri may undergo the most varied transformations. Thus the dorsal cirri, or their lateral branches, frequently become gills, which are often delicately branched and provided with blood-vessels. In the *Aphroditidæ* they become broad dorsal scales (**elytra**). In some cases (*e.g. Capitellidæ*, *Glyceridæ*) the dorsal parapodia may carry, besides the typical cirrus or the cirrus transformed into a lateral organ, a gill, which, in contradistinction to the gill which arises from the cirrus, is called a lymph gill; it is provided with hæmolymph by continuations of the body cavity (in the absence of a blood-vascular system). The cirri may stand at the base of the parapodia, or may even move away from them. They may even be retained in those cases where the parapodia disappear.

The **head** of the *Polychæta* is characterised by special appendages, the front ones being called feelers, the back ones feeler-cirri. They never stand on parapodia, which are just as constantly wanting in the true oral segment as are setæ. In most of the delicate tubicolous *Polychæta* a reduction of the parapodial cirri or parapodial gills goes hand in hand with the reduction of the parapodia on the trunk; they are retained only in the anterior segments. In the *Serpulidæ* all the parapodial appendages are reduced, and therefore the head appendages are transformed into greatly developed tentacle gills which often form a stately crown. In *Sternaspis* on each side of the anus there is a tuft of gills.

In the *Oligochæta*, *Archiannelida*, *Echiuridæ*, and some of the *Capitellidæ*, not only the parapodia but their appendages (cirri, gills) are wanting. Only, *Alma nilotica*, a very insufficiently known *Oligochæte* which is found in muddy ditches in Egypt, carries dorsal gills on the hinder part of its body. In all these divisions the head appendages are also wanting. Only the *Archiannelida* (*Polygordius*, *Protodrilus*) possess two feelers at the extreme front of the head. In the *Echiuridæ* the head is produced in front of and over the mouth into a long process provided with a longitudinal furrow or channel on the ventral side (proboscis, prostomium); this in *Bonellia* is forked at its end.

The inner segmentation is reflected outwardly in most *Chætopoda*, not only by the regular repetition of the setæ (and the parapodia of the *Polychæta*), but also by an outer division of the body into rings, which is caused by the occurrence of more or less distinct regularly-repeated constrictions. These constrictions are generally found between 2 consecutive segments, and thus the rings, in number and position, answer to the real segments. It only seldom occurs that each segment is again ringed. In many of the lower *Oligochæta*, indeed in the *Archiannelida* and some of the *Echiuridæ*, no distinct mark of rings or segmentation is recognisable on the integument.

The body of the *Chætopoda* is outwardly either **homonomously segmented**, *i.e.* all consecutive segments of the trunk are alike, or **heteronomously segmented**, when the segments in different regions are differently developed, both as concerns their outer shape and their provision with various setæ, parapodia, cirri, gills, etc. We can in the latter case distinguish different regions of the body (*e.g.* thoracic region, branchial region, abdominal region, etc.) The integument of the *Chæto-*

poda is covered with a chitinous cuticle which is specially strongly developed in the *Polychæta Errantia.* The cuticle is weaker and much more delicate in most of the *Oligochæta* which live in mud, and in the tubicolous *Polychæta.*

For the general form of body and outer organisation of the *Myzostomidæ* compare the systematic review.

The form of the body in the *Prosopygia* is extremely varied. The most important points have already been referred to in the systematic review. The body is as little segmented externally as internally.

In the *Sipunculacea* (*Sipunculus*, *Priapulus*, *Halicryptus*) a regular outward ringing of the trunk occurs. The rings, at least in some cases, correspond with the muscle bundles of the circular musculature and with the lateral nerves which proceed from the ventral strand. In *Sipunculus* there are, in addition to the circular furrows on the trunk, still deeper and more distinct longitudinal furrows, so that the whole skin seems divided into regular die-shaped areas. There are similar longitudinal furrows on the "proboscis" of *Priapulus.* Papillæ are very wide spread on the bodies of the *Sipunculacea*, principally on the proboscis.

A closer comparison of the proboscis of the *Sipunculacea* with the similarly named organ of the *Echiuridæ* (which formerly were united with them in the class of the **Gephyrea**) shows great morphological difference between the two organs. The proboscis of the *Sipunculacea* is the front portion of the body, which can be invaginated into the hinder portion. The mouth lies at its anterior end. The proboscis of the *Echiuridæ* is a prolongation of the head portion (prostomium), which lies in front of and above the mouth and cannot be invaginated. The mouth lies at its base. In the proboscis of the *Sipunculacea* runs the fore-gut, while the fore-gut is in no way connected with the prostomium of the *Echiuridæ.*

The *Sipunculacea* possess a rough cuticle; in *Phoronis* it is delicate, and the skin therefore secretes a detached chitinous envelope, which serves as a dwelling tube. The *Bryozoa* generally form a rough hard cuticle (cell, ectocyst) whose aperture can be closed by a cover, and which often calcifies. In a similar way the mantle of the *Brachiopoda* secretes a bivalve shell which is generally calcareous, less frequently horny.

This shell of the *Brachiopoda* (Fig. 125) cannot be compared with the similarly bivalved shell of the *Mussel* (*Lamellibranchiata, Cochlidæ*). The two shell valves of the former are dorsal and ventral; each valve is symmetrical; the median plane of the body divides each valve into two lateral congruent halves. In the mussels, on the contrary, we distinguish a right and a left shell. The median plane passes between the two shell valves. Each valve is asymmetrical. The gaping edge of the shell in the mussels is ventral, in the *Brachiopoda* anterior; the closed edge where the two valves are joined by a hinge is dorsal in the mussels, in the *Brachiopoda* it is posterior.

We have already, in the systematic review, said what is most important concerning the oral tentacles and oral arms, which are very characteristic of the *Prosopygia*; the various positions of the anus were also described. Refer to it also for the outer form and organisation of the *Rotatoria* and *Chætognatha*.

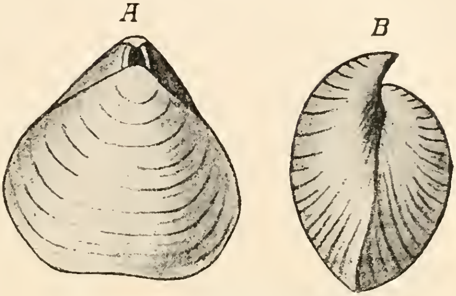


Fig. 125.—**Rhynconella psittacea.** *A*, From above. *B*, From the left side.

II. The Integument.

The integument of the worms consists first of the **outer cuticle**, and second of the subjacent **body epithelium**, which secretes the cuticle, and which in most worms (just as in the *Arthropoda*) is called the **hypodermis**.

The cuticle is very variously developed. It is thin and delicate in the soft-bodied forms, especially in the *Nemertina*, where it is perforated by very fine pores to allow the cilia to pass through. Where it is strongly developed, as in many *Annulata*, *Prosopygia*, *Nematoda*, and *Rotatoria*, it gives protection and support to the body, and as skeleton offers support and surfaces of attachment to the body musculature. It consists of a substance allied to chitin, and occasionally calcifies (in *Bryozoa*, *Brachiopoda*) into a very hard envelope or shell. It often shows stratification, and seems to be composed of various crossing systems of very fine adhering fibrillæ. It may in general be conceived of as a secretory product of the glandular hypodermis cells which underlie it, or as a product of metabolism of the protoplasm of these cells. To the same category as the cuticle belong various sorts of tubes and envelopes which, detached from the integument, surround the bodies of many *Annelida* (tube-worms) and possess a chitinous substratum. We must further consider the **setæ** of the *Chætopoda* as cuticular formations of certain hypodermal glands, which can be seen, at least when they first appear, to be composed of fibrillæ and fibres in close contact and glued together.

The cellular **hypodermis**, which usually consists of one layer, can best be examined in the *Annulata*, where it is composed of the two following principal elements—(1) **gland cells**; these are naked and large, and yield the material for cuticular formations; over each gland cell there is generally a pore in the cuticle; (2) **thread-like cells**; these are generally slender cells whose protoplasm is strongly modified and falls into fibres. They often lose their nuclei, and are arranged round the gland cells in such a way as to form for the latter a loose supporting tissue, in whose meshes the gland cells lie. Gland cells of the hypodermis form the chief component part of the subdermal setiparous sacs of the *Chætopoda;* these are the setiparous glands which produce the setæ.

The setiparous glands may undergo important transformations. In *Polyodontes* (*Aphroditidæ*), for example, the setiparous glands of the dorsal branch of the parapodia are changed into large **spinning glands**, whose thread-like secretion yields the material for the structure of the tubes they inhabit. In *Aphrodite* the dorsal setiparous glands produce setæ and hairs, which form the hairy felt covering the respiratory chambers. The setiparous glands may again become simple dermal glands. *Anachæta*, for example, no longer possesses setæ, but, in place of the 4 rows of setæ of the related *Enchytræus* species, has 4 rows of flask-shaped hypodermal glands projecting into the body cavity. The mucous glands are peculiar dermal glands which are common, especially in naked and soft worms (*Nemertina, Hirudinea*).

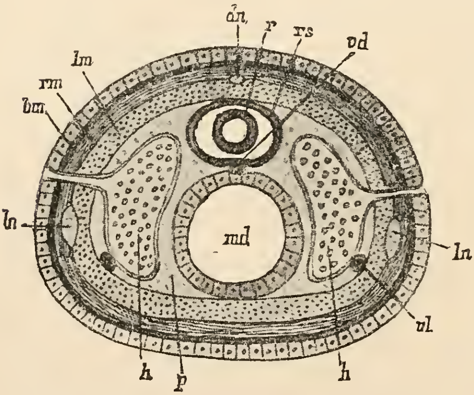


FIG. 126.—**Transverse section through the middle part of the body of a Nemertian**, half diagrammatic. *ln*, Lateral longitudinal nerves ; *dn*, medio dorsal nerve ; *bm*, basal membrane ; *rm*,' circular muscle layer ; *lm*, longitudinal muscle layer ; *rs*, proboscis sheath ; *r*, proboscis ; *vd*, dorsal vessel ; *vl*, lateral vessels ; *h*, testes ; *p*, parenchyma ; *md*, mid-gut.

The hypodermis may be very insignificant in comparison with the cuticle. Its elements may fuse into a subcuticular layer of protoplasm. In the *Gordiidæ* among the *Nemathelmia* we still find it clearly developed into an epithelial layer at the anterior and posterior ends of the body, while in the rest of the body it is reduced to a subcuticular finely granulated layer containing scattered nuclei. In this reduced form we meet with the hypodermis in all other *Nemathelmia*, where it is often hardly recognisable. It seems here to be almost entirely taken up in the formation of the strong cuticle. The same is the case in the *Bryozoa*.

In the *Hirudinea* and in most *Oligochæta*, as sexual maturity begins, the hypodermis undergoes a peculiar metamorphosis in a series of the segments near the genital apertures (in the *Hirudinea* always the tenth, eleventh, and twelfth.) The gland cells here swell greatly and come to lie in several superimposed layers, and there thus arises a girdle-like thickening of the body which is outwardly visible (the **clitellum**).

In the gill-less *Annulata* (higher *Oligochæta, Hirudinea*) capillaries of the blood-vascular system may penetrate as far as into the hypodermis, and so enter the service of the general cutaneous respiration.

In *Chætopoda*, a plexus of ganglionic cells lying immediately under the hypodermis can be demonstrated, which is connected by nerve fibrillæ with the thread-like cells of the hypodermis.

In many worms (*Aphanoneura*, *Archiannelida*, *Saccocirrus*, *Opheliacea*, various *Polychæta* of families widely separated, and further in the *Priapulidæ*, *Phoronidæ*, and *Sagitta*) the central nervous system lies in the hypodermis in such a way that no sharp distinction can be seen between the usual hypodermis cells and the nerve elements. In many *Annulata* whose central nervous system lies *under* the hypodermis, the former nevertheless passes into the hypodermis at the most anterior and posterior ends, the anterior part of the brain into the hypodermis of the prostomium, and the most posterior end of the ventral chord into the hypodermis of the tail segment.

The sensory organs of most worms, which will be described elsewhere, belong to the hypodermis.

The hypodermis is often separated from the underlying tissues by a thin supporting or basal membrane.

III. The Dermo-muscular Tube.

Immediately under the outer integument in most worms the body musculature lies in the form of a dermo-muscular tube, which repeats the shape of the body. It consists in general of two well-developed layers, an **outer layer of circular fibres** and an **inner layer of longitudinal fibres.**

These two layers are found in all *Nemertina*, except *Cephalothrix*, where the circular muscle layer may be wanting. In the *Schizonemertina*, and further in *Polia* and *Valencinia*, there is, in addition, an outer longitudinal layer, which may even be more strongly developed than the inner layer; in *Carinina*, *Carinella*, and *Carinoma* there is also an additional circular layer. All these layers form in the *Nemertina* a continuous tube, nowhere broken through in any way worth mentioning.

Among the *Nemathelminths*, all the *Nematoda* possess only the longitudinal muscular layer (Fig. 127, *lm*). This is broken through in 4 lines running in the longitudinal direction, and thus falls into 4 longitudinal portions. Two of the 4 longitudinal lines are median (dorsal and ventral) and 2 lateral. In these lines of interruption the subcuticular granulated dermal layer (hypodermis) is thickened, and in it lie definite organs of which we shall speak later. In the *Gordiidæ* the ventral line only is clearly marked.

In the *Acanthocephala*, besides the longitudinal muscular layer, an outer circular muscular layer is added.

In the *Annulata* the dermal musculature almost everywhere appears in the typical form. The circular layer is very rarely

(*Archiannelida*) wanting. Other layers are, however, sometimes added to the two typical layers, for instance, a layer of fibres which cross each other diagonally in the *Hirudinea* and *Echiuridæ*. The circular layer is everywhere continuous; the longitudinal layer, however, is almost always broken through at different places in the *Chætopoda*. These breaches are often very dissimilar in different genera and families, so that they cannot all be comprised in the same description. The most frequent are those in the dorsal and ventral lines, then in the longitudinal lines formed by the bundles of setæ and the parapodia. The various arrangement of these latter naturally causes variety in the arrangement of the lines or areas of interruption. As a rule in the *Annulata*, the longitudinal musculature is more strongly developed than the circular musculature.

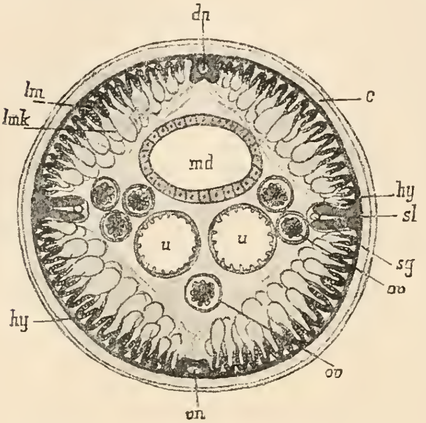


Fig. 127.—**Transverse section through a Nematode (Ascaris).** *dn*, Medio-dorsal, *vn*, medio-ventral longitudinal nerve in the line which represents the middle line of the body; *sl*, lateral lines; *c*, cuticle; *hy*, hypodermis; *sg*, lateral vessels; *ov*, ovarial tubes; *lm*, longitudinal musculature; *lmk*, cell elements of the longitudinal muscular fibres; *u*, uterus; *md*, mid-gut.

The dermal musculature of the *Myzostomidæ* is difficult to make out. We may perhaps distinguish: (1) a system of fibres which radiate from the centre to the circumference; (2) a system of fibres concentrically arranged, and running parallel to the edge of the body. The first system must represent the circular musculature of the *Annulata*, the second their longitudinal musculature.

The various groups of muscles which serve in the *Chætopoda* for moving the bundles of setæ, the parapodia and their appendages, must be regarded as special local modifications of the dermal musculature. In the *Sternaspidæ*, as in the *Sipunculidæ*, we find parts of the longitudinal musculature differentiated into dorsal and ventral retractors of the anterior introvertible portion of the body.

The general body musculature is developed in a very different manner in the *Prosopygia*. The naked *Sipunculacea* possess a strong and typically developed dermo-muscular tube, consisting of an outer circular and an inner longitudinal layer (Fig. 128). Between these two, in the *Sipunculidæ*, a thin layer of diagonal fibres is interposed. The longitudinal and circular muscles generally run in regular bundles or bands lying side by side, and these correspond with the outwardly visible longitudinal and circular ridges. The longitudinal musculature supplies the retractors of the proboscis (Fig. 138, p. 208); the number of these retractors varies, and is of great importance for classification; they are attached to the dermo-muscular tube on the one hand at the anterior end of the proboscis (anterior portion of the head), and on the other at the anterior or middle portion of the trunk, and run freely through the body cavity.

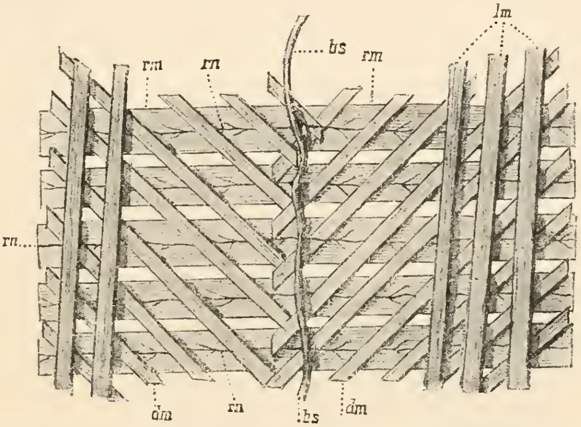


Fig. 128.—**Portion of the musculature of the body wall of Sipunculus,** diagrammatic (after **Andreae**). *lm*, Longitudinal muscles, partly left out; *rm*, circular muscles; *dm*, diagonal muscles, cut away in the middle line; *bs*, ventral chord; *rn*, nerve rings.

In the *Phoronidæ* which live in chitinous tubes there is a typical bilaminar dermo-muscular tube.

In the *Bryozoa* we can no longer speak of a dermo-muscular tube. Its extreme reduction is to be referred to the development of a stiff skeleton (shells, cells, ectocysts), which deprives a dermo-muscular tube of its function. Only such portions of the general musculature remain as are necessary for the withdrawal and protrusion of the soft-skinned anterior end with its tentacles, or (*Rhabdopleura*) for the contraction of the stalk of the body, which is movable within its tube (longitudinal muscles of the stalk). In the *Endoprocta* also there is, especially in the stalk, a delicate longitudinal muscular layer immediately under the skin. The elastic cuticle (which takes the place of the circular musculature), or (*Pterobranchia*) a cartilaginous substance which forms an axial strand in the stalk, serves to counteract these muscles.

The muscular apparatus which serves for the protrusion and withdrawal of the anterior tentacle-bearing end of the body out of and into the cells, in those *Bryozoa* provided with a temporary or permanent tentacle sheath, has been best observed in the fresh-water forms (Fig. 139, p. 208). It consists esentially of 3 parts: (1) of retractors which run in a longitudinal direction (like those of the *Sipunculacea*) through the body cavity, and are attached on one hand to the anterior end of the body near the tentacles, on the other to the body wall at the base of the cell;

(2) of a system of fibres stretched between the invaginated wall of the proboscis sheath and the neighbouring outer body wall (parieto-vaginal muscles); (3) of circular muscles, generally developed only on the anterior body wall, though in *Paludicella* they appear as subdermal muscular hoops in the whole body, and by their contraction cause the protrusion out of the cells of the withdrawn anterior end of the body with its tentacles. All these circular muscles are to be considered as remains of the circular muscle layer; the retractors and parieto-vaginal muscles as remains of the longitudinal musculature of a dermo-muscular tube.

In the *Brachiopoda* a typical dermo-muscular tube is as little developed as in the *Bryozoa;* its absence is here also evidently to be referred to the development of a shell. As remains of a dermo-muscular tube, there are: (1) lying under the integument of the mantle, weakly-developed fibres running transversely and longitudinally; (2) the arm muscles (protractors and retractors); and (3) the longitudinal muscles of the peduncle, which, in the almost universal absence of a circular musculature, are counteracted by its elastic wall.

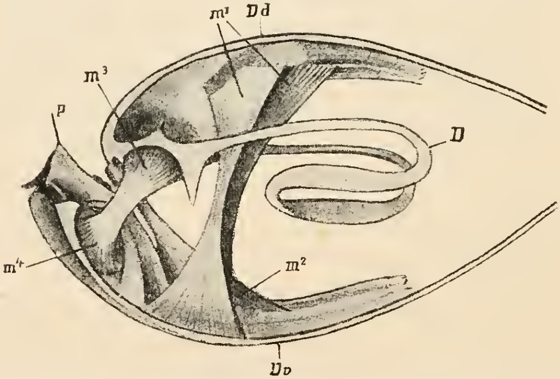


Fig. 129.—**Preparation of Waldheimia flavescens** (after **Owen**), seen from the right side, to demonstrate the musculature, the peduncle (*p*) and the calcareous framework (*D*) which serves to support the arms. *Dd*, Dorsal, *Dv*, ventral shell valve; m_1, m_2, m_3, m_4, muscles for opening and closing the shell.

In the *Brachiopoda* a system of strong dorso-ventral muscles passing through the body cavity (Fig. 129) serve for closing and opening the two valves of the shell (adductors and divaricators). They are attached to both the shell valves in the posterior region of the body in the neighbourhood of the hinge (where this is present). These muscles cannot be regarded as dislocated or modified portions of the dermo-muscular tube.

In *Dinophilus* there is found under the body epithelium a very weakly developed dermo-muscular tube (circular and longitudinal muscle layers).

The muscles of the *Rotatoria* mostly run as isolated fibres in the longitudinal direction, or circularly round the body. The longitudinal muscles are always more strongly developed, attach themselves at both ends to the integument, and serve chiefly for drawing in the anterior end with the wheel organ, for shortening the tail or foot, and, in tubicolous forms, for withdrawing the body into its case.

The dermo-muscular tube of the *Chætognatha*, which swim with arrow-like speed, is very strongly developed, in keeping with its high degree of activity. A circular muscle layer is, however, wanting. The longitudinal musculature (Fig. 130, *lm*) is divided by 4 longitudinal lines of interruption (2 lateral, 1 medio-dorsal, and 1 medio-ventral) into 4 areas (2 dorsal and 2 ventral).

Worm-like contractions do not occur, in consequence of the want of a circular muscle layer. By alternate contractions of dorsal and ventral musculature, and by the co-operation of the horizontal fins, the elastic body is quickly propelled forwards. It was chiefly the similarity of the muscular arrangement of the *Chætognatha* with that of the *Nematoda* which caused many zoologists to place the former with the *Nemathelminths*.

In the genus *Spadella* there is a thin layer of transverse muscle fibrillæ lying in the body cavity, closely applied to the ventral musculature. The arrangement of the musculature in the head of the *Chætognatha* undergoes a marked complication. The most important head muscles are those which serve for moving the seizing hooks.

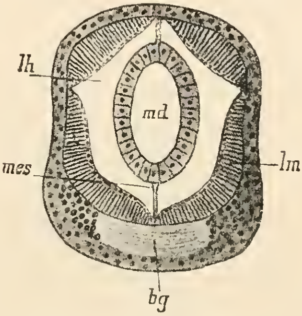


FIG. 130. — **Transverse section through the trunk of a Sagitta** (after **O. Hertwig**). *lh*, Body cavity; *mes*, mesentery of the intestine; *md*, mid-gut; *lm*, longitudinal musculature; *bg*, ventral ganglion.

IV. The Proboscis of the Nemertina and Acanthocephala.

These organs may be treated of together, although they arise quite independently, and are not homologous.

In the **proboscidal apparatus** of the *Nemertina* (Fig. 131) we distinguish the following principal parts: (1) the proboscis sheath; (2) the proboscis; (3) the retractor muscle of the proboscis.

The **proboscis sheath** (*rs*) is a tube closed on all sides which lies above the intestinal canal in the parenchyma of the body. Its muscular walls consist principally of a circular and a longitudinal muscle layer. The proboscis sheath stretches more or less far back, often to near the hindermost end of the body.

The **proboscis** (*r*) is also a cylindrical tube. It lies invaginated into the proboscis sheath. The space, closed in on all sides, between proboscis sheath and proboscis is filled with fluid. The walls of the proboscis sheath and of the proboscis join each other not far behind the foremost end of the body. From this point a short tube (**rhyncho-**

dæum, *rd*) stretches to the most anterior end of the body, to emerge generally separately from the oral aperture in front of and above it. The whole proboscidal apparatus is entirely separate from the intestinal canal. The rhynchodæum thus leads through the proboscidal aperture into the central cavity of the proboscis which closes blindly behind. The wall of the long proboscis is extremely muscular, the arrangement of the fibres being occasionally very complicated. It is internally lined with epithelium which is continued on to the rhynchodæum,

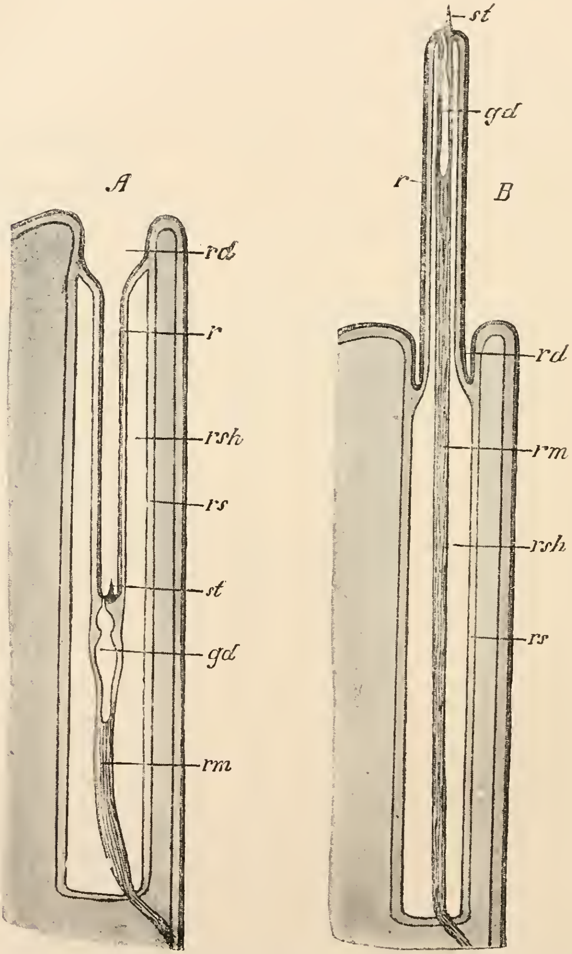


FIG. 131.—Diagrammatic representation of the proboscidal apparatus of the Nemertina. *A*, Proboscis withdrawn. *B*, Proboscis protruded. *r*, Proboscis; *rs*, proboscis sheath; *rsh*, cavity of the latter; *st*, stylet; *gd*, poison gland; *rm*, retractor muscle; *rd*, rhynchodæum.

and which, at the external aperture of the latter, passes into the outer body epithelium.

At the blind posterior end of the proboscis a strand of muscle fibres is inserted, the **retractor** (*rm*) of the proboscis, which runs freely inside the proboscis sheath to its posterior end, breaking through its walls to lose itself in the dorsal longitudinal musculature. The proboscis can be evaginated from the proboscis sheath. This occurs principally by a contraction of the muscular walls of the proboscis sheath. In an evaginated condition the proboscis projects from the anterior end of the body as a long tube, while the rhynchodæum remains in its position. The inner wall then lies outside, the outer wall inside; the blind posterior end is at the extreme point of the protruded proboscis, and its epithelium then represents still more clearly than before a simple continuation of the outer body epithelium. The anterior part of the extended retractor then lies in the central cavity of the proboscis into which the fluid of the proboscis sheath penetrates. By contraction of the retractor the proboscis is again invaginated.

At the blind end of the invaginated proboscis there is found in the *Hoplonemertina* a stylet (*st*) projecting into the proboscidal cavity, and at its side accessory stylets, mostly small and in the course of formation. These stylets, when the proboscis is fully protruded, come to lie at its foremost end and project freely. Further, the duct of a sac-like gland (poison gland) (*gd*) to whose posterior end the retractor is attached, is also often found at the end of the proboscis. In the unarmed *Nemertina* numerous rod-shaped bodies or stinging capsules lie in the epithelium of the proboscis. Only in *Amphiporus*, *Malacobdella*, and *Geonemertes palaensis* the proboscidal aperture opens into the œsophagus from above, so that the proboscis is protruded through the mouth. Few observations have been made as to the function of the *Nemertian* proboscis, which when irritated is generally so energetically projected that it tears itself off at its edge of insertion in the rhynchodæum. It probably serves as a weapon both for defence and offence.

We have already in the *Platodes* become acquainted with organs similar to the proboscidal apparatus of the *Nemertina*. The proboscis of the *Proboscidea* (p. 150) among the *Rhabdocœla* (*Turbellaria*), representing an invagination of the most anterior body wall which has become permanent, may possibly be homologous with the *Nemertian* proboscis. There is a further extraordinary correspondence in general arrangement between the proboscidal apparatus of the *Nemertina* and each of the 4 proboscidal apparati of the *Tetrarhynchidæ* among the *Cestoda*.

The proboscidal apparatus of the *Acanthocephala* (Fig. 172, p. 258) consists of the following principal parts: (1) the proboscis, (2) the proboscis sheath, (3) the proboscis retractor, (4) the retractors of the proboscis sheath, (5) the retinacula.

The **proboscis** in its evaginated condition represents the cylindrical or conical anterior end of the body, narrowed and outwardly armed with numerous hooks or stylets. The **proboscis sheath** is a muscular pouch with a double wall, closed on all sides. It is attached at the base of the proboscis to the body wall, and projects thence backwards into the body cavity. It receives the proboscis when the latter is invaginated. By its contraction the proboscis is protruded. The

proboscis retractor consists of longitudinal muscles, which, running inside the proboscis sheath, are attached on one side to the base (posterior wall) of the proboscis sheath, and on the other to the apex of the proboscis. By its contraction the proboscis is invaginated. The proboscis retractor is continued at the posterior end of the proboscis sheath into the two muscular **retractors of the proboscis sheath**, which run through the body cavity, one being dorsal and the other ventral, to attach themselves to the dermo-muscular tube. These retractors hold the proboscis sheath in its place. At the base of the proboscis sheath there arise further two occasionally muscular strands, the **retinacula**, which run laterally through the body cavity into the body wall, and carry back within them lateral nerve strands which come from the cerebral ganglion lying in the base of the proboscis sheath.

V. The Intestinal Canal.

The intestinal canal in the Worms is, in general, well developed and provided with an anus. Only in the endoparasitic *Acanthocephala* every trace of an intestinal canal has disappeared. In the males of the *Rotatoria* also, and the males of certain species of *Dinophilus*, the intestine is more or less completely degenerated. The intestine of the dwarf male of *Bonellia*, which lives parasitically in the female, is without mouth or anus. In the sexually mature *Gordiidæ* also the mouth is closed by an overgrowth of the cuticle. An anus is wanting in various *Nematoda*, such as *Mermithidæ*, *Ichthyonema*, and *Filaria medinensis*. In the hermaphrodite generation of *Allantonema mirabile* the intestine is quite reduced. A more or less far-reaching reduction of the intestine can also be found in other *Nematoda*, *e.g. Atractonema*, *Sphærularia*. The intestine ends blindly in the *Testicardines* among the *Brachiopoda*, and in *Asplanchna* among the *Rotatoria*. All these defects and degenerations represent a derived condition, in contrast with the well-developed intestine which is provided with an anus. The degeneration can for the most part be ontogenetically established.

The walls of the intestine consist almost everywhere of 2 layers, an outer muscular layer, which we might name the intestino-muscular tube in contradistinction to the dermo-muscular tube, and an inner epithelial layer turned towards the intestinal lumen.

We can, from an ontogenetic point of view, distinguish three divisions in this intestine, the first two being already known to us in the *Cœlenterata* and *Platodes*. (1) The **fore-gut** which proceeds from the stomodæum of the larva or embryo. Its epithelium is of ectodermal origin, and it seems chiefly to supply the various adaptations for seizing food, for reducing it into smaller pieces, and for passing it on further (pharynx, jaws, teeth). (2) The **mid-gut** comes from the mid-gut (mesenteron) of the larva; its epithelium is of endodermal origin. It forms the principal digesting portion of the intestine. (3)

The **hind-gut**, mostly short, often hardly distinguishable, comes from the proctodæum of the larva or embryo; its epithelium is derived from the ectoderm. It ejects the undigestible remains of food through the anal aperture. We will treat of these three divisions separately, taking the worms in order.

A. The Fore-gut.

The fore-gut is called the **gullet** or **œsophagus** in the *Nemertina*. It is chiefly to be distinguished from the mid-gut which follows it by the finer structure of its walls. Here and there glands have been observed entering it; these are salivary glands. There are no special muscular swellings in the œsophagus of the *Nemertina*, a want which is compensated for by the development of a special proboscidal apparatus.

The œsophagus of the *Nematoda* is always distinctly separated from the mid-gut, and lined by a strong cuticle, a continuation of the cuticle of the outer integument. Its muscular wall is always thickened into a generally round or egg-shaped **pharynx**, which consists principally of muscle fibres placed radially to its axis. The mouth often lies at the base of a variously shaped buccal cavity, provided with hard teeth, lips, papillæ, etc., and the pharynx itself may fall into two consecutive parts by means of a transverse constriction. Less frequently glandular tubes entering the buccal cavity have been observed.

The fore-gut of the *Annulata* shows very various adaptations. In the *Hirudinea* we can already distinguish two types. In the *Rhynchobdellidæ* a pharyngeal apparatus is developed, which agrees even in details with that of the *Triclada*, *Alloiocœla*, and many *Polyclada* among the *Platodes*. The mouth leads into a cylindrical pharyngeal pouch proceeding backwards, at whose posterior end a muscular cylindrical tube, the pharynx, rises, and projects freely forwards into the pharyngeal pouch. We have then—to use the terminology adopted in connection with the *Platodes*—a tubular pharynx plicatus, which is protruded (not evaginated) from the oral aperture. In the *Gnathobdellidæ*, on the contrary, the muscular wall of the œsophagus itself is thickened and projects into the lumen, generally in the form of three longitudinal folds or ridges. These ridges are often very strongly developed (jaws), and at their anterior projecting edges they are finely and sharply toothed (jaw teeth). The use made of jaw and teeth by the medicinal leech is well known. From the wall of the pharynx many strong muscle fibres radiate out to the body wall. The ducts of well-developed salivary glands enter into the pharynx.

Æolosoma among the *Oligochæta* shows a very simple arrangement. The fore-gut is limited to the head segment, and forms a single pharyngeal cavity with a weakly developed muscular wall. In all other *Oligochæta* the fore-gut stretches through several segments, and is divided into two parts by a transverse constriction, an anterior part, the buccal cavity, and a posterior part, the pharyngeal cavity or pouch. The dorsal wall of the pharyngeal cavity is nearly always considerably thickened, and projects into the pharyngeal cavity in the form of a variously shaped muscular pharynx. The pharynx is attached by muscles to the body wall, and can be protruded in order to take in food, the pharyngeal pouch being at the same time necessarily everted. Various glands—pharyngeal glands, salivary glands, and septal glands—may enter the pharyngeal pouch. The part of the intestine which in the Oligochæta follows the pharyngeal pouch and is generally termed the œsophagus belongs, according to recent ontogenetic investigations, to the (endodermal) mid-gut, and will thus be treated of later.

Among the *Polychæta* we again come upon very various forms of the fore-gut. In most of the tubicolous forms it is a short soft-skinned division which follows the mouth and is called the œsophagus. In *Terebellidæ* the œsophagus carries a ventral muscular appendage, the œsophageal sac. Most of the *Polychæta*, however, are characterised by the possession of a pharyngeal apparatus, which, especially in the *Errantia*, reaches a high degree of complication and can stretch through many segments. We may in a general way distinguish three modifications of this pharyngeal apparatus.

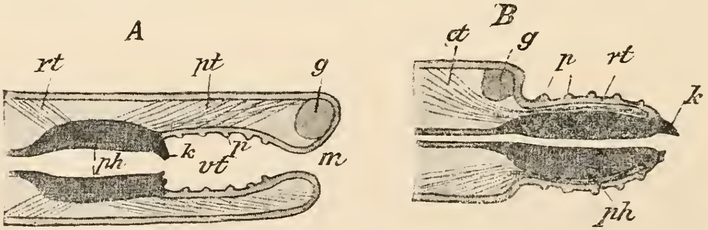


Fig. 132.—**Diagrammatic representation of the pharyngeal apparatus of a carnivorous Annelid.** *g*, Brain; *ph*, pharynx; *k*, jaw; *m*, mouth; *rt*, retractors; *pt*, protractors; *vt*, anterior soft-skinned portion of the pharyngeal apparatus; *p*, its papillæ. *A*, Pharyngeal apparatus in a withdrawn condition. *B*, In a protruded condition. In *B*, *ct* indicates retractors; *rt*, anterior soft-skinned portion of the pharyngeal apparatus.

1. The pharyngeal apparatus consists of two portions. The anterior portion, into which the mouth leads, is a soft-skinned tube, which is often provided internally with papillæ. The wall of the posterior portion is thick, on account of the strong development of its muscular layers, and represents the actual pharynx (generally called proboscis). Its anterior end carries papillæ projecting inwards or a conical process, or besides these (*Errantia*) two hard chitinous jaws. This pharynx can be so pushed forward that its anterior end which is thus armed projects freely outwards, and is then everywhere surrounded by the

anterior soft-skinned portion, whose papillæ then lie externally. The anterior soft-skinned portion, therefore, is turned outwards like the finger of a glove, and the pharynx proper is pushed after it. The protrusion takes place either through pressure of the perienteric fluid in consequence of a contraction of the dermo-muscular tube, or by the contraction of special protractors of the pharynx. The withdrawal is effected by means of special retractors. This is the most common arrangement of the pharyngeal apparatus (Fig. 132).

2. The anterior soft-skinned portion is wanting, or is very weakly developed. The mouth then leads almost directly into the muscular pharynx, which is itself evaginated so that when protruded its inner surface comes to lie outside (*e.g.* in the *Capitellidæ*, Fig. 133).

3. The pharyngeal apparatus consists of two portions, one above the other, the upper one of which (œsophagus) is less muscular and forms the communication between mouth and intestine; while the under one (jaw-carrier), which is blindly closed and enters the œsophagus in front, is extremely muscular and carries hard jaws, which are generally numerous, in special folds and sacs. These jaws come to the exterior when the pharynx is protruded, and can be moved one against the other (*Eunicidæ*, Fig. 134).

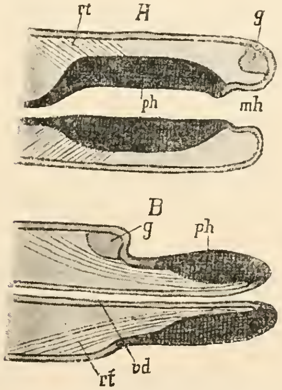


Fig. 133.—**Representation of the pharyngeal apparatus of an Annelid**, second diagram. *g*, Brain; *ph*, pharynx; *rt*, retractors; *mh*, buccal cavity; *vd*, œsophagus. *A*, In a withdrawn condition. *B*, In a protruded condition.

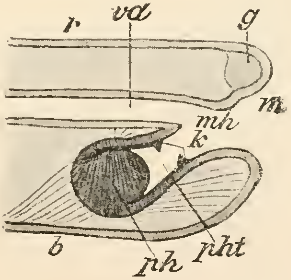


Fig. 134.—**Third diagram of the pharyngeal apparatus of an Annelid (Eunicide)**, withdrawn. *g*, Brain; *vd*, œsophagus; *ph*, pharynx; *pht*, pharyngeal sac; *k*, jaws; *mh*, buccal cavity; *m*, mouth; *r*, dorsal, *b*, ventral side.

Among the so-called *Archiannelida*, *Histriodrilus* approaches nearest to the third type on account of its ventral pharyngeal bulb armed with jaws. The pharynx (œsophagus) of *Polygordius* is distinguished by the want of a muscular layer, and by the great thickening of its epithelial wall, which is very thin only in the ventral middle line. Under the pharynx there lies a thin-walled channel, closing blindly and communicating by a longitudinal slit with the pharynx. In *Protodrilus* a muscular accessory organ, bent in the shape of a U, and lying under the beginning of the intestine, enters the pouch-shaped non-muscular œsophagus quite to the front, behind the oral aperture. *Polygordius* and *Protodrilus* thus approach the *Terebellidæ* in the arrangement of their fore-gut.

The genus *Sternaspis*, which possesses a strongly muscular pharynx, is distinguished by the fact that the seven anterior segments of the body can be invaginated.

Glands entering various parts of the pharyngeal apparatus have been observed in many *Polychæta*.

In the *Echiuridæ* the fore-gut is, relatively speaking, little distinguished from the mid-gut, and it even takes part in the formation of the loops which the intestinal canal makes in the body cavity. Three divisions are distinguished in it from before backward—the pharynx, the œsophagus, and the crop. It is the œsophagus in which the muscular layer is specially strongly developed. It is not certain whether any part of the fore-gut can be protruded. Food is in any case seized by means of the prostomium (proboscis) and conducted to the mouth along its ventral groove.

The *Myzostomidæ* possess a pharyngeal apparatus, constructed on the plan of that of the *Rhynchobdellidæ* among the *Hirudinea*. At the free end of the pharynx there are tentacle-like processes.

In the *Prosopygia* the fore-gut is in general very short and not strikingly developed. This is evidently in keeping with the manner of taking food of these mostly attached animals; their feeding is chiefly accomplished by the help of special outer appendages of the head (tentacles, arms). (In a similar way we found that in the *Chætopoda* inhabiting tubes or living in mud and provided with a crown of tentacles or a prostomium, the pharyngeal apparatus is far less developed than in the other forms.) Among the *Sipunculacea* a well-developed œsophageal bulb is present in the *Priapulidæ* only; its inner cuticle forms numerous teeth projecting into the lumen. The musculature is very powerful, and consists principally of circular and radial muscles. In the *Phoronidæ*, *Bryozoa*, and *Brachiopoda* the fore-gut is represented by the connective piece between mouth and intestine surrounded by a muscular layer, and is not very well marked; this is generally described as the œsophagus.

In the *Rotatoria* (Fig. 161, p. 245) the mouth leads first into a narrow ciliated buccal cavity (œsophagus), in connection with which a muscular layer is only rarely found. The buccal cavity is followed by the distinctly separate œsophageal bulb or pharynx, which is provided with a chitinous masticatory apparatus and strong musculature for moving it. The masticatory apparatus consists of a middle part (incus) and 2 lateral parts (mallei), each of which again consists of 2 pieces connected by a hinge (uncus and manubrium). The buccal cavity and the pharynx together ought to be considered as the fore-gut. In the pharynx of various *Rotatoria* salivary glands enter.

The fore-gut of the species *Dinophilus* (Fig. 162, p. 246), by its ventral muscular appendage whose hollow anterior end enters the œsophagus directly behind the mouth, recalls in a striking manner the arrangement found in the *Archiannelida* and the *Terebellidæ*. The ciliated fore-gut itself falls into 2 parts, a straight anterior œsophagus, and a short posterior fore-stomach into which 2 lateral salivary glands enter.

In the *Chætognatha* the very simple fore-gut which lies in the head is compressed transversely, and provided externally with a muscular layer whose fibres run dorso-ventrally.

B. The Mid-gut.

The mid-gut comes from the endodermal mesenteron of the larva or embryo. The relations of the various divisions of the gut to the embryonic gut are, however, clearly established in only a few cases, so that the demarcation of the mid-gut from the fore- and hind-guts is to a great extent arbitrary. In the epithelium of the mid-gut numerous gland cells are universally found.

The mid-gut of the *Nemertina* runs through the whole body, generally in a straight line, from the œsophagus to near the anus. It lies under the proboscis. It usually has numerous unbranched lateral sacs or diverticula, which occasionally lie one behind the other pretty regularly, and so cause a segmentation of the gut similar to that in the *Triclada*. In the *Hoplonemertina* the gut sends off towards the front an unpaired diverticulum under the œsophagus.

A musculature peculiar to the mid-gut has not yet been discovered in the *Nemertina*.

The mid-gut of *Malacobdella* possesses no lateral diverticula; it has instead a serpentine course.

In the *Nematoda* also the mid-gut has a straight course through the body. A special enteric musculature seems everywhere wanting.

With few exceptions the mid-gut of the *Annulata* also runs in a straight line through the body. It is almost everywhere surrounded outwardly by a muscular layer, consisting of circular and longitudinal muscle fibres.

The mid-gut of the *Hirudinea* shows mostly paired, lateral, segmentally arranged cæca or diverticula, the last pair of which is often very long and extends backwards on both sides of the hind-gut. Sometimes only this last pair of diverticula is retained, or the diverticula may be altogether wanting (*e.g. Nephelis, Lumbricobdella*).

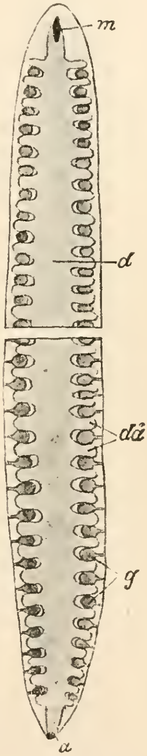


FIG. 135. – **Intestinal canal and genital organs of a Nemertian,** diagrammatic. *m*, Mouth; *a*, anus; *d*, gut; *dä*, intestinal diverticula; *g*, genital glands opening outwards by lateral pores.

In the mid-gut of the *Oligochæta* we distinguish two principal divisions, the œsophagus (which according to recent observations also comes from the endodermal mesenteron) and the stomach-intestine. The œsophagus is generally a tube with narrow lumen and weak walls. In the terrestrial *Oligochæta* and the *Naidomorpha* the œsophagus has somewhere in its course a muscular swelling (seldom double), the **muscular stomach** (gizzard). Besides this, 3 pairs of glandular lateral sacs enter the posterior portion of the œsophagus of the *Lumbricidæ* and related terrestrial *Oligochæta*; these are known as the lime-secreting glands, or **Morren's glands.**

The large **stomach-intestine** often shows constrictions between the consecutive segments. In the *Lumbricidæ* the absorbing surface of the stomach intestine is increased by the fact that its dorsal wall is folded longitudinally into the lumen of the intestine, and so forms a tube lying in the dorsal middle line of the gut, but open longitudinally towards the body cavity; this is the **typhlosolis** (Fig. 165, p. 250, *ty*).

In the mid-gut of the *Polychæta* also we can distinguish an anterior division, mostly shorter and narrower, from the posterior wider **stomach-intestine.** At the boundary between the two special glands may enter, like the Morren's glands of the *Oligochæta.* The stomach intestine usually shows successive segmental swellings, caused by constrictions at the partitions between the segments. These swellings are often prolonged laterally into cæca; these are particularly long in *Aphrodite* and the peculiar species *Sphincter;* in *Aphrodite* the cæca themselves are again branched (hepatic tubes).

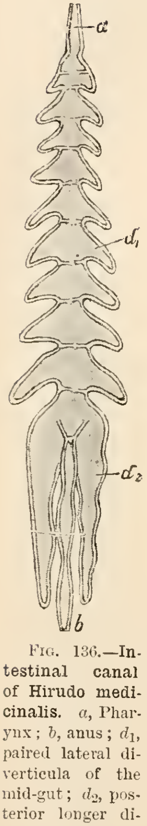


FIG. 136.—**Intestinal canal of Hirudo medicinalis.** *a*, Pharynx; *b*, anus; d_1, paired lateral diverticula of the mid-gut; d_2, posterior longer diverticula.

In the *Syllidæ* and *Hesionidæ* two lateral sacs enter the anterior end of the mid-gut (or posterior end of the fore-gut?); these can be filled with air like a swim-bladder. The mid-gut usually has a straight course, but in the *Chlorhæmidæ*, *Amphictenidæ*, and above all in *Sternaspis*, it forms more or less striking loops.

The *Capitellidæ* and a few *Eunicidæ* are distinguished by the possession of an **accessory intestine** ventral to the main intestine, and opening into it anteriorly and posteriorly in the *Capitellidæ*, but in the *Eunicidæ*, as it appears, only anteriorly. In *Capitella* ventral ciliated channels run forwards along the œsophagus and backwards along the hind-gut from these openings. The constituents of food are never met with in this accessory intestine, and it probably has a respiratory function.

In the *Echiuridæ* (Fig. 137) a very striking mid-gut lies in numerous loops and windings around the longitudinal axis of the body.

It has an accessory intestine lying close to it which passes anteriorly and posteriorly into longitudinal ciliated channels in the main intestine, and is justly considered as the connecting piece of these channels arched over and thus separated from the intestine.

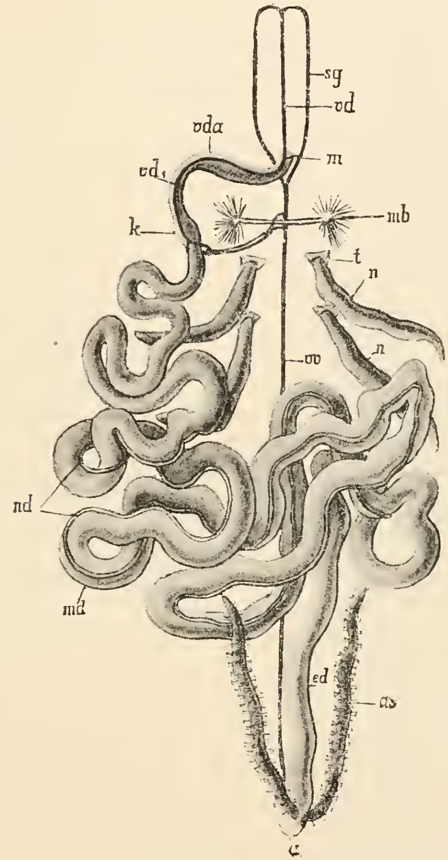
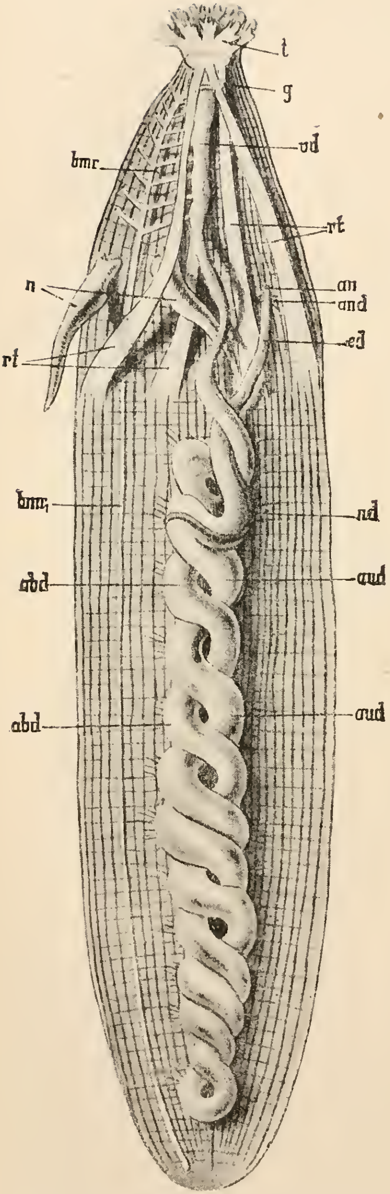


FIG. 137.—**Enteric canal, vascular system, and nephridia of Echiurus.** *sg*, Lateral vessels of the prostomium; *vd*, dorsal vessel of the prostomium: vd_1, dorsal vessel of the fore-gut (*vda*); *k*, crop; *md*, mid-gut, with the accessory intestine (*nd*); *vv*, ventral vessel; *n*, nephridia; *t*, their funnel; *as*, anal glands; *ed*, hind-gut; *a*, anus; *mb*, muscles of the anterior hooked setæ; *m*, mouth.

The mid-gut of the *Myzostomidæ* (Fig. 175, p. 262), with its branched diverticula which stretch as far as the lateral edge of the body, recalls the mid-gut of the *Annelid* species *Sphincter*, whose body is also broad and disc-like.

While among the *Sipunculacea* the mid-gut in the *Priapulidæ* runs in a straight line through the body, in the *Sipunculidæ* (Fig. 138) it forms a descending limb which runs through the trunk to the posterior



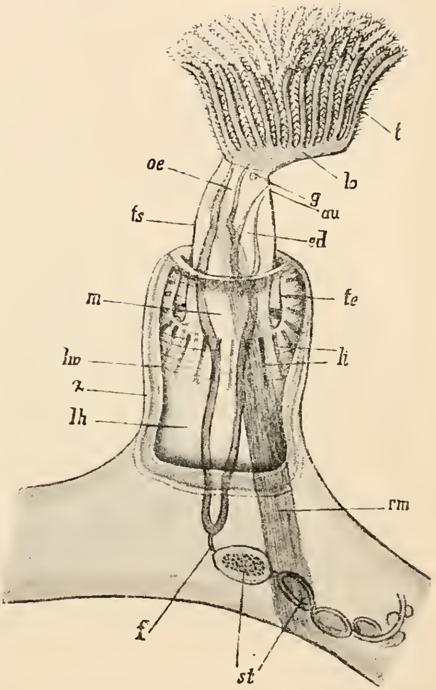


Fig. 139.—**Organisation of an individual of Plumatella repens, with protruded crown of tentacles.** *t*, Tentacles; *lo*, lophophore or tentacle carrier; *ts*, tentacle sheath (wall of anterior body); *te*, constant invaginated portion of the tentacle sheath; *lw*, posterior portion of body wall, covered with a cuticular envelope (cell *z*); *au*, anus; *ed*, hind-gut; *li*, muscular (?) bands, which fasten the invaginated part of the tentacle sheath to the body wall; *rm*, larger retractor muscles for withdrawing the tentacle crown into the cell; *f*, funiculus; *st*, statoblasts; *m*, stomach with cæcum; *lh*, body cavity; *g*, brain.

Fig. 138.—**Anatomy of Sipunculus with protruded proboscis**, partly after **Vogt and Jung**; the body is cut open longitudinally. *t*, Tentacles; *g*, brain; *vd*, fore-gut; *rt*, proboscis retractor; *n*, nephridia; *bmr*, that portion of the ventral chord which lies in the proboscis and runs freely in the body cavity; bmr_1, ventral chord of the trunk, marking the ventral middle line; *an*, anus; *and*, anal glands; *ed*, hind-gut; *nd*, accessory intestine; *abd*, descending limb; *aud*, ascending limb of the mid-gut.

end of the body, and then bends round to run forwards as an ascending limb. The two limbs twist round each other and form a spiral. A ciliated channel runs along the whole course of the mid-gut. Where this ceases, at its posterior end, a blindly closed diverticulum is attached to the gut, winding round its end; this may be homologous with the accessory intestine of the *Chætopoda*.

The intestine of *Phoronis*, like that of the *Sipunculacea*, forms a descending limb, and on the dorsal side of this an ascending limb.

The arrangement in the *Bryozoa* (Fig. 139) is closely connected with that in the already described *Prosopygia*. A descending limb of the intestine, not very sharply distinguished from the fore-gut, leads into the expanded stomach, from which arises an ascending limb which passes into the hind-gut. The stomach is occasionally prolonged into a somewhat sharply demarcated cæcum directed backwards.

In the mid-gut of the *Brachiopoda* we distinguish an anterior widened part, the stomach, into which the œsophagus enters, and an adjoining narrower part, the stomach-intestine. The stomach carries one or more pairs of lateral diverticula which branch and divide into massive glandular lobes, called the liver; these envelop the stomach on all sides. The stomach-intestine forms either a simple or complicated coil and then runs backwards (*Crania*), or bends on one side round to the front (the other *Ecardines*), or ends blindly (*Testicardines*).

In *Dinophilus* (Fig. 162, p. 246) and the *Rotatoria* (Fig. 123, p. 185; Fig. 161, p. 245) the mid-gut forms in the female a well-developed pouch-shaped stomach, which is sharply divided from the fore- and hind-guts. The epithelium of the stomach is either itself glandular, or there are special large glandular appendages. An intestinal musculature is either wanting or very slightly developed.

The mid-gut of the *Chætognatha* (Fig. 152, p. 227) takes a straight course through the trunk cavity of the body, without lateral appendages. A muscular layer is wanting.

C. The Hind-gut and the Anus.

The hind-gut comes from the proctodæum of the larva, and forms in the worms a tube, often very short, but generally clearly separated from the mid-gut; this tube opens externally through the anus, and is frequently called the **rectum**. The anus is either a separate aperture, or else it unites with the apertures of other organs of the body. This union is brought about through pit- or sac-like depressions of that region of the body wall in which these apertures lie near each other; a **cloaca** is thus formed, which then opens externally by a new common aperture, the cloacal aperture.

The juxtaposition of the external apertures of inner organs and the invagination of the region common to these apertures are very frequent in the animal kingdom. We will give only a few cases in illustration. In many *Platodes* the originally separate male and female genital apertures come to lie at the base of a common genital cloaca. The male genital aperture may even be combined with the mouth (*e.g.* in *Stylostomum* among the *Polyclada* and in *Prorhynchus* among the *Rhabdocœla*). In the *Mesostomidæ* among the *Rhabdocœla* the longitudinal branches of the water-vascular system, which generally emerge independently at the surface of the body, enter the pharyngeal pouch, which itself represents an invagination of the outer body wall (*stomodæum*). In a few *Nemertina* the otherwise universally separated proboscidal and oral apertures may be united (*Amphiporus, Malacobdella, Geonemertes palaensis*).

The following are the most important combinations of the anal aperture with the apertures of other organs. There are three kinds of such combinations.

1. **Union of the anal aperture with the apertures of the nephridia or excretory organs.**—In the *Priapulidæ* the two anal organs which serve primarily for excretion and secondarily as genital ducts emerge quite near the anus. In *Sipunculus* slightly developed anal glands have been observed entering the end of the hind-gut; these are perhaps (?) homologous with the anal organs of the *Priapulidæ.* In the *Echiuridæ*, which in many ways occupy a position intermediate between the *Chætopoda* and the *Sipunculacea*, both the anal glands (anal nephridia) also enter the hind-gut. In the *Rotatoria* also anus and nephridia enter a common cloaca.

2. **Union of the anal with genital apertures.**—In the *male Nematoda* the genital aperture emerges with the anus into a common cloaca; and the same is the case in the *female Rotatoria.*

3. **Union of the anal with both nephridial and genital apertures.**—This occurs, as may be seen from 1 and 2, in the *female* Rotatoria, where all three apertures open into a common cloaca.

The position of the anus and the cloaca.—The anus has a terminal position in the *Nemertina*, *Nematoda*, and *Annulata.* In the *Nematoda* it lies ventrally at a little distance from the posterior end of the body; in the *Annulata* generally dorsally, but always in the last segment, except in *Notopygos* (*Amphinomidæ*), where it lies several segments from the posterior end on the back. In the *Chætognatha* it lies ventrally at the boundary between the trunk and the tail regions; in the *Rotatoria* dorsally at the boundary between trunk and foot. In attached tubicolous *Rotatoria* it has moved somewhat forwards on the back, so that the hind-gut bends round forwards. The *Prosopygia* are distinguished by the fact that the anus lies on the back, moved far forward; and in the *Sipunculidæ* it even lies at the boundary between proboscis and trunk; in *Phoronis* and the *Bryozoa* quite anteriorly on the back, either (*Ectoprocta*) outside the tentacle carrier or (*Endoprocta*) inside it. Where an anal aperture is retained in the *Brachiopoda* it lies anteriorly, to the right, near the mouth. There are, however, a few exceptions to the rule which generally holds for the *Prosopygia.* In the *Priapulidæ* and in the *Brachiopod* genus *Crania* the anus lies behind.

VI. The Body Cavity, the Musculature which passes transversely through it, the Dissepiments and Mesenteries.

In the *Nemertina* we cannot yet speak of a body cavity (cœlome). Apart from the connective tissue, which penetrates between the muscles of the dermo-muscular tube, the space between the intestine and that tube is everywhere filled by a gelatinous tissue which is morphologically equivalent to the gelatinous tissue of the *Cœlenterata* and the parenchyma of the *Platodes.* The various organs—genital glands, blood-vessels, nephridia—are imbedded in this gelatinous tissue. Dorso-ventral muscle fibres pass through it and form (1) a sort of enteric musculature, the intestine passing between them and holding them apart, and (2) passing between the enteric diverticula a sort of muscular septa separating them; these septa, just like the diverticula themselves, lie one behind the other with more or less regularity, and recall the septa which are developed between the gastro-canals of the *Platodes.*

In the *Nemathelmia* there is a very spacious body cavity filled with fluid, which, in the *Nematoda*, occupies the whole space between the dermo-muscular tube and the intestine; and in the *Acanthocephala*, where an intestine is wanting, it is represented by the whole interior of the body, which is surrounded by the dermo-muscular tube. In this cavity lie the genital organs, bathed on all sides by the body fluid, and further, in the *Acanthocephala*, the lemnisci. In the latter the genital organs are attached by a muscular band or ligament to the posterior end of the proboscis sheath, and also by lateral muscular bands to the dermo-muscular tube. The body cavity of the *Nemathelmia* is not lined with a special epithelium (endothelium), but is limited directly—externally by the body musculature, and internally by the walls of the intestine.

The *Gordiidæ* occupy an isolated position among the *Nemathelminths* in the morphological condition of the cœlome, as in many other points of their organisation. In animals not quite sexually mature we find between the intestine and the body wall a considerable mass of cells, which disappears for the most part at the time of the development of the genital glands, and is probably used as material for nourishing these glands. We then find, in place of the cell mass, a spacious body cavity, which, however, in contradistinction to other *Nemathelminths*, is lined on all sides by an epithelium, often of several layers, lying on the inside of the dermo-muscular tube (Fig. 170, p. 256). This epithelium, in contrast to the epithelium of the intestinal canal and to the outer body epithelium, we call the **peritoneal endothelium.** This endothelium forms, in the median plane of the body, a partition wall which separates into 2 lamellæ; these run dorso-ventrally, having the intestine between them. At the sides of the ventral median nerve they unite with the endothelium of the body wall. By the special arrangement of this partition wall (mesentery) the body cavity is divided into 3 principal chambers; 2 lateral, and 1 unpaired ventral chambers, in which the intestine runs. We shall return to some peculiarities of this mesentery later on, when treating of the genital organs.

The presence of an endothelium and of a dorso-ventral median mesentery raises the *Gordiidæ* almost to the level of the higher worms, and supports the view that they should be considered as such (probably *Annulata*) degenerated by parasitism.

We cannot yet decide what should be considered as the body cavity in the *Hirudinea* among the *Annulata*. The space between the intestine and the body wall is filled by a connective tissue or parenchyma whose elements undergo the most varied transformations. We find pigment cells, fat cells, fibres. Blood-vessels and blood-sinuses arise by the flowing together of the contents of neighbouring cells. The collective mass of the connective tissue elements is more strongly developed in the *Gnathobdellidæ* than in the *Rhynchobdellidæ*. In the latter division a connected system of blood-sinuses, whose walls are not muscular but lined with an endothelium, and in which the central nervous system lies, must be considered as a slightly developed or else much reduced body cavity. In the *Gnathobdellidæ* the sinus, which contains the ventral chord, the œsophageal commissures, and the brain, seems to be such a reduced body cavity. This sinus, however, is not lined with an endothelium. The fact that in all *Hirudinea* the blood-vascular system is in open communication with the sinuses makes it difficult to decide whether the canal and sinus systems represent parts of the body cavity; and if so, to what extent this is the case. The sinuses are filled with a fluid which, in the *Rhynchobdellidæ*, contains colourless blood corpuscles.

Muscle fibres, branched at both ends and attached to the dorsal and ventral body walls, run through the body parenchyma. They form muscular dissepiments between the enteric diverticula, the arrangement of which recalls that of the dissepiments in the *Nemertina* and *Turbellaria*, and, in correspondence with the metameric arrangement of these diverticula, are themselves metameric.

For the *Chætopoda* we can establish a general morphological scheme of the body cavity, which, however, undergoes considerable modifications in a few divisions. Between the intestine and the body wall there is always a body cavity filled with fluid, which is entirely separated from the blood-vascular system. The body cavity is divided in the following way. A **dorsal mesentery** connecting the intestine with the dorsal middle line, and a **ventral mesentery** connecting it with the ventral middle line of the body wall, divide the body cavity into 2 lateral chambers, a right and a left. **Muscular partition walls, septa,** or **dissepiments,** comparable to the dissepiments of the *Turbellaria*, *Nemertina*, and *Hirudinea*, divide the body cavity into as many consecutive chambers as there are segments. These transverse partition walls always run between 2 consecutive segments. They are bored through by those organs which run longitudinally through several segments; viz. the enteric canal, the blood-vessels, and the nephridia. It is the septa which bring about the segmental constrictions of the intestine. The consecutive chambers of the body cavity are seldom completely separated from one another, the septa being mostly perforated, so that a free communication of the cœlomic fluid in adjacent chambers of the body cavity is possible.

All the walls of the body cavity and the organs lying in it are lined with a peritoneal endothelium, which undergoes the most various modifications. The endothelium of the body wall is distinguished as the parietal layer; that of the intestine as the visceral layer.

The **chloragogen cells** are peritoneal cells with definite excretory functions; they are especially strongly developed in the *Oligochæta*, and are attached to the dorsal vessel and its branches, particularly to the network of blood-vessels which surround the intestine. The brown granules which they contain are products of excretion taken from the blood, and most probably reach the exterior through the nephridia by the detachment and dissolution of the chloragogen cells. We find such cells also in the *Polychæta*. The excretory organs probably also draw the excretory substances direct from the blood, *i.e.* from the network of vessels which surround the renal tube.

The division of the body cavity may vary greatly in details. The dissepiments may become reduced or wholly disappear in large tracts of the body, so that consecutive chambers of the body cavity coalesce. Especially where a protrusible proboscis is developed, the segments through which this organ stretches undergo a reduction of their dissepiments. Dissepiments and mesenteries are generally typically developed in an early stage, even where in the adult condition great transformations take place.

The mesenteries may be reduced to isolated bands, fastening the intestine to the body wall, and these may also be developed only in certain regions of the body. On the other hand, the body cavity may undergo a still greater process of division (especially in *Polychæta*). For example, a membrane running under the intestine, attached on each side near the ventral chord to the body wall, often divides the body cavity into an upper chamber containing the intestine, and a lower chamber in which the ventral chord runs. Further, 2 lateral lamellæ often run through the body in a dorso-ventral direction, slanting upwards and outwards from both sides of the ventral middle line; these cut off 2 lateral cavities from the body cavity, which may be described as renal chambers, as they generally contain the greater part of the nephridia. These lamellæ enclose transverse muscle fibres (Fig. 158, p. 237).

The dissepiments undergo a striking reduction, especially in the bodies of those *Chætopoda* in which the enteric canal forms loops, and in which the segmentation of the body is more or less obscured (*Chlorhæmidæ*, *Sternaspidæ*, *Echiuridæ*). A spacious body cavity is thus formed. In the *Capitellidæ* the want of a separate blood-vascular system is compensated for by a strikingly pronounced partitioning of the body cavity.

Communication between the body cavity and the outer world takes place in two ways. Firstly, by the **nephridial canals**, which will be described later, and which are originally present in pairs in each segment, and, secondly, by the **dorsal pores.** These have been clearly observed in the *Lumbricidæ* and related land *Oligochæta*, and are medio-dorsal perforations in the body wall, lying in the anterior end of each segment. They are wanting in the head segment and in a certain number of the subsequent anterior segments.

According to some writers, dorsal pores are present also in *Enchytræidæ*; and cephalic pores leading into the head cavity are to be found in different families of the *Oligochæta*. But the presenee of these pores has again recently been disputed.

In the *Myzostomidæ* a body cavity filled with fluid is wanting. The organs found between the intestine and the body wall, above all the genital organs, are embedded in a body-parenchyma of connective tissue. Still the question remains to be decided, whether the space in which the sexual products lie does not answer to the body cavity of other worms. Dorso-ventral muscle fibres run through the parenchyma and form, in the same way as in the *Hirudinea*, *Nemertina*, and *Turbellaria*, a kind of muscle septa between which secondary muscle septa coming from the edge are intercalated, in the spaces between the sexual organs and the enteric diverticula. In the middle region of the body the septa leave a considerable space open in which we find the intestine, with the uterus dorsally above it and the ganglionic mass of the ventral chord under it.

In the manner of division of the body cavity the *Chætognatha* are closely allied to the *Chætopoda*. The body cavity is divided by 2 dissepiments into 3 consecutive chambers. The first dissepiment lies at the boundary between head and trunk, the second between trunk and tail, and the 3 chambers separated by the septa are the head, trunk, and caudal cavities. The enteric canal divides the head and trunk cavities into 2 lateral portions; in the trunk cavity the intestine is often fastened to the body wall by a dorsal and a ventral mesentery; a dorso-ventral mesentery-like partition of the caudal cavity is also found, although the intestine is there wanting. The parietal and visceral layers of the peritoneal endothelium are continued on to the mesenteries and the dissepiments, and form their chief component part, as they are not provided with muscles.

The body cavity of the *Prosopygia* shows very different arrangements. That of the *Sipunculacea* is large and spacious, like that of the *Echiuridæ*; dissepiments are wanting. The intestine, in the *Sipunculidæ*, is fastened to the body wall by delicate mesenterial strands which are wanting in the *Priapulidæ*. In *Priapulus* the body cavity is continued into the caudal appendage. A large expanse of the peritoneal covering of the intestine is ciliated in the *Sipunculidæ*, and, as in the *Echiuridæ*, a longitudinal muscular band runs along the intestine. The cœlomic fluid generally contains amœboid lymph cells; and besides these, in the *Sipunculidæ*, the sexual products and other peculiar bodies whose significance is not yet clear are found floating in it. In *Phoronis* also the body cavity is well developed, and lined throughout by a peritoneal endothelium. At the most anterior end of the body there is a septum which separates the cavity of the prostomium and the tentacles from the body cavity. The descending limb of the intestine is fastened to the body wall by a ventral mesentery, which, on the limb which ascends forwards to the anus, becomes a dorsal mesentery. The descending limb is further connected with the body wall by 2 lateral mesenteries. Among the *Bryozoa* the body cavity in the *Pterobranchia* and *Endoprocta* is extremely reduced, but in the *Ectoprocta* well developed. It is continued into the tentacles, and is often lined with a ciliated endothelium, at least this can be demonstrated in the fresh-water *Bryozoa.* The intestine is fastened to the body wall on all sides by fibres which are considered to be muscular. The gastric cæcum is also suspended from the posterior body wall by a strong non-muscular strand, the **funiculus.** In *Paludicella* there is also a second funiculus. In the *Brachiopoda* the cavity containing the viscera is lined by an endothelium generally ciliated over a great part of its surface. The enteric canal is fastened to the body wall by a more or less complete dorso-ventral mesentery, which, when complete (*e.g.* in *Crania*), divides the body cavity into two lateral halves. There are often lateral membranes or bands as well fastening the intestine to the body wall—a gastro-parietal band in the region of the stomach, and an ileo-parietal band in the region of the hind-gut. These bands have been compared with septa, which implies that the *Brachiopod* body was originally composed of three segments. This view is supported by other anatomical and ontogenetic facts. The body cavity in the *Brachiopoda* is continued in the hollow spaces of the mantle. An endothelial lining of the body cavities of *Rotatoria* and *Dinophilus* has not yet been proved. Distinct mesenteries and septa are wanting. Fine fibres of connective tissue here and there connect the organs lying in the body cavity with its walls; no constant arrangement, however, is found.

The phylogenetic origin of the body cavity of the worms, and generally of the higher *Metazoa*, is not at present certainly established; it is also impossible to say decidedly how far the hollow spaces in the body, called body cavities, are homologous in the various divisions of the Vermes. In the *Annulata* and many other higher animals it has long been known that special parts of the peritoneal epithelium are the places of formation of the sexual products. We are therefore justified in asking the question, whether the ovaries and testes of the lower acœlomous worms out of whose germinal epithelium the sexual products are formed, do not correspond with the chambers of the body cavity (cœlome) of the higher worms.

VII. The Nervous System.

The **Nemertina** (Figs. 140, 141).—The central nervous system consists of the brain, which is placed in front of or over the œsophagus and under the anterior portion of the proboscidal apparatus, and of two longitudinal trunks, proceeding from the brain and running somewhat ventrally in the lateral parts of the body; these end near the anus, or else coalesce immediately in front of the anus above the hind-gut. The brain consists of two large lateral ganglia connected by a transverse commissure and further united by a commissure which runs over the proboscis, so that the proboscis at its anterior end is embraced by a nerve ring. Each cerebral ganglion carries a lobe, usually sharply demarcated and placed behind, seldom to the side or in front; the relations of this with the lateral grooves (ciliated organs, olfactory organs) will be described later. These are known as the olfactory lobes, and usually lie above the first portion of the lateral nerves. From the brain various nerves proceed forwards to the apex of the head, to the eyes, and so on. Special nerves innervate the œsophagus and the proboscis. In *Paleonemertina* and *Schizonemertina*, between the longitudinal and circular muscle layers, there is a continuous nerve sheath (nerve plexus) entering the longitudinal trunks. A nerve arising anteriorly in the dorsal cerebral commissures often runs in the dorsal middle line; beneath this nerve we can occasionally observe a second dorso-median nerve, the nerve of the proboscis sheath. In the general nerve sheath, which innervates the dermo-muscular tube, we can, in the *Schizonemertina*, observe thicker strands, which form annular commissures between the three principal nerves running in the longitudinal direction. In the *Hoplonemertina* the nerve sheath is wanting; the commissures run separately, and sometimes show a markedly metameric arrangement.

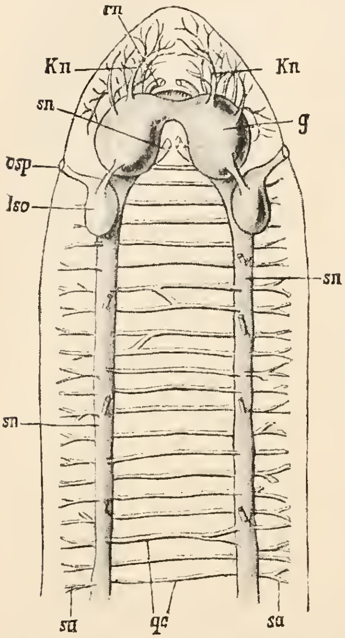


Fig. 140.—**Nervous system of the anerior part of the body of a Nemertian (Drepanophorus Lankesteri), after Hubrecht.** *g*, Cerebral ganglia; *osp*, aperture of the lateral organs (ciliated grooves); *lso*, cerebral lobes of the ciliated organs; *rn*, proximal portion of the proboscis nerves; *kn*, nerves of the head; *sn*, œsophageal nerves; *sn* (further down), lateral longitudinal trunks; *qc*, transverse commissures; *sa*, lateral branches of the longitudinal trunks.

In the whole structure of this nervous system a considerable agreement with that of the *Platodes* (*Polyclada*, *Triclada*, *Trematoda*) cannot be ignored. The brain and the longitudinal trunks of the *Nemertina* answer to the brain and the ventral longitudinal trunks of the *Platodes*. Whether the unpaired dorso-median longitudinal nerve of the *Nemertina* answers to the two dorsal longitudinal nerves of the *Platodes* cannot yet be decided. The longitudinal trunks (and also the brain) lie either imbedded in, or directly under the epithelium (*Carinina*, *Carinella*), or they are enclosed in the musculature of the body wall (*Cephalothrix*, *Cerebratulus*), or they lie on the inner side of the musculature (*Amphiporus*).

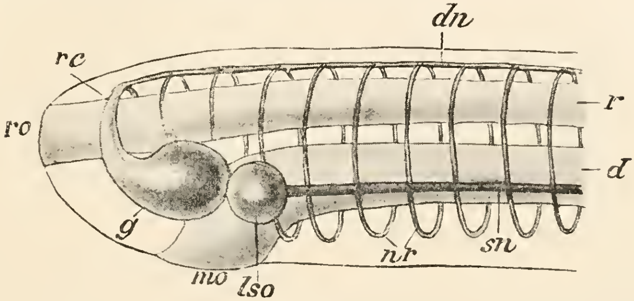


FIG. 141.—**Anterior end of the body of a Nemertian from the side,** diagrammatic (partly after **Hubrecht**). *g*, Brain; *rc*, proboscis commissure; *dn*, medio-dorsal nerve; *lso*, cerebral lobe of the lateral organ; *sn*, lateral nerve; *mo*, mouth; *r*, proboscis; *d*, intestine; *nr*, nerve rings, commissures between lateral nerves and the medio-dorsal nerve; *ro*, proboscidal aperture.

In *Malacobdella* ganglionic swellings were formerly erroneously described as occurring in the course of the longitudinal trunks.

Nemathelminths.—The nervous system of the *Nematoda* (Fig. 142) consists of a ring surrounding the œsophagus, the sides of which often swell out into a ganglion. A dorsal and a ventral longitudinal nerve arise out of the ring, and these run in the middle line to the posterior end of the body. The two nerves are connected together by transverse commissures which run under the cuticle outside the musculature. The transverse commissures of the right and left sides of the body do not exactly correspond. Numerous nerves proceed forwards from the œsophageal ring towards the apex of the head.

Attempts have been made to trace back the nervous system of the *Nematoda* to that of the *Platodes* in the following way. By union of the dorsal longitudinal trunks in the middle line the medio-dorsal nerve of the *Nematoda* arose, and by the union of the ventral longitudinal trunks the medio-ventral, which in young *Ascaridæ* and in a *Plectus* is still distinctly paired. The dorsal half of the *Nematodan* œsophageal ring answers to the brain of the *Platodes* with its often distinct lateral swellings. The ventral half of the œsophageal ring answers to the proximal portions of the ventral longitudinal trunks, still separated in the region of the œsophagus, but fused in the ventral middle line to form the medio-ventral nerve. The lateral nerves which run a short distance at the anterior end of the *Nematoda* are considered to be the remains of the lateral longitudinal nerves. The transverse commissures of the *Nematoda* correspond with the transverse commissures which connect the various longitudinal nerves of the *Platodes*. We prefer, however, to compare the nervous system of the *Nematoda* with that of the *Nemertina*, because there we have an unpaired dorso-median nerve, and the nerves corresponding with the outer lateral longitudinal nerves of the *Platodes* are wanting. The lateral swellings of the brain also are developed more clearly as lateral ganglia connected by a transverse commissure than is the case in the *Platodes*.

In the *Acanthocephala* (Fig. 172, p. 258) there lies at the base of the proboscis sheath a ganglion which sends several nerves forwards to the proboscis sheath, the proboscis, and the neck. Posteriorly there proceed from the ganglion two lateral longitudinal nerves, which first enter the retinacula at the posterior end of the proboscis sheath and run in them to the body wall, and then to the posterior end of the body. A dorso-median longitudinal nerve has also been observed. In the male, besides the anterior ganglion, another ganglion in the region of the genital apparatus (lying anteriorly on the base of the withdrawn bursa) has been described; this gives off nerves to the genital apparatus, and is also connected by two nerves with the posterior ends of the lateral longitudinal nerves of the body.

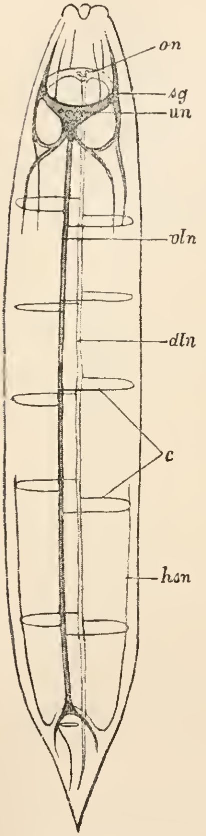


Fig. 142.—**Diagrammatic representation of the nervous system of the Nematoda, after Bütschli.** *on*, Upper, *un*, under portion of the œsophageal ring; *sg*, lateral swellings of the same; *vln*, medio-ventral; *dln*, medio-dorsal longitudinal nerve; *c*, commissures between the two; *hsn*, posterior lateral nerves (bursal nerves).

Fig. 143.—**Central nervous system of Hirudo medicinalis, after Hermann.**

The nervous system of the *Acanthocephala* is up to the present time not clearly understood. If there really is a medio-dorsal longitudinal nerve it perhaps corresponds with the medio-dorsal nerve of the *Nematoda*, and then the lateral longitudinal nerves perhaps represent the ventral longitudinal nerves, which fuse in the middle line in most *Nematoda*. What the relations are between the œsophageal ring of the *Nematoda* and the ganglion of the proboscis sheath of the *Acanthocephala*, or whether any such relations exist, are questions which must be left on one side.

The *Gordiidæ* also deviate from other *Nematoda* in the structure of the nervous system. Round the rudimentary pharynx lies a ganglionic mass (peripharyngeal ganglion) which is much thickened, chiefly ventrally, and is produced into a ventral chord (Fig. 170, p. 256). This runs backward in the middle line and swells into a caudal ganglion under the terminal portion of the genital ducts. In the male it divides at the most posterior end of the body into two strong branches which run into the caudal bifurcation. The peripharyngeal ganglion is connected on each side with the hypodermis, as is the ventral strand at the extreme posterior end of the body, in the caudal bifurcation, and indeed along its whole length by means of numerous unpaired median nerves. Nerve fibres radiate forwards from the peripharyngeal ganglion. A medio-dorsal nerve is wanting. It is probable that the peripharyngeal ganglion and the ventral strand of the *Gordiidæ* are homologous with the œsophageal ring and ventral chord of the *Annulata.*

Annulata.—Here we can establish a general scheme for the central nervous system. It consists (1) of a brain which lies over the anterior portion of the enteric canal, and (2) of the segmented ventral chord, running through the body in the ventral middle line. These two are connected by 2 commissures, the œsophageal commissures, which embrace the fore-gut between them. The anterior end of the intestine is thus surrounded by a nerve ring, the so-called œsophageal ring, which enters the brain dorsally, and the first ganglion of the ventral chord ventrally (Figs. 144, 146). The brain (supra-œsophageal ganglion), whose composition out of 2 lateral halves connected by transverse commissures can generally be seen, lies originally in the first, the cephalic or oral segment. The anterior ganglion, or rather double ganglion, of the ventral chord (infra-œsophageal ganglion) probably originally belonged to the second segment of the body. The remaining double ganglia of the ventral chord follow the infra-

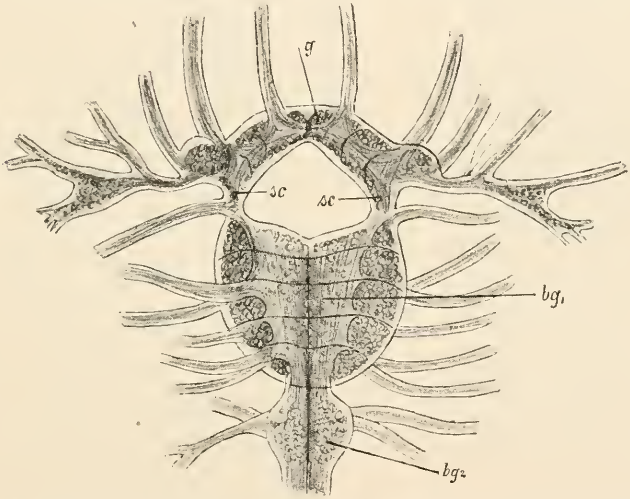


FIG. 144.—**Œsophageal ring with diverging nerves of Hirudo,** enlarged (after **Hermann**). *g*, Brain; *sc*, œsophageal commissure; bg_1, first ganglion of the ventral chord (infra-œsophageal ganglion); bg_2, second ventral ganglion.

œsophageal ganglion, one in each segment. The 2 ganglia of each double ganglion are connected together by short transverse commissures, and with the corresponding ganglia of the preceding and succeeding double ganglia by longitudinal commissures.

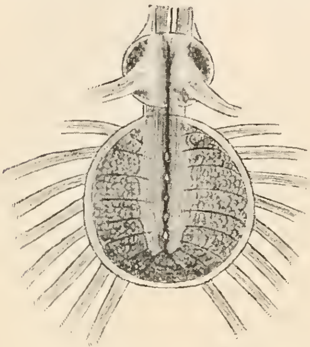


FIG. 145.—**Terminal or (sucker) ganglion of Hirudo, with preceding ganglion, after Hermann.**

Besides the œsophageal commissures nerves proceed from the brain to the integument and the sensory organs of the head; and from the ganglia of the ventral chord nerves supply the integument, sensory organs, and musculature of the segments to which they belong.

The musculature of the fore-gut (pharynx, proboscis, etc.) is provided with nerves arising either direct from the brain or from the œsophageal commissures. These nerves are called œsophageal nerves (often also nervi vagi), and the plexus they form in the fore-gut is called the **œsophageal nervous system.** In the most various divisions there is also a further plexus of ganglionic cells and nerve fibres in the walls of the mid-gut (**visceral nervous system, sympathetic nervous system**) whose connection with the central nervous system requires further investigation.

Difference of opinion prevails as to the phylogenetic origin of the nervous system of the *Annulata*. We prefer that view which not only derives the brain of the *Annulata* from that of the *Nemertina* and *Platodes*, but also sees in the segmented ventral chord with œsophageal commissures the further developed ladder nervous system formed in these lower divisions by the longitudinal ventral trunks and their transverse commissures. Ganglionic cells are found in the *Platodes* and *Nemertina* everywhere in the larger longitudinal trunks, and are present in great numbers in the *Polyclada* and *Triclada* at the points of divergence of the transverse commissures and lateral branches. These latter are repeated in an extremely regular manner and in a segmental arrangement as early as in certain *Triclada* (*Gunda*) and *Nemertina* (*Drepanophorus*). If we imagine the ganglionic cells of the longitudinal trunks crowded together at the points of divergence of the transverse commissures and side branches, and their number perhaps increased still further, these points of divergence must swell into ganglia and the longitudinal trunks become longitudinal commissures between the successive ganglia. The longitudinal trunks with their ganglia only need to move together into the ventral middle line, so as to become the typical ventral chord of the *Annulata*. The mouth and œsophagus prevent such a moving together in the anterior part of the body, and so the first part of the longitudinal trunks becomes the œsophageal commissures of the *Annulata*.

An approximation of the longitudinal trunks, which, it is true, never leads to direct contact, may be observed as early as the *Nemertina*, not to speak of the *Platodes*. Whereas as a rule among these forms the paired longitudinal trunks lie laterally, sometimes even over the enteric diverticula (*Amphiporus Moseleyi*), they are found in *Drepanophorus* placed somewhat ventrally and nearer each other. On the other hand, the ventral chord of the *Annelida* can, by the separation of its symmetrical halves, assume the appearance of a ladder nervous system (*e.g.* in the *Hermellidæ*, Fig. 147).

In very many *Annulata* (many *Oligochæta* and *Polychæta*) the brain stands in direct connection with the hypodermis of the head segment. It often shows more or less distinct lobes, always symmetrically arranged, which look like special ganglia. The brain, which originally (and also ontogenetically) belongs to the head segment, can in some cases stretch into the second segment; it can even move back into the

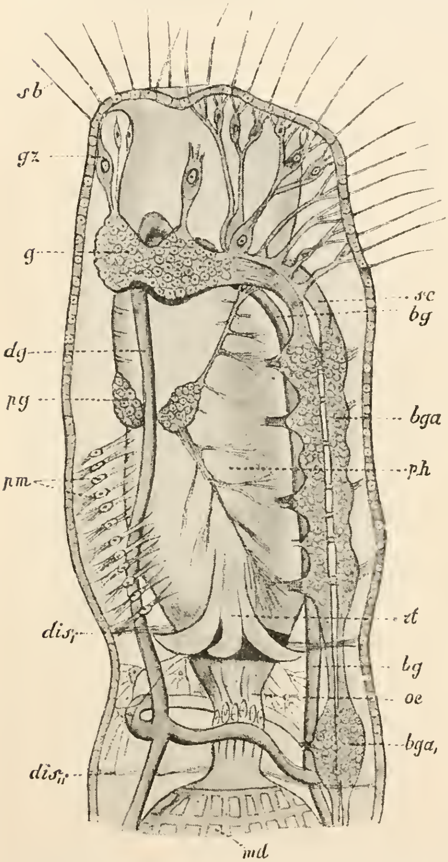


FIG. 146.—**Anterior part of the body of Chætogaster diaphanus, from the side, after Vejdovsky.** *sb*, Sensory setæ; *gz*, ganglionic cells of the cup-shaped organ; *bga*, ladder-like ventral chord of the pharyngeal region; dis_1, dis_2, first and second dissepiments; *pm*, pharyngeal muscles; bga_1, ventral ganglion in the œsophageal segment; *g*, brain; *pg*, pharyngeal ganglion; *md*, stomach-intestine; *rt*, retractors (?) of the pharynx; *sc*, œsophageal commissure; *dg*, dorsal vessel; *bg*, ventral vessel; *œ*, œsophagus; *ph*, pharynx.

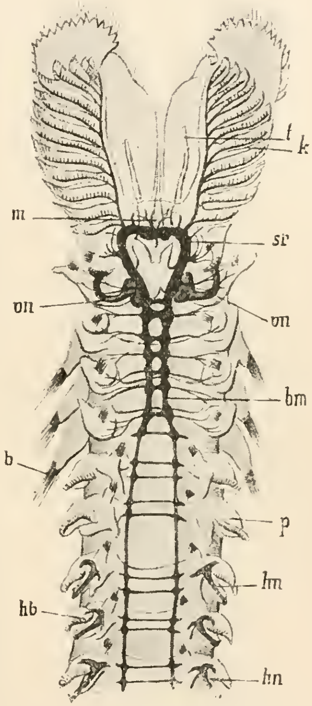


FIG. 147.—**Nervous and nephridial systems in the anterior portion of the body of Sabellaria alveolata, from the ventral side, after E. Meyer.** The nervous system is made black. *sr*, Œsophageal ring; *bm*, ventral chord; *t*, tentacles; *k*, feeler gills; *m*, mouth; *b*, bundles of setæ; *hb*, hooked setæ; *p*, parapodia; *vn*, anterior pair of nephridia; *hn*, posterior nephridia through which the sexual products are discharged.

second, third, or fourth segment (in certain earthworms). The infra-œsophageal ganglion is also by no means always placed in the second segment of the body; here and there it lies in the head segment, or in the first and second segment, or it moves farther back—farthest of all in *Pleione*, where it lies in the fifth or seventh segment. In the *Hirudinea* (Figs. 143 to 145) the infra-œsophageal ganglion fuses with a few of the subsequent ganglia of the ventral chord, forming a considerable infra-œsophageal ganglionic mass, in which, however, by the number and arrangement of the diverging peripheral nerves, and by the arrangement of the ganglionic cells and fibre commissures, its composition out of several ganglia can be more or less distinctly recognised. The same is true of the large posterior (sucker) ganglion (Fig. 145), which is composed of six fused ganglia.

As far as the ventral chord is concerned, the presence of a single ganglion in each segment is the rule; but there are exceptions to this rule in the most varied groups. Sometimes one or two accessory ganglia are added to the principal ganglion, *e.g.* in the *Serpulidæ* two ganglia are typically present in each segment. On the other hand the ganglionic masses may become very indistinct or be altogether wanting (*Archiannelida*, and isolated forms in the most varied groups). In *Sternaspis* the ventral chord shows ganglionic swellings only in the most posterior part of the body. The fusion of the two lateral halves of the ventral chord is often limited to the ganglia, whilst the longitudinal commissures run as completely separated strands. These again may lie so close to each other that they appear externally to be one single strand. It may even in various forms come to a fusing of the two commissures, so that the ventral chord then consists of a single strand, which, *e.g.* in the *Archiannelida*, does not even show the segmental ganglionic swellings, and then recalls in a striking manner the ventral strand of the *Gordiidæ*. From the ganglia of the ventral chord there arise on each side nerves, generally 2 or 3, which run upwards in the body wall and innervate the musculature, the integument, and the segmental sensory organs, where such are present. It has been shown in some cases that this innervation takes place by means of a sub-epithelial nerve plexus developed all over the body. Lateral nerves may also diverge from the longitudinal commissures between 2 consecutive ganglia. The same is the case in the most anterior longitudinal commissures—the œsophageal commissures.

There is often (especially in *Hirudinea*) in the ventral chord a delicate median strand of longitudinal fibres which is called the intermediate nerve. The ventral chord is nearly always covered by a single or double sheath of connective tissue (neurilemma sheath), in which longitudinal muscle fibres run, principally in *Oligochæta* and *Hirudinea*.

Certain tubes with a wide lumen and wall formed of neurilemma, which run back in varying but always small numbers on the dorsal side of the ventral chord, deserve special attention. These tubes, which are called **neurochord strands** or **giant nerve tubes**, begin anteriorly in the œsophageal commissures or in the infra-œsophageal ganglion, and stretch to the most posterior end of the ventral chord. They were in all probability originally the neurilemma sheaths of giant nerve fibres, arising from larger ganglionic cells which lay in the ganglia at different parts of the ventral chord. Various observations make it probable that the nerve fibres in the neurochord tubes in various *Annulata* degenerate, the neurochord tubes themselves persisting as elastic organs of support, containing a watery fluid mixed with the remains of the original nerve substance. Such degeneration is, however, denied by some authorities.

The typical position of the ventral chord, and generally of the whole central nervous system of the *Annulata*, is in the body cavity on the inner side of the musculature. As the brain very often passes into the hypodermis of the head without sharp limitation, so the posterior end of the ventral chord in most *Oligochæta* and *Polychæta* passes without sharp limitation into the hypodermis of the anal segment. In many *Chætopoda* of the most varied divisions, indeed in single genera of different families, the nervous system even in adult animals shows an embryonic condition, in so far as it lies outside the body musculature in the deeper part of the epidermis. This position of the central nervous system is thus far from being characteristic of the so-called *Archiannelida*, and we can in general give it no special systematic significance. We find besides in various divisions all transition stages, from the position of the ventral chord in the body cavity to its hypodermal position, since it can lie in the body musculature between the hypodermis and the body cavity. Moreover, in *Capitella*, anteriorly, the ventral chord lies in the body cavity, then passes in between the musculature, and finally, posteriorly, comes to lie in the hypodermis.

The symmetrical halves of the ventral chord may separate in some cases, and the ventral chord can thus assume the form of a ladder nervous system (Figs. 146 and 147) (*Hermella*, many *Serpulidæ*, *Spinther*, and in the pharyngeal region in the *Chætogastridæ*). In the *Aphanoneura* (*Æolosoma*) the ventral chord is said to be entirely wanting, or it lies in a quite embryonic condition imbedded in the hypodermis.

The nervous system of the *Echiuridæ* (Fig. 148) deserves special attention. A distinctly marked supra-œsophageal ganglion or brain is wanting. The œsophageal ring is very much elongated, in keeping with the great length of the prostomium. Its two limbs (œsophageal commissures), which run laterally in the prostomium (proboscis), and which coalesce at its anterior end, give off numerous branches towards both the exterior and interior; those branches which run dorsally inwards may represent transverse commissures between the limbs of the œsophageal ring. Below and behind the mouth the limbs of the œsophageal ring coalesce to form an unpaired ventral strand, which in adult animals has no ganglion swellings, but is supplied with ganglionic cells throughout its whole course; this strand runs in the ventral middle line on the body wall to the posterior end of the body, and gives off to the right and left at short intervals lateral branches which correspond with the rings of the outer integument. The corresponding right and left lateral

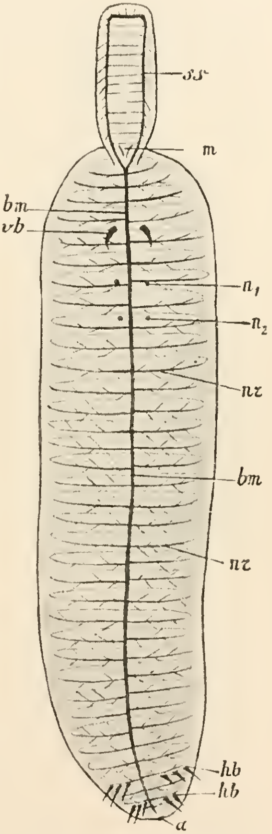


Fig. 148.—Nervous system of **Echiurus**, diagrammatic. *ss*, The two limbs of the œsophageal ring, which join at the anterior end of the prostomium and enter the extreme anterior end of the ventral chord (*bm*) behind the mouth; *nr*, nerve rings; *vb*, anterior hooked setæ; *hb*, the two posterior circles of setæ; n_1, n_2, apertures of the nephridia; *a*, anus.

branches pass into each other dorsally, and thus form in the body wall numerous consecutive nerve rings.

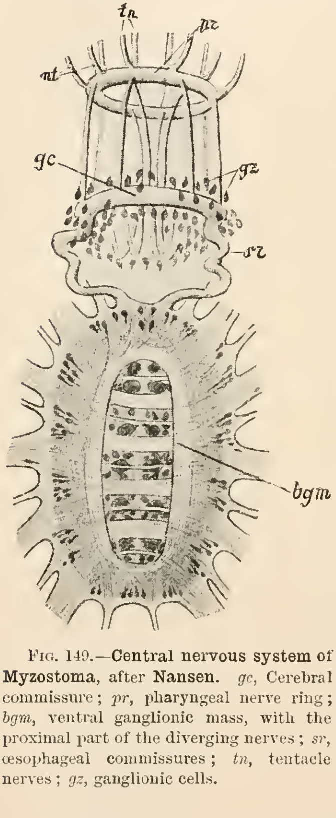


Fig. 149.—**Central nervous system of Myzostoma,** after **Nansen.** *gc*, Cerebral commissure; *pr*, pharyngeal nerve ring; *bgm*, ventral ganglionic mass, with the proximal part of the diverging nerves; *sr*, œsophageal commissures; *tn*, tentacle nerves; *gz*, ganglionic cells.

The nervous system of the *Myzostomidæ* (Fig. 149) is now very exactly known. It consists of an œsophageal ring surrounding the base of the pharynx, whose dorsal lateral portions are somewhat thickened, and so represent a weakly developed brain. Close to the œsophageal ring lie ganglionic cells. Further forward in the pharynx a second nerve ring (pharyngeal ring) is found, which is connected with the œsophageal ring by several longitudinal nerves, and gives off nerves to the tentacles at the free anterior edge of the pharynx. On the ventral side, under the integument, lies a large, elongated, ganglionic mass, from whose anterior end the two commissures (limbs) of the œsophageal ring arise. The ganglionic mass represents a ventral chord which consists of several (probably 6) fused pairs of ganglia, and in which an intermediate nerve is to be found. From this ganglionic mass 11 alternately stronger and weaker nerves radiate on each side towards the circumference of the disc-shaped body; these nerves branch in a complicated manner and innervate especially the musculature of the parapodia, the hooks, the cirri at the edge of the body, and the integument and its musculature. The existence of a sympathetic nervous system also seems probable.

Prosopygia.—The nervous system of the *Sipunculacea* is in many respects closely related to that of the *Echiuridæ*. As there is no long prostomium, the œsophageal ring is also not elongated anteriorly, but forms a simple ring at the anterior end of the enteric canal. This ring in the *Priapulidæ* is only a little thickened dorsally, while in the *Sipunculidæ* it enters a well-developed brain. Nerves diverge from the brain to the anterior end of the body and to the tentacles (where the latter are present). Nerves also diverge from the œsophageal ring; 2 of these in *Sipunculus* supply the intestine, forming a ganglion on each side, while in *Priapulus* 4 penetrate the pharynx. The ventral strand, which is covered with ganglionic cells along its whole course, runs in the ventral middle line of the body to its extreme posterior end, where it swells somewhat. In its whole course it gives off, just as in the *Echiuridæ*, corresponding right and left lateral nerves, which, running in the body cavity, unite dorsally to form nerve rings (at least in *Sipunculus*). Each pair of nerves corresponds with one of the circular muscle bundles and with one of the more or less distinct rings of the outer integument. In the *Priapulidæ* it is said that there are weak but regularly recurring swellings of the ventral chord which correspond with the circular muscle bands. While in the *Sipunculidæ* the central nervous system lies in the body cavity, in the *Priapulidæ* it is in close connection with the hypodermis.

Whereas in the *Echiuridæ* the ventral chord is distinctly segmented in the early stages of development, such a segmentation is wanting in the *Sipunculacea* even in those stages. The ventral strand of the latter is nevertheless homologous with that of the *Echiuridæ* and with the ventral chord of the *Annulata* in general. The nerve rings of the *Sipunculacea* evidently correspond with those of the *Echiuridæ*. There can be no doubt as to the homology of the brain and œsophageal ring. We have also seen that the ventral chord, even in true *Chætopoda*, may present no ganglionic swellings, and may fuse into a single median ventral strand. It is a question whether the nerve rings of the *Echiuridæ* and *Sipunculacea* are repeated segmentally. In the *Echiuridæ* several body rings with smaller papillæ alternate with one with larger papillæ. The setæ only occur on the rings which carry the larger papillæ. We also find that the nerve rings in the body rings with the larger dermal papillæ, are stronger than the others. It seems probable that several rings go to one segment, and that the number of these rings with larger papillæ and stronger nerve rings corresponds with the true number of the segments. In the *Chætopoda* also (apart from the *Hirudinea*) one segment is sometimes externally divided into 2 or more rings, and more than one ganglion of the ventral chord may lie in one segment. In the *Hermellidæ* and *Serpulidæ* we find typically 2 pairs of ganglia in each segment, and further 2 transverse commissures and 2 lateral branches on each side, which ascend in the body wall towards the dorsal middle line.

The nervous system in other *Prosopygia* is remarkably weakly developed. The ventral chord is reduced to the infra-œsophageal ganglion, and even this may be wanting. The small development of the nervous system is probably to be traced to the stationary manner of life, which results in a reduction of the specific sensory organs, and—by the development of tube-dwellings, shells, or cases—of the general body musculature (dermo-muscular tube).

Phoronis possesses a nerve ring surrounding the mouth at the base of the tentacles. The anus lies outside the nerve ring. From the dorsal part of the ring a nerve arises which runs backwards asymmetrically on the left side, through about two-thirds of the length of the body, and with a tube (notochord ?) passing through it. The morphological significance of this nerve is unknown. The whole nervous system lies in the hypodermis outside the basal membrane.

The nervous system of the *Brachiopoda* (Fig. 150) is weakly developed. It consists of a delicate œsophageal ring, whose upper portion is only very slightly swollen into a supra-œsophageal ganglion. The infra-œsophageal ganglion is indicated by a thickening of the ventral portion of the œsophageal ring, and in some cases two lateral swellings can be made out.

From the supra-œsophageal ganglion two nerves run into the arms; from the infra-œsophageal ganglion nerves run also to the arms, to the mantle, and to the opening and closing muscles of the shell. The arm nerves are connected with a plexus of ganglionic cells and nerve fibres, which spread out in the supporting substance of the arm walls close under the epithelium. Each of the mantle nerves divides into a dorsal branch for the dorsal fold of the mantle, and a ventral branch for the ventral fold. They are again richly branched, and their branches anastomose forming a plexus. The nervous system of the *Brachiopoda* lies under the integument.

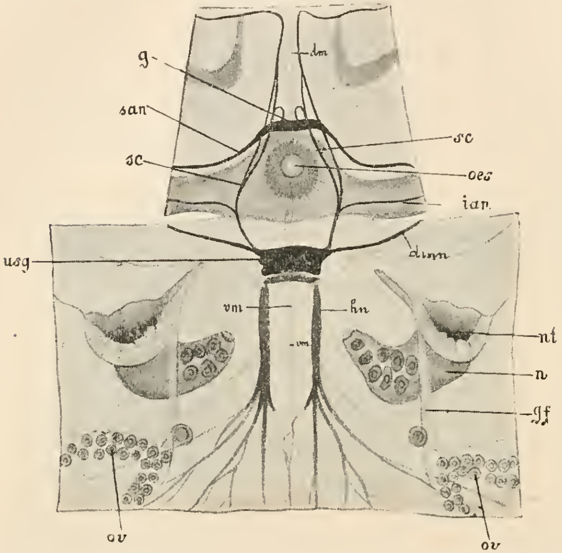


Fig. 150.—**Preparation of Terebratula vitrea for demonstration of the nervous system, the ovaries, and the nephridia, after van Bemmelen.** Anterior body wall after removal of the arm apparatus, the enteric canal, and the closing muscles, spread out and seen from within. Above lies a part of the dorsal body wall; below, a part of the ventral body wall. *g*, Brain; *sc*, œsophageal commissures; *usg*, infra-œsophageal ganglion; *san*, arm nerve proceeding from the supra-œsophageal ganglion; *ian*, ditto from infra-œsophageal ganglion; *œs*, œsophagus; *dmn*, dorsal mantle nerves; *hn*, nerves proceeding backwards from infra-œsophageal ganglion; *n*, nephridia (oviducts); *nt*, nephridial funnel; *gf*, genital folds; *ov*, ovaries; *dm*, dorsal mesentery; *vm*, ventral mesentery.

In the *Bryozoa*, only the supra-œsophageal ganglion of the œsophageal ring is retained; it lies as a generally inconsiderable mass (occasionally with thickened lateral parts) dorsally over the fore-gut, between mouth and anus, under the integument. From this ganglion nerves run chiefly into the tentacles, and further to the two ciliated pits, when such are present.

Rotatoria.—Over the œsophagus there lies a ganglion (supra-œsophageal ganglion) which sends off nerves to the wheel organ, the cutaneous organs of touch, and the muscles. It lies under the integument.

In *Dinophilus* also, in front of and above the mouth (in the prostomium), is found a mass of fibres surrounded by ganglionic cells, which represents the supra-œsophageal ganglion. In *Dinophilus gigas* two longitudinal nerves rise out of it, which pass by the mouth, and run on both sides of the body immediately beneath the integument to its posterior end. These longitudinal nerves must represent the separated lateral halves of the ventral chord of the *Annulata*. Transverse commissures seem to be wanting.

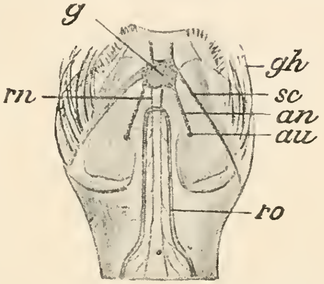


Fig. 151.—**Head of Sagitta bipunctata, seen from above, with closed seizing hooks, after O. Hertwig.** *g*, Brain; *gh*, seizing hooks; *sc*, commissure between brain and ventral ganglion; *an*, optic nerve; *au*, eye; *ro*, anterior portion of the olfactory organ; *rn*, olfactory nerve.

Chætognatha (Figs. 151 and 152).—The nervous system is here well developed. The central nervous system and the peripheral nerves lie, with the exception of a single portion, external to the musculature in the body epithelium. The brain or supra-œsophageal ganglion lies dorsally in the head segment, while the infra-œsophageal ganglion lies ventrally in the trunk segment and surpasses the cephalic ganglion in size. The cephalic and ventral ganglia are connected by 2 long commissures. Besides these 2 commissures, the supra-œsophageal ganglion gives off 2 strong nerves which penetrate the mesoderm forwards and downwards, and which we may call motor nerves, 2 lateral nerves which supply the integument of the head, 2 outer posterior nerves which, after a short course, reach the 2 eyes behind the supra-œsophageal ganglion (nervi optici), and 2 inner posterior nerves which supply the unpaired sensory organ lying behind the eyes which is supposed to be the olfactory organ (nervi olfactorii). A great number of nerves radiate from the ventral ganglion, among which the continuations of the 2 œsophageal commissures, after running through the ventral ganglion, are found as 2 strong longitudinal strands, which, after giving off numerous lateral nerves, themselves end in fine nerve fibres. All nerves diverging from the ventral ganglion and the posterior longitudinal nerves pass finally into a plexus of ganglionic cells and nerve fibres, which is developed

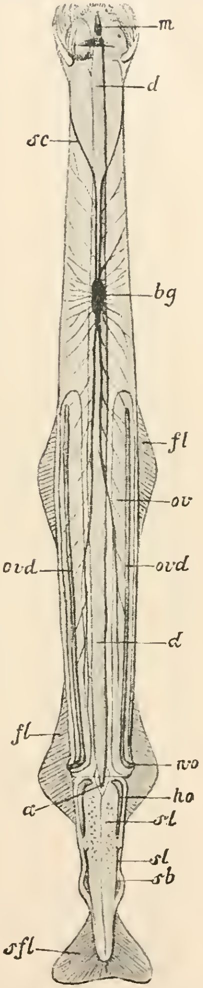


Fig. 152. — **Sagitta hexaptera, seen from the ventral side, after O. Hertwig.** *m*, Mouth; *d*, intestine; *sc*, œsophageal commissure; *bg*, ventral ganglion; *fl*, fins; *or*, ovarium; *ovd*, oviducts; *wo*, female genital aperture; *a*, anus; *ho*, testes; *sh*, tail cavity; *sl*, sperm duct; *sb*, sperm vesicle; *sfl*, caudal fin.

in the epithelium all over the body. The motor nerves of the supra-œsophageal ganglion form a ganglion each on the sides of the fore-gut in the cephalic segment (lateral cephalic ganglia), with small accessory ganglia. The musculature of the head and the fore-gut are supplied with nerves by these ganglia. This mesodermal part of the nervous system of *Sagitta* recalls the œsophageal nervous system of other worms. We do not yet know how the trunk and caudal musculature are supplied with nerves.

VIII. Sensory Organs.

All the different kinds of sensory organs are found in the worms—organs of touch, sight, hearing, smell, and taste. Besides these, in a few divisions we meet with sensory organs which cannot at present be classed in any of the above categories—the lateral organs of the *Chætopoda*, the lateral eyes of *Polyophthalmus*, and the segmental organs of the *Hirudinea*. It must not be forgotten that the functions of the sensory organs of the worms are as little experimentally established as are those of most other invertebrate animals; and that it is almost entirely their position and structure which lead us to consider them auditory, olfactory, etc. The function of the organs of touch indeed is more surely established. That the worms in some way or other see with the sensory organs which have been indicated as eyes may also be considered certain, though we do not know what and how they see.

The sensory organs are most numerous and best developed in animals leading a free aquatic life (*Polychæta*, *Errantia*, *Chætognatha*), and among these again the good swimmers take the first place. The worms which are attached at the bottom of the water and those which lurk in holes are not quite so fully provided. In worms living in mud and sand or in earth the sensory organs are much reduced, and this is the case in the highest degree in parasitic and attached animals. In the latter, however, the strongly developed organs of touch form an exception. Where the sensory organs are reduced in adult, stationary, or parasitic animals we often meet with them well developed in their young stages, when they as larvæ move about freely. In order of frequency we have the organs of touch, which are universally distributed, then the eyes, then the olfactory organs and organs of taste. Organs of hearing have been certainly observed only in a few cases (*Arenicolidæ*, *Serpulacea*, *Terebelloidea*).

A. Organs of Touch.

Everywhere, except in the worms provided with a thick shell, the entire integument is the seat of a highly developed sense of feeling or touch. This sense is served in a special manner by epithelial sensory cells, which carry at their free end sensory hairs or setæ, and at their basal ends are continued as nerve fibres, which are themselves generally processes of peripheral ganglion cells. A plexus of nerve fibres and ganglion cells lying immediately under the body epithelium can now be proved with certainty to exist in various worms, especially in the *Chætopoda* and *Chætognatha*. In parasites with a thick outer cuticle papillæ, rod- or seta-like processes of this cuticle, which are principally developed at the anterior end and near the genital apertures, play the part of organs of touch. As a rule the tactile cells are most numerously present in that part of the integument of the worm where the body has most points of contact with its immediate surroundings. Such points are, above all, the anterior end of the body, the neighbourhood of the mouth, and the various appendages. There are some such appendages which, on account of their position and their specially rich provision of tactile cells, may be regarded as specific organs of touch. We may mention in illustration the feelers on the heads of the *Chætopoda*, especially of the *Polychæta*, the cirri of the parapodia, the prostomium of the *Echiuridæ*, the tentacles of the *Prosopygia* (cirri on the oral arms of the *Brachiopoda*), and the wheel organ of the *Rotatoria*. It is obvious that such organs of touch in worms inhabiting tubes or shells can only attain development at the anterior end of the body, which carries on the relations with the outer world; and it is equally intelligible that in such worms these same organs should carry on other relations to the outer world as well (prehension of food, respiration). Hence the strong development of the tentacular apparatus in the tubicolous and shelled worms (tubicolous *Annelids*, most *Prosopygia*, and the tubicolous *Rotatoria*).

The sense of touch is very strongly developed in the *Hirudinea*. The tactile cells, each of which is provided with a fine hair, form groups (tactile cones), which are arranged in 18 longitudinal rows. They are developed on the warts or papillæ, when such occur (Fig. 156).

B. Eyes.

Their occurrence, number, and arrangement.—In many genera and species of *Nemertina* the eyes are wanting. In others small eyes occur in varying numbers (2, 4, or many) at the anterior end of the body. In the *Nematoda* the absence of eyes is the rule, the presence of 2 simple eye-spots at the anterior end of the body (in some of the free-living forms) the exception. The *Acanthocephala* are without eyes. In the *Annulata* the presence of eyes is the rule, their absence the exception. The *Hirudinea* possess 1 to 5 pairs of eyes in the anterior rings of the body. Among the *Oligochæta*, which mostly live in mud or earth, only the *Naidomorpha* possess eyes—one pair in the head segment. In the *Archiannelida* which have a similar mode of life, or are, like *Histriodrilus*, parasitic, the eyes are either wanting or reduced in the adult animal. Most of the *Polychæta* are provided with eyes, which lie, with very few exceptions, in the head segment. Most of the *Errantia* have 1 or 2 pairs of well-developed eyes, which in the *Alciopidæ* reach a remarkable size; many *Sedentaria* are eyeless; where, however, eyes occur they lie as small so-called eye-spots, generally in great numbers, in the prostomium, at the part where the brain is connected with the hypodermis. In *Fabricia* eye-spots occur at the posterior end of the body; in some species of *Sabella* on the tentacle gills. For the so-called lateral eyes of *Polyophthalmus* see below. The *Echiuridæ*, which live in mud or lurk in holes, and the parasitic *Myzostomidæ*, are blind. The absence of eyes is characteristic of the whole class of the *Prosopygia*. The *Rotatoria* possess an unpaired or a paired eye-spot lying on the brain, but this is wanting or rudimentary in the adult condition in stationary forms. *Dinophilus* has 2 eye-spots in the prostomium. In the *Chætognatha* 2 eyes lie on the dorsal side of the head, behind the brain, in the body epithelium.

Structure of the eyes.—A comparative morphology of the eyes of worms is at the present time a desideratum. At any rate it now appears certain that the eyes in the various divisions need not be homologous. The eyes which appear in pairs are perhaps homologous, such as those developed in larvæ of the *Trochophora* type in close connection with the cerebral rudiment; these very often disappear through metamorphosis, or degenerate. As a detailed account of these always more or less complicated organs is here impossible, we select a few for brief description, viz. the eyes in *Capitella*, in *Alciope* (the most highly developed eye among worms), in a *Chætognathan*, and in *Hirudo*.

1. The eye of *Capitella*.—The numerous eyes (ocelli) of *Capitella* lie in the prostomium at the part where the brain fuses with the hypodermis. The following are the elements of a single eye. We find slipper-shaped refracting cells, whose outer portion is homogeneous and transparent, while the inner part contains pigment. Each of these cells is continued as a nerve fibre towards the brain, this nerve fibre entering a ganglion cell of the central optic lobe. The refracting cells of the eyes are connected together by thread cells of the hypodermis. The cuticle is arched over the eye.

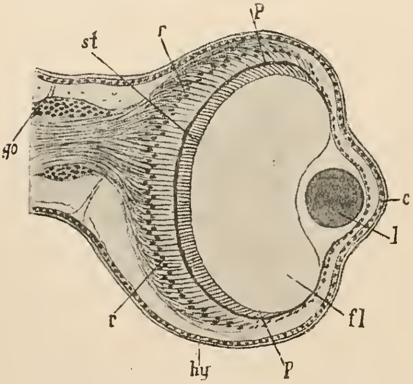


FIG. 153.—Section through the eye of an Alciope (Callizona Grubei). *hy*, Hypodermis; *c*, cornea; *l*, lens; *fl*, eye fluid; *p*, pigment of the retina; *r*, retinal cells; *st*, rods; *go*, ganglion opticum of the brain (after Carrière).

2. The eye of *Alciope* (Fig. 153).—The two eyes of *Alciope* stand out spherically, one on each side of the head. They are covered by a thin layer of hypo-

dermis with its cuticle, which form the **outer cornea** over the centre of the protruding eye. The eye itself is a vesicle whose posterior thicker wall forms the **retina**, while the anterior thinner wall is the **inner cornea**. The elements of the retina are long cells standing closely pressed together, in which three parts can be distinguished: (1) towards the brain, the cell body with a nucleus; (2) the rod, which is directed towards the hollow of the bulb; and (3), between these two, a thin layer of pigment. Under the cornea lies the spherical lens. The rest of the eye is filled with fluid. The retinal cells are continued into nerve fibres, which soon enter the ganglion cells of the optic lobe (ganglion opticum); the latter is connected with the brain by a mass of nerve fibres.

3. The *Chætognathan* eye (Fig. 154) is spherical. In the centre of the sphere lie 3 bi-convex lenses imbedded in pigment; to the outside of each of these 3 lenses a third part of the whole retina is applied in such a way that the three parts together form the wall of the sphere. The retina consists of cells; the portion of each of these cells which is in contact with the lens is rod-like, and the part which is turned outwards is the cell-body with its nucleus. At the circumference of the sphere, each retinal cell is continued as a nerve-fibre. All the nerve fibres unite in the nervus opticus (Fig. 151, p. 227). The *Chætognathan* eye may be considered to have come from 3 simple fused ocelli.

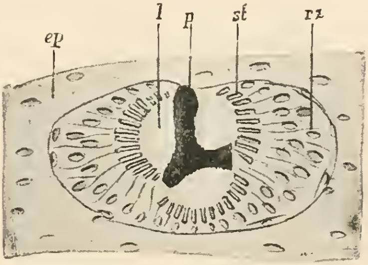


FIG. 154.—**Section through the eye of Sagitta hexaptera, after O. Hertwig.** *ep*, Body epithelium; *l*, lens; *p*, pigment; *st* rods; *rz*, retinal cells.

A comparison of the three eyes just described shows how greatly the eyes of worms may vary in structure.

4. The eyes of *Hirudo* (Figs. 155, 156) lie in the anterior rings of the body and vary in number. They are cylindrical and stand at right angles to the somewhat modified hypodermis with which they are in contact. The optic nerve enters at the base, its fibres passing into long sensory cells which lie in the axis of the eye. Around the axis are arranged large clear cells, each containing a nucleus and a refractive substance. The whole organ is imbedded in strongly pigmented connective tissue. Our present knowledge of the structure of these organs hardly justifies us in calling them eyes; morphologically they are transformed tactile organs.

C. Olfactory Organs (Ciliated Organs).

In many worms of the *Nemertian* and *Chætopodan* divisions there are found, at the anterior end of the body, 2 lateral strongly ciliated parts of the hypodermis, the so-called ciliated organs, ciliated clefts, ciliated pits, ciliated prominences, which are regarded as olfactory organs. The body epithelium at these points consists of ciliated sensory cells, whose bases are prolonged as nerve fibres. These nerve fibres are connected under the sensory epithelium with a plexus of ganglion cells, which is itself again connected with the brain. In the *Chætopoda* the ciliated parts just mentioned are frequently depressed in the form of pits or sacs, and are often protrusible. A special olfactory lobe (ganglion olfactorium) may be developed on the brain in close proximity to the ciliated organ, this lobe bearing the same relation to the olfactory organ that the lobus opticus or ganglion opticum bears to the eye. In the *Nemertina* these olfactory lobes are very strongly developed, and often sharply separated from the brain (*cf.* p. 216 and Figs. 140, 141). The ciliated organs here are pits which open outwardly by means of longitudinal clefts at the sides of the head, and which in the *Schizonemertina* are continued inwardly as ciliated canals, penetrating to the interior of the cerebral olfactory lobes. It is probable that all these ciliated organs are homologous formations, and correspond with the ciliated grooves at the extremity of the head in the *Turbellaria*.

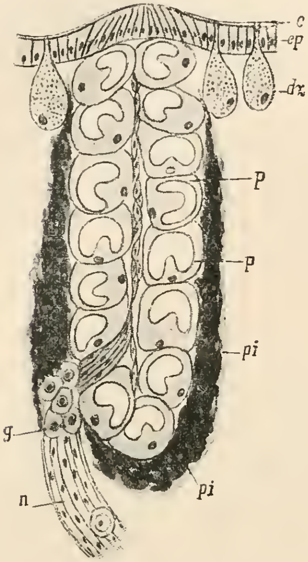


FIG. 155.—**Section through the eye of a land leech.** *c*, Cuticle ; *ep*, hypodermis ; *p*, large clear cells ; *g*, ganglion cells ; *n*, nerve ; *dz*, cutaneous gland cells ; *pi*, pigment (after **Whitman**).

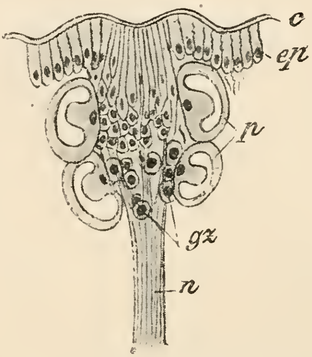


FIG. 156.—**Section through a tactile sensory organ of Macrobdella, after Whitman.** *c*, Cuticle ; *ep*, hypodermis ; *p*, large clear cells ; *gz*, ganglion cells ; *n*, nerve. The sensory cells are here clearly seen to be long hypodermis cells, the tactile hairs which they carry are not depicted.

In the *Chætopoda* such organs have been found more or less developed in the *Capitellidæ*, *Eunicidæ*, *Nereidæ*, *Phyllodocidæ*, *Syllidæ*, *Opheliacea*, *Typhloscolecidæ*, *Sabellidæ*, *Archiannelida*, *Tomopteridæ*, *Ctenodrilus*, and *Aphanoneura*. Sensory organs of similar structure and in a similar position have been observed in *Bryozoa* (*Loxosoma Rhabdopleura*) and in *Phoronis*.

In the *Chætognatha* (Fig. 151, p. 227) a circular band, partly consisting of ciliated epithelial cells, lies like a ridge on the ordinary epithelium cells. It is considered to be an olfactory organ, and lies behind the eyes between the head and the trunk; this unpaired sensory organ is innervated by a pair of olfactory nerves running between the nervi optici.

D. **Organs of Taste (Cup-shaped Organs).**

There occur also certain sensory prominences of the body epithelium, essentially similar in structure to the olfactory organs just described, and called cup-shaped organs from the fact that they can be withdrawn into pit- or cup-shaped depressions of the integument. They always occur in large numbers and widely scattered. As, however, they are specially numerous at the edge of the mouth, in the oral cavity, and also in the pharynx, they are held to be organs of taste.

The structure and distribution of these organs in the *Capitellidæ* is well known. In *Notomastus*, *Dasybranchus*, and *Heteromastus* they occur only in the prostomium, thorax, and pharynx, in *Mastobranchus* and *Capitella* on the abdomen also. Similar sensory organs are found also in *Oligochæta* (*Lumbricidæ*, *Chætogastridæ*, *Enchytræidæ*), especially numerous in the head, chiefly on the upper lip. Among the *Polychæta* they have been observed in the *Nereidæ* (*Nephthys*) and the *Eunicidæ* (on the pharynx and in the buccal cavity). In the *Hirudinea*, where they were first observed and exactly described, they are always found on the lips. Cutaneous sensory organs, which are found in great numbers in the *Sipunculidæ* and *Echiuridæ* on the papillæ not only of the body, but of the proboscis as well (often arranged, like the papillæ themselves, in longitudinal or transverse rows), probably also belong to the category of cup-shaped organs.

E. **Lateral Organs.**

These retractile sensory organs only occur in the *Chætopoda* and agree essentially in structure with the cup-shaped organs. The numerous thread-like sensory cells of these organs carry sensory hairs, and are connected on the one hand with transverse muscle fibrillæ which together form a retractor for the organ, and on the other hand with a plexus of ganglion cells which is again connected by a special nerve with the ventral chord. The above is the case in those *Capitellidæ* which have been most carefully examined in this connection. The lateral organs are most clearly distinguished from the cup-shaped organs by their strictly segmental arrangement. There is a pair in each segment, one on each side between the dorsal and the ventral parapodia. They are found not only in the *Capitellidæ*, but also in *Polyophthalmus* and the *Amphictenidæ*, and among the *Oligochæta* in the *Lumbriculidæ*. There are many reasons for considering the lateral organs to be homologous with the dorsal cirri of the ventral parapodia of other *Polychæta*, and in the family of the *Glyceridæ* we can follow, almost step by step, the transformation of these cirri into lateral organs. The cirri, being sensory organs, their gradual reduction into papillæ causes the tactile cells scattered in their hypodermis to collect together to form the compact sensory epithelium of the lateral organs.

Strands of lateral ganglion cells appear always to occur in the lateral lines of the *Oligochæta*, entering the brain anteriorly. They are closely connected with the hypodermis, and in the *Lumbriculidæ* supply the lateral organs with nerves. They are probably also connected with the intestinal nervous system.

The function of the lateral organs is at present an unsolved problem.

F. Auditory Organs.

There is a remarkable absence of auditory organs in the *Vermes*. They only occur in the *Polychæta*, and there also only occasionally in a few families, viz. in the *Arenicolidæ*, in the *Terebellidæ* (*Lanice*), and *Serpulidæ* (*Myxicola*, *Amphiglene*, *Fabricia*). Their occurrence has also been proved in several *Terebellid* larvæ, in the larvæ of *Eupomatus* (*Serpulidæ*), and in a nearly related *Chætopodan* larva. They are paired, and lie in *Arenicola* on the œsophageal commissures in the head segment, and in this case receive their nerves from the brain. In other forms they lie, as it appears, in the first trunk segment, and are supplied with nerves by the infra-œsophageal ganglion. In this point, as well as in their development, they recall the auditory organs of the mollusca. In adult animals they are vesicular (otocysts), the wall being formed by epithelial cells (sensory cells, auditory cells). The vesicles contain a fluid in which one or more otoliths are suspended.

G. The Lateral Eyes of Polyophthalmus.

Eye-like organs are found in strictly segmental order somewhat beneath the insertion of the transverse muscular bands in the lateral line of *Polyophthalmus*. They occur in *P. pictus* in the 8th to the 19th body segments, and are closely connected with the hypodermis which is free from pigment, and which with the cuticle covers each eye. Each eye consists of a lens, a pigment cup, and a body which consists of prismatic cells placed in this cup. The pigment cup and cell body together perhaps form a sort of retina (?) It must be expressly noticed that besides the lateral eyes, *Polyophthalmus* possesses cephalic eyes as well (3 in number) and lateral organs, and that it is very doubtful whether the lateral eyes are visual organs.

IX. Excretory Organs—Nephridia.

(Occasionally Ducts for the transmission of the Sexual Products.)

Nemertina.—The excretory apparatus, which is always paired, consists of canals lined with epithelium and mostly ciliated, which as a rule rise in the blood sinuses of the body and open externally. It is limited to the anterior portion of the body. The efferent ducts always lie laterally over the longitudinal trunks of the nervous system. Its arrangement differs greatly in details. In all *Nemertina*, the epithelial walls of the excretory canals (nephridia) are glandular.

In *Carinella* (*Paleonemertina*) an excretory portion separates itself from the lateral vessels of the blood-vascular system, and falls into two parts, a glandular part and a reservoir. On the one side it is connected with the lateral vessels at two points, on the other with a canal which opens externally. In *Carinoma* the nephridium on each side consists of (1) a very short longitudinal canal which communicates with the lateral vessels at three points, and (2) an efferent duct which opens externally. In *Carinina* also the nephridial system on each side consists of two parts: (1) a compact mass of small canals, which projects inwards towards the blood sinus of the œsophageal region, and which (2) is connected with a nephridial cavity narrowing at its posterior end into a canal which opens externally.

While in the *Paleonemertina* (with the exception of *Carinina*) the nephridia are in open communication with the blood-vascular system, such a communication has till now not been proved in other *Nemertina*. In the *Schizonemertina* on each side of the anterior region of the body there is either a single longitudinal canal or else a longitudinal network of canals, in which, however, one principal canal can generally be distinguished. These longitudinal canals, which lie in or on the blood sinuses or lateral vessels on the inner side of the longitudinal muscle layers, reach the exterior on each side either (1) posteriorly through an efferent duct, or (2) through two ducts opening near the middle of their course, or (3) through several often very numerous lateral ducts which are more or less metamerically arranged.

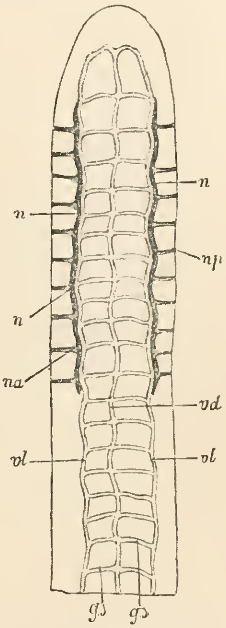


Fig. 157.—**Nephridial and circulatory system in the anterior portion of the body of a Nemertian,** diagrammatic. *n*, Longitudinal canals of the nephridial system; *np*, lateral apertures of the same; *na*, efferent ducts; *vd*, dorsal vessel; *vl*, lateral vessel; *gs*, transverse vessels between the dorsal and lateral vessels.

In the *Hoplonemertina* and *Malacobdellidæ* also, on each side, in the anterior region of the body, a longitudinal canal is found. This gives off, along its whole length, branches which again ramify. The longitudinal canals and their branches lie neither on nor in the blood sinuses, but are directly imbedded in the gelatinous connective tissue (body parenchyma). The longitudinal canals either open externally through several lateral efferent ducts, or on each side by one lateral canal, which may branch off from the longitudinal trunk either anteriorly, in the middle, or posteriorly.

The nephridial system of the *Schizonemertina* and *Hoplonemertina* shows a certain agreement with that of the *Platodes*. Here, as there, we meet with lateral longitudinal trunks which open externally on each side, either through one aperture (*e.g.* in the *Platodes* among the *Rhabdocœlida : Derostoma*, *Prorhynchus*, *Gyrator*, *Mesostoma ;* and among the *Trematoda : Polystomidæ*), or through numerous lateral ducts in more or less segmental arrangement (*e.g.* in *Platodes* among the *Triclada*). The longitudinal trunks of the *Nemertina* may even, as in the *Platodes*, be broken up into a plexus, or they may be present in numbers. Where the nephridial system in the *Nemertina* (*Hoplonemertina*) is neither in direct nor indirect communication with the blood-vascular system, it belongs to the branched type, as in the *Platodes*, which have no blood-vascular system. In the *Nemertina*, it is true, the nephridial system lies only in the front or foremost portion of the body. Terminal excretory cells have not been proved to exist, and the canals are lined with a ciliated epithelium, while in the *Platodes* (everywhere and in all divisions ?) each canal runs within cells arranged in a single row (intracellular). These differences, however, ought not to prevent a recognition of the homology between the excretory systems of the *Platodes* and the *Nemertina*.

Nemathelmia.—The *Nematoda* and *Acanthocephala* must be described separately. In the first, longitudinal canals occur in the lateral lines ; till now no inner lining of epithelium has been proved to exist. The two longitudinal canals unite at the anterior end of the body to form a longer or shorter unpaired canal, which opens externally near the brain by a ventral median pore. The homologies of these canals, which are considered to be excretory canals, are quite uncertain. In the *Gordiidæ* they are wanting. The canal-like space (section of the body cavity) which surrounds the intestine of these animals is said to divide (in *Gordius Preslii*) in front of the cloaca into two branches, and these perhaps open into the cloaca. Whether this canal is an excretory tube is, however, quite uncertain.

In the *Acanthocephala*, in the subcuticle of the integument, a system of canals is found which will be described in the section on the vascular system. The anterior part of this canal system, which is quite separated from the posterior part, was formerly claimed as an excretory system ; but there are difficulties in the way of accepting this view, chiefly because it has no external aperture.

Annulata.—The following scheme may be given as of general application to the excretory or nephridial system. It consists of paired tubes (nephridia), open at both ends, which are repeated segmentally. Each nephridium is in open communication with the body cavity or blood sinuses by an inner aperture ; the external aperture lies in the integument. The nephridia therefore form an open communication between the body cavity and the exterior, and serve chiefly for conducting the waste products of metabolism out of the body. Since the genital products are, in many *Annulata*, developed out of the endothelium of the body cavity, then free themselves from the matrix, and ripen when floating freely in the cœlomic fluid, an opportunity is given to them also of reaching the exterior through the nephridia. The nephridia thus frequently undertake, in addition to their purely excretory function, the transmission of the genital products to the exterior. This secondary function may often become the principal function in some of the nephridia, which may then undergo a complete transformation, and in the *Polychæta* are called genital tubes.

As already explained, paired nephridia originally occur in all the segments of the *Annulate* body, even in the cephalic or oral segment. It may, however, happen that the nephridia in a smaller or greater number of segments do not attain development. It is further very generally found that some of the nephridia begin to form early in the embryo or larva or young animal, and function as embryonic or larval kidneys, but afterwards entirely disappear when the permanent nephridia attain development. We shall call those which temporarily appear in the ontogenetic development **provisional** or **embryonic nephridia**. We can again distinguish two sorts of such provisional nephridia. (1) Those which appear in that region of the embryo or larva which corresponds with the subsequent head segment, and lie at the anterior end of the cell mass (mesoderm streaks), from which the most important organs of the segmented mesoderm come; these are

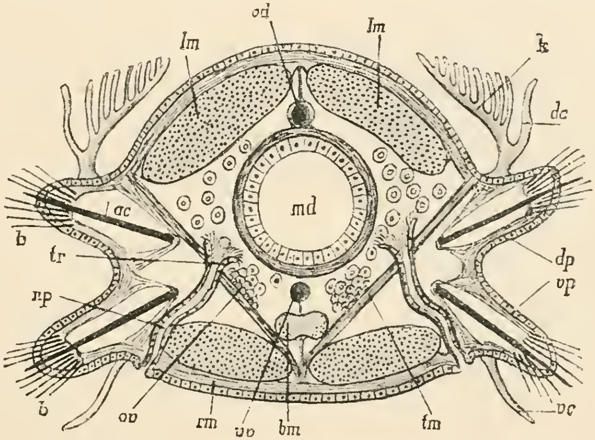


FIG. 158.—**Transverse section through a trunk segment of a carnivorous Annelid,** diagrammatic. *b*, Setæ; *ac*, aciculum (supporting seta); *lm*, longitudinal musculature; *vd*, dorsal vessel; *k*, gill; *dc*, dorsal cirrus; *dp*, dorsal parapodium; *vp*, ventral parapodium; *vc*, ventral cirrus; *tm*, transverse muscles; *bm*, ventral chord; *vo*, ventral vessel; *rm*, circular musculature; *ov*, ovary; *np*, nephridia; *tr*, nephridial funnel; *md*, mid-gut. In the body cavity are eggs.

the **embryonic head nephridia** or the **head kidneys.** (2) Those which appear in the trunk segments; these are the **provisional trunk kidneys.** The permanent nephridia, on account of their frequently strict segmental arrangement, are often called segmental organs, or on account of their looped or winding course (in *Oligochæta* and *Hirudinea*) looped canals.

We will first describe the three sorts of nephridia separately, and then discuss their morphological significance and their relations to each other.

A. The embryonic **head nephridia (head kidneys).**—These appear temporarily in the larva or embryo, and are paired. Their inner end lies in the embryonic head cavity. They have been observed in many *Oligochæta* and *Polychæta.* They are ciliated canals, which are not in open communication with the head cavity. The lumen of these canals is intracellular, *i.e.* the nephridia are rows of consecutive cells perforated to form a canal. In this point the embryonic head nephridia agree with the permanent nephridia of the *Oligochæta* and *Hirudinea*, and with the canals of the water-vascular system of the *Platodes.* They are occasionally branched (*e.g.* in the larvæ of *Echiurus* and *Polygordius*), like the water-vascular system of the *Platodes* and the nephridia of many *Nemertina.* Lateral branchings of the principal canals also occur in the permanent nephridia of the *Hirudinea* and *Oligochæta.* Terminal cells provided with bundles of cilia (flames) often occur at the inner ends of the branched or simple nephridia; the flames project into the lumen of the canal, in which they undulate. These terminal cells resemble those of the water-vascular system in the *Platodes.*

B. **The embryonic or provisional trunk nephridia.**—These have till now been observed in comparatively few cases; it is, however, probable that they are widely distributed. They occur (like permanent nephridia) in strictly segmental arrangement as paired canals in those generally anterior segments, in which in adults permanent nephridia are wanting.

Among the *Oligochæta* it has been proved that in *Rhynchelmis*, in the 5 anterior trunk segments in which nephridia are wanting in adult animals, 5 pairs of provisional nephridia, which degenerate later, attain development in the embryo. In the *Capitellidæ* the nephridia are always wanting in a large number of anterior segments (thorax and anterior part of the abdomen), but this is only the case in adult animals. In the young animals, however, we meet with provisional nephridia in most of these segments, which are the better developed the younger the animal, and the further forward the segment to which they belong. In other words, the nephridia arise first anteriorly, and their degeneration proceeds in order from before backward (in the thoracic and in some of the anterior abdominal segments) in proportion as the permanent nephridia of the abdominal region attain development. In *Nereis cultrifera* (Fig. 159) there are found in the larval stage 5 pairs of provisional or larval trunk nephridia in the 5 anterior segments, in which in adult animals we meet with no nephridia. As in most *Oligochæta* nephridia are wanting in some of the anterior segments, it is probable that provisional nephridia occur in these segments in the larval forms. The same may be conjectured of the *Polychæta.* In the *Oligochæta* the nephridia are wanting in the genital segments, except in the *Lumbricidæ.* But here also provisional nephridia attain development in these segments at early stages. In the *Hirudinea* provisional nephridia are developed in early embryonic or larval stages (2 pairs in *Nephelis*, 3 pairs in *Hirudo*, 4 pairs in *Aulostoma*) which disappear early. As the larvæ are, at the time when provisional nephridia are present, still unsegmented, it cannot be certainly decided what is their morphological significance. A certain number of the anterior and of the posterior segments of the adult *Hirudo* are without nephridia. This fact favours the conjecture that the larval nephridia of the *Hirudinea* are the provisional nephridia of the anterior trunk segments. Possibly the foremost pair of larval nephridia of the *Hirudinea* represent the embryonic head nephridia (head kidneys) of other *Annulata*.

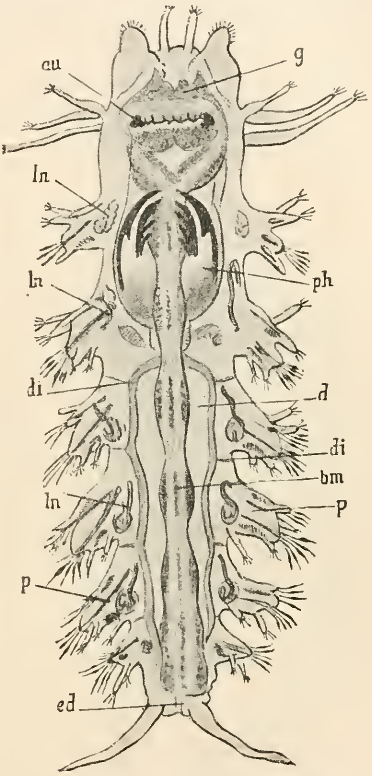


Fig. 159.—**Diagram of a very young specimen of Nereis cultrifera, after Edward Meyer.** *g*, Brain; *au*, eyes; *ln*, larval trunk nephridia; *ph*, pharynx with jaws; *di*, dissepiments; *d*, intestine; *bm*, ventral chord; *ed*, hind-gut; *p*, parapodia with cirri and setæ. On the head are the tentacles and sensory cirri.

Concerning the structure of the provisional trunk nephridia, the following may be said. In the *Capitellidæ* and *Oligochæta* they show in general the same structure as the permanent trunk nephridia. In *Nereis* they are distinguished from the permanent nephridia by the want of an inner aperture opening into the body cavity, *i.e.* of a funnel; both by this fact and the fact that the nephridial canal is intracellular they recall the larval head nephridia of many *Annulata*. The larval nephridia of the *Hirudinea* have neither inner nor outer aperture.

C. **The permanent nephridia.**—In every *Annulate* nephridium, if we for the time ignore the numerous complications and modifications presented by the different divisions, the following three portions may be distinguished:—(1) an inner ciliated aperture opening into the body cavity or into a blood sinus; this from its shape is often called the funnel; (2) a canal connected with the above, which is generally ciliated, and often has glandular walls; and (3) a terminal portion opening externally. The central part or nephridial canal is intracellular in the *Hirudinea* and *Oligochæta*, and generally much coiled (looped canal) (Fig. 160). In the *Polychæta* it is usually intercellular (lined with a many-celled epithelium) and not coiled in a complicated manner. The portion of the *Annulate* nephridium which projects into the body cavity is outwardly covered by a continuation of the peritoneal endothelium.

In the *Hirudinea* the permanent nephridia are wanting in a number of the anterior and posterior segments. In the rest of the body they are found in strictly segmental arrangement, one pair in each segment. The position of the funnels in the body varies very much; they lie either in the ventral blood sinus (*Clepsine*), or in those sinuses in which the testes lie (*Hirudo*, *Aulostoma*), or in other blood sinuses of the body. The nephridial canal has many windings and loops which lie close together, the finer details of which it is extremely difficult to make out. Finally, it opens externally either directly without terminal swelling (*Clepsine*), or it opens into a vesicle lined with epithelium (ciliated in *H.*

medicinalis), which opens externally through a pore. That part of the nephridial canal which comes after the funnel is distinguished by the fact that fine, branched, and often anastomosing canals enter its intracellular principal lumen. The cells of this portion are in fact perforated by branching canals. In *Hirudo* the funnel is closed towards the blood sinus in which it lies.

The nephridia in the genera *Pontobdella*, *Branchellion*, and *Piscicola* differ much from the above, as they form in each segment a complicated network of canals which are always intracellular, this network opening outwardly by 2 apertures and entering the blood sinuses of the body through 2 funnels.

The nephridia of other *Oligochæta* show (Fig. 160) great correspondence with those of the *Hirudinea*. The funnel of a nephridium projects from the anterior wall of each dissepiment into the cavity of the segment lying anterior to that in which the nephridium lies. Starting from the funnel, the nephridial canal, which is everywhere intracellular, first passes through the dissepiment, forms more or less complicated loops in that segment of the body cavity which lies posteriorly (in these coils we can generally distinguish several different portions), and finally emerges through a terminal portion into a vesicle which opens outwardly. This vesicle is often provided with muscular walls. The funnel and external aperture of a nephridium thus always lie in two different segments; the two external apertures of a pair of nephridia lie in the same segment as the inner funnels of the pair of nephridia which come next in order posteriorly. This position of the inner and outer apertures of the nephridia in 2 consecutive segments is maintained even in those cases where, as in the middle body segments of *Phreatothrix*, the nephridial canal passes through several dissepiments, running back from its ciliated funnels through several segments; it then forms a loop and bends forwards again. In the nephridia of the *Chætogastridæ* the ciliated funnels are wanting. In them, as in the *Hirudinea*, numerous branched and anastomosing intracellular canals enter the central canal. In a species of *Acanthodrilus* (*Lumbricidæ*) there are typically 4 pairs of nephridia in each segment (even in the genital segments). There is said to be a similar arrangement of nephridia in the anterior segments of *Perichæta mirabilis*.

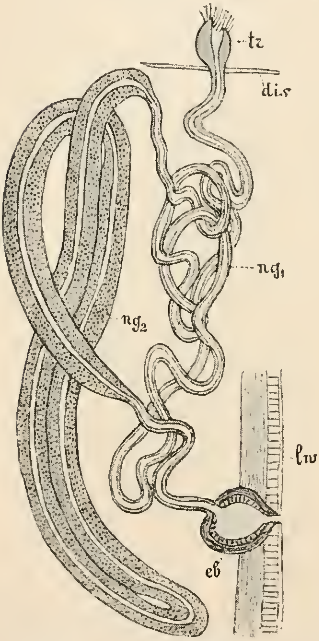


Fig. 160.—**Nephridium of an Oligochæte**, diagrammatic. *tr*, Funnel; *dis*, dissepiment; ng_2, glandular; ng_1, non-glandular portion of the nephridial duct; *eb*, terminal vesicle; *lw*, body wall (partly after **Vejdovsky**).

The permanent nephridia of the *Polychæta* are tubes with cellular walls; their often ciliated central canal is thus as a rule, in opposition to that of the *Oligochæta* and *Hirudinea*, intercellular. (Intracellular nephridial canals, however, also occur.) The nephridial tube is almost always so bent that we can distinguish in it two limbs, one centripetal, at whose inner end lies the funnel, which is mostly wide open and provided with cilia, and another centrifugal, which opens outwardly by breaking through the body wall. The nephridia lie in the nephridial or renal chambers of the body cavity which have already been described (p. 213), and they may lie wholly in one segment, or else, as in the *Oligochæta*, each pair of nephridia belongs to two consecutive segments.

Although there are many *Polychæta* in which the pairs of nephridia are repeated throughout the greater part of the body with great uniformity and in strictly segmental arrangement, there are, on the other hand, many groups in which we find great deviations from this arrangement. We can only mention the most important.

In the *Capitellidæ* permanent nephridia occur, as a rule, only in the abdominal region, either in the greater part of that region or only in the anterior, or only in the posterior portion. There is either one pair in each segment or several (*Capitella*); even as many as 6 pairs may occur in each segment. In most *Capitellidæ* more or less numerous pairs of nephridia are changed into genital tubes, which will be further described below, and it is always the anterior pairs of nephridia which undergo such a transformation. The permanent nephridia of *Capitella* are distinguished by the fact that they possess, as a rule, more than one funnel.

In the *Terebelloidea* the nephridia only occur in the thoracic region, and in strictly segmental arrangement. In this region the dissepiments are wanting, with the exception of a strongly developed diaphragm which divides the cœlome of the thoracic region into an anterior and a posterior cavity. The nephridia of the anterior thoracic cavity function as organs of excretion; those of the posterior conduct the genital products to the exterior. In *Lanice conchilega* there is a very striking nephridial arrangement. The 3 pairs of nephridia of the anterior thoracic cavity do not emerge externally direct, but the 3 nephridia of each side enter a short nephridial duct which has a single external aperture. In a similar way the 4 nephridia of the posterior thoracic cavity enter on each side a longitudinal nephridial duct, which, however, has not 1 opening but 4. It may therefore be said that the 4 nephridia on each side are connected by a longitudinal canal.

In the *Cirratulidæ*, *Serpulacea*, and *Hermella* (Fig. 147, p. 221) an anterior sterile region and a posterior genital region may be distinguished, the genital products attaining development in the latter. In the anterior sterile region, which consists of a varying number of segments, only one pair of nephridia occurs. This pair alone has an excretory function. They are long, and extend through several segments. In the *Cirratulidæ* they emerge ventrally by separate apertures in the third segment; in the *Serpulacea* and *Hermella*, however, they unite anteriorly to form an unpaired duct, which reaches the exterior near the extreme anterior part of the body in the dorsal middle line. In the genital region the nephridia are repeated in strictly segmental arrangement, and serve as genital tubes for conducting the sexual products to the exterior.

In *Sternaspis*, two brown lobate bodies lying in the 5th and 6th segments are regarded as nephridia; these possess neither a lumen nor an internal aperture, and end in the integument between the sixth and seventh segments.

In the *Echiuridæ* (Fig. 137, p. 207) there are two sorts of organs which have been considered as nephridia, the so-called segmental organs and the anal tubes. The segmental organs have quite the structure of the permanent Polychætan nephridia, and we can hardly doubt their homology with the latter. They occur either in 2 pairs (*Echiurus*), or 3 pairs (*Thalassema*), or unpaired and singly (*Bonellia*), and possess well-developed internal funnels. Their outer apertures lie behind the anterior hooked setæ. Their principal function is the transmission of the genital products out of the body cavity. The **anal tubes** are 2 long tubes which on the one hand enter the hind-gut, and on the other are in open communication with the body cavity by means of numerous ciliated funnel apertures, one of which always lies terminally. An excretory function is ascribed to them. Whether they represent a pair of modified nephridia cannot at present be decided. The fact that they are supplied with numerous funnel apertures ought not to stand in the way of such a view, as typical permanent nephridia in the *Polychæta* (*Capitella*) and *Oligochæta* (*Anachæta*) may be provided with accessory funnels.

Organs which may with certainty be pointed to as nephridia have until now not been observed in the **Myzostomidæ**.

The problem of the morphological relations between the permanent nephridia, the provisional trunk nephridia, and the embryonic head nephridia, is still unsolved. It is closely connected with the questions as to the significance of segmentation in the *Annulate* body and the morphological significance of the body cavity and the mesoderm. It is very probable that the permanent segmentally-arranged nephridia in all the *Annulata* are homologous. The histological difference between the nephridia of the *Hirudinea* and *Oligochæta* on the one hand and those of the *Polychæta* on the other, which consists in the fact that in the former the nephridia are perforated rows of cells and in the latter as a rule tubes with epithelial walls, would in that case be unessential, as also would be the absence or presence of branchings. It is further probable that the provisional trunk nephridia are morphologically equivalent to the permanent nephridia. They are distinguished from the latter only in that they appear earlier and disappear in proportion as the permanent nephridia appear and assume their functions. The homology between provisional trunk nephridia and permanent nephridia is supported by the circumstance that no case has as yet been known in which permanent nephridia have attained development in a segment where provisional nephridia have previously appeared and then disappeared. *Capitella*, in which in the tenth and eleventh segments both provisional and permanent nephridia develop, is an exception, but only an apparent exception, for we have seen that in this animal several pairs of permanent nephridia occur in one segment. It is probable that the embryonic head nephridia are homologous with the trunk nephridia (provisional and permanent). The whole nephridial apparatus would then have to be judged of in the following way. Originally a pair of nephridia occurs in each segment of the segmented *Annulate* body, even in the head segment. All the pairs of nephridia are segmentally homologous with each other. The larva or embryo of the now living *Annulata* consists of the embryonic head segment and the unsegmented rudiment of the trunk. The differentiation of the trunk occurs from before backward; the first and oldest segment to be developed is the first trunk segment; then follows the second trunk segment, and so on. In correspondence with this, the pair of nephridia of the head segment first appears (embryonic head kidneys), then the pairs of nephridia of the anterior trunk segments, several of which (provisional trunk nephridia) may degenerate gradually as new nephridia, the permanent trunk nephridia, begin to form behind them. The cause of the disappearance of the head and the provisional trunk nephridia in the course of development is perhaps to be found in the fact that the foremost body segments in the adult animal are crowded with organs (pharynx, brain, etc.) Besides this, in the whole animal kingdom organs which attain development very early and function during larval or embryonic life show a tendency to degenerate early, as if they were soon worn out. Further in the *Oligochæta* (excepting the *Lumbricidæ*) the nephridia in the genital segments degenerate when the various sexual organs attain development.

The nephridia as organs of excretion.—The original and most general function of the nephridia is that of excretion. The discharge of the excretory products occurs in two ways. The nephridia may either take up the excretory products direct out of the body fluid or out of the blood by means of the open funnels, or the excretory products may collect in the walls of the nephridia and thence reach the nephridial cavity. The nephridia are often surrounded by a rich network of blood-vessels which yield up to the nephridial walls the excretory material they contain.

The nephridia as ducts for the sexual products.—Since the nephridia establish an open means of communication between the body cavity and the outer world, an opportunity is offered to the sexual products floating in the cœlomic fluid to choose this way of reaching the exterior. In the *Polychæta* the nephridia in fact act at the same time as sperm ducts and oviducts. In the simplest cases this new function does not bring about any marked variation in the form and structure of the nephridia, the funnels at most showing slight enlargement at the time of sexual maturity. It often happens, however, that some of the nephridia act almost exclusively as sperm ducts and oviducts. Their funnels are then strikingly enlarged, while at the same time the (excretory) nephridial canal diminishes in size and becomes simplified. Some of the nephridia in the *Capitellidæ* undergo even more profound modification. The funnel becomes enormously enlarged, and connected with the exterior by means of a new canal, which breaks through the body wall and opens outwardly through a genital pore, while at the same time the nephridial canal may become reduced and may quite disappear. Thus arise the **genital tubes**; they act as ducts for the sexual products and as copulatory organs. The sperm ducts and oviducts of the *Oligochæta* have also long been considered as modified nephridia, and it cannot be denied that they show great agreement with nephridia in their structure and composition (funnel, canal, or duct and terminal vesicle) as well as in their development. Nevertheless it is a striking fact that in the *Oligochæta*, where the nephridia occur in strictly segmental arrangement (one pair in each segment), either permanent (*Lumbricidæ*) or provisional nephridia (other *Oligochæta*) are found in the genital segments also, side by side with the sperm ducts and oviducts. In *Acanthodrilus*, where 4 pairs of nephridia occur typically in each segment, there are also 4 pairs in the genital segments. These are difficulties which cannot be ignored in the way of establishing a homology between the oviducts and sperm ducts of the *Oligochæta* and nephridia. The ducts for the sexual products in the *Hirudinea* and *Myzostomidæ* can certainly not as yet be considered as modified nephridia.

The phylogenetic origin of the nephridial system of the Annulata is still quite uncertain. There are three different views. According to one of these, the whole nephridial system of the *Annulata* corresponds with the water-vascular system of the *Platodes* and with the excretory system of the *Nemertina*, which (in the

Triclada and certain *Nemertina*) already shows a more or less distinct segmentation, in that the efferent ducts are segmentally repeated. In all *Platodes* and *Nemertina*, however, longitudinal canals are present throughout the whole body or in the anterior part of the body, which can open externally through more or less distinctly paired and segmentally arranged ducts, whilst in all *Annulata* the nephridia are separate at their first appearance, and with a very few exceptions (*Lanice*) remain separate during life. While the water-vascular system of the *Platodes* is markedly branched, such branching is less marked even in the *Nemertina*, and in the *Annulata* (*Oligochæta*, *Polychæta*) is generally altogether wanting. This may be explained by the fact that in the parenchymatous *Platodes* the excretory organs have to seek out the excretory products all over the body, while the development of a blood-vascular system and a body cavity affords spaces for collecting these products, out of which the nephridia can take them direct. The nephridial funnel in the *Annulata*, which ontogenetically originates quite separately from the other parts of the nephridium, would then be a new adaptation, a collecting apparatus, suited for taking up the excretory material out of the blood sinuses or body cavity, and for discharging it through the nephridial canals. According to a second view, only the embryonic head kidneys of the *Annulata* correspond with the water-vascular system of the *Platodes*, with which they certainly often show a great structural resemblance. A third supposition is that the head kidneys of the *Chætopoda* and the embryonic kidneys of the *Hirudinea* answer to the excretory organs of the *Nemertina*, while the permanent nephridia may have arisen from the efferent ducts of the ovaries and testes of the *Nemertina*. This last conjecture is opposed by the fact, which is unanimously supported by all recent investigations, that the original function of the *Annulatan* nephridium is excretory, and that only secondarily some of the nephridia undertake the transmission of the sexual products.

Prosopygia.—The number of the nephridia is everywhere in this class very small; there are never more than two pairs. In the *Sipunculidæ* (Fig. 138, p. 208) there are two large tubular nephridia like the permanent nephridia of the *Polychæta*, especially of the *Echiuridæ*. They emerge laterally at the limit between the proboscis and the trunk (near the anus). Less frequently (*Phascolion*) only one nephridium occurs. The nephridia, besides their excretory functions, serve as ducts for the transmission of the genital products. In *Sipunculus* anal tubes which enter the hind-gut have been observed, which are perhaps homologous with the anal tubes of the *Echiuridæ* and the *Priapulidæ*. The *Priapulidæ* have only two richly-branched anal tubes emerging near the anus. At the blind ends of the branches are found terminal cells with long flagella projecting into the canals, similar to those which are characteristic of the water-vascular system of the *Platodes* and of some of the embryonic head nephridia and the provisional trunk nephridia of the *Annulata*. The anal tubes of the *Priapulidæ* are said to act as excretory organs in youth, and in later stages as places of formation and ducts for the transmission of the sexual products. *Phoronis* possesses one pair of nephridia which open outwardly and anteriorly by two lateral apertures, and besides their excretory function also undertake the transmission of the genital products out of the body cavity. Among the *Bryozoa* nephridia have till now been found only in the *Endoprocta*. They are paired canals like the embryonic head nephridia of the *Annulata*, which issue between mouth and anus into the so-called vestibulum. The *Brachiopoda* (Fig. 150, p. 226) possess one pair, less frequently (*Rhynchonella*) two pairs like those permanent nephridia which in the *Polychæta*, *Sipunculidæ*, and *Phoronis* discharge the sexual products. They emerge to the right and left of the mouth into the mantle cavity.

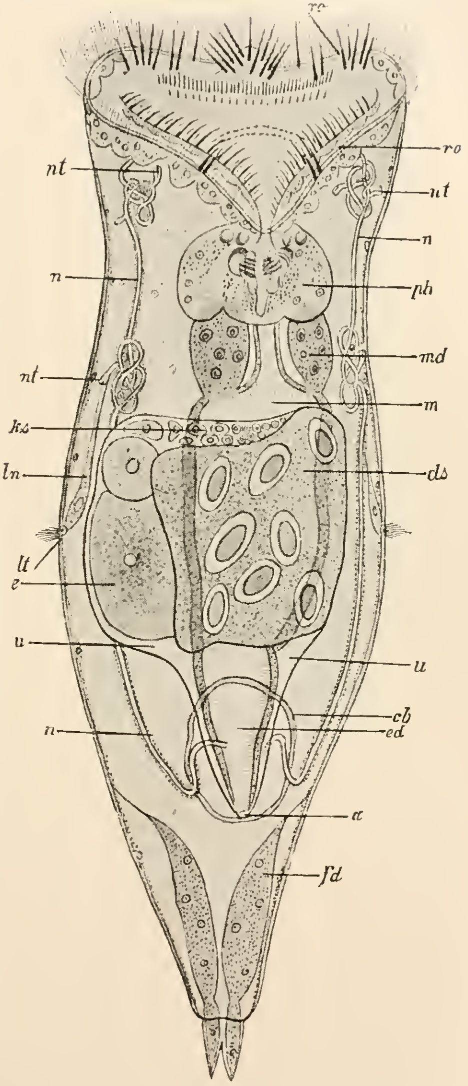


FIG. 161.—**Organisation of Hydatina senta, after Plate.** *ro*, Wheel organ; *nt*, nephridial ciliated cells; *n*, nephridia; *ph*, pharynx; *md*, gastric glands; *m*, stomach; *ds*, vitellarium; *ks*, germarium; *cb*, outline of the contractile vesicle; *ed*, hind-gut; *u*, uterus; *a*, anus; *fd*, cement or pedal glands; *lt*, lateral feeler; *ln*, nerve of the same; *e*, advanced egg.

Rotatoria and Dinophilus.—*Dinophilus gyrociliatus* (Fig. 162) possesses five pairs of nephridia, which show a remarkable agreement with the provisional trunk nephridia of certain *Polychæta* (*Nereis cultrifera*, Fig. 159, p. 239). They lie one behind the other in the trunk region in those segments which are outwardly indicated and demarcated by ciliated rings. The nephridia of the *Rotatoria* (Fig. 161) consist of two looped, and in certain places much convoluted canals, which run longitudinally near the intestine; these open into the cloaca, generally forming a contractile terminal vesicle. The longitudinal canals usually have short accessory branches, whose ends (ciliated lobes, vibratile organs) seem to be constructed like the ends of the water-vascular system of the *Platodes*, and of the embryonic head nephridia of the

Annulata. This correspondence indeed is apparent in the whole nephridium.

The only organs which can perhaps be pointed to as transformed nephridia in the *Chætognatha* are the oviducts and the sperm ducts; these are paired tubes, the oviducts opening outwardly at the posterior end of the trunk segment, the sperm ducts in the tail segment by paired lateral apertures. The latter are provided with funnel-like ciliated inner apertures.

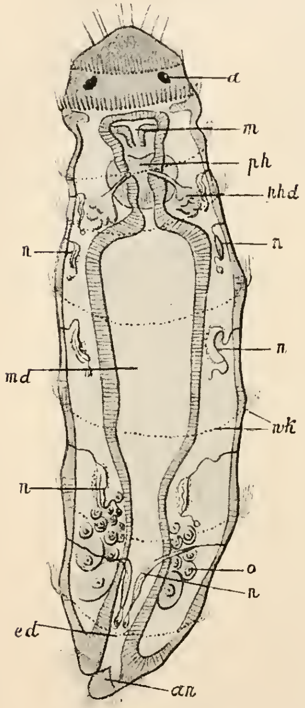


FIG. 162.—**Organisation of Dinophilus gyrociliatus, female, after E. Meyer.** *a*, Eye; *m*, mouth; *ph*, pharynx; *phd*, pharyngeal glands; *n*, nephridia; *md*, mid-gut; *wk*, ciliated rings; *o*, ovarium; *an*, anus; *ed*, hind-gut.

X. Respiratory Organs.

In many worms no specific respiratory organs are developed. Respiration is performed by means of the integument, and also often by the walls of the intestine. The general ciliation of the body in the *Nemertina* is of great assistance for respiration in water. In the *Hirudinea* and many *Oligochæta* cutaneous respiration is facilitated by the presence in the integument of numerous fine blood-vessels. But we can only speak of specific respiratory organs where definite organs have been developed whose exclusive or most important function is respiration. Among the *Hirudinea* we see in *Pontobdella* the integumental capillaries of the blood-vascular system already localised in elevations and papillæ of the body, which may therefore be called the branchial papillæ. In *Branchellion* each ring carries on each side a branched appendage into which blood-vessels enter. Specific respiratory organs are wanting in the *Oligochæta* and the *Archiannelida.* Among the *Oligochæta*, only the insufficiently known *Alma nilotica* possesses branchial appendages at the posterior part of the body. The *Polychæta*, on the contrary, are pretty generally supplied with gills, which are usually branched appendages of the Parapodia (Fig. 124, p. 188; Fig. 158, p. 237); these in some cases, however, may emancipate themselves from the parapodia and may be independently inserted on the back. The comparative morphology of the gills of the *Polychæta* has not yet been thoroughly worked out. We may perhaps at once distinguish two sorts of gills—lymph gills and blood gills. The **lymph gills** are processes of the parapodia which are distinct from the parapodial cirri; they may occur simultaneously on the ventral and dorsal parapodia. They are found in the *Capitellidæ* and the *Glyceridæ*, and in the absence of a separate blood-vascular system are provided with continuations of the body cavity carrying hæmolymph. The **blood gills,** on the contrary, are often branched appendages of the parapodia which are penetrated throughout by blood-vessels. We can again distinguish two sorts of blood gills—dorsal gills and cephalic gills. The dorsal gills are transformed cirri of the dorsal parapodia, or transformed lateral off-shoots of such cirri. They occur, like the parapodia themselves, in segmental order, but may often attain development only in certain regions of the body (branchial regions). The cephalic gills, on the other hand, which we meet with specially in tubicolous *Annelids*, are transformed tentacles or feeler-cirri of the head, and often form a beautiful crown of gills or tentacles projecting above the aperture of the tube. These crowns are at the same time also the seat of a fine sense of touch, and, further, organs for the drawing in of nourishment. In the *Sabellidæ* (*Branchiomma*) eyes may be developed on the cephalic gills. Where gills attain development they are almost always either ciliated or mobile, so that a constant exchange of the respirable medium, oxygenated water, is secured. In the thoracic membrane of the *Serpulidæ* there is a rich network of vessels, and this no doubt has a respiratory significance. In *Sternaspis*, on each side of the anus, there is a tuft of filamentous gills. We do not find special respiratory organs in the *Myzostomidæ*, the *Chætognatha*, and the *Rotatoria*, in whom a blood-vascular system also is wanting. In all these forms cutaneous respiration must take place, facilitated in the wheel animalculæ by the activity of the wheel organ. The cutaneous respiration in the *Echiuridæ* is principally localised in the prostomium. In the *Prosopygia* the tentacles which stand round the mouth, or the oral arms furnished with cirri (*Brachiopoda*) chiefly act as gills, and these organs are either penetrated by blood-vessels (*Phoronis*, *Brachiopoda?*) or supplied with canal or vessel-like processes of the body cavity (*Sipunculidæ*, *Bryozoa*). In the *Brachiopoda* the inner surface of the mantle has in all cases an additional respiratory significance. The *Priapulidæ* among the *Sipunculacea* possess no oral tentacles; in them respiration takes place through the integument. Besides this, however, there can be little doubt that in *Priapulus* the deeply-lobed caudal appendage into which, in the absence of a blood-vascular system, a continuation of the body cavity extends, may be regarded as a respiratory organ.

Just as the cutaneous respiration may be concentrated in certain localised parts of the integument, in which places the principle of in-increase of surface is applied, accompanied by a richer vascularisation, the enteric respiration also may be localised. The accessory intestine which is found in some *Polychæta* and *Sipunculacea* is said to represent such a respiratory portion of the enteric canal. Respiratory organs are wanting in the *Nemathelminths*.

XI. Blood-Vascular System.

There is no organic system in the worms which is so variable as the blood-vascular system. It is sometimes wanting, sometimes highly-developed. We even find that it may be wanting in certain groups whose nearest relations possess it. Thus, as we find a blood-vascular system sometimes present, sometimes absent, in the most different orders of the most different classes, its small morphological worth is evident. Even where worms are supplied with a circulatory apparatus it varies so much in structure that no morphological comparison is possible, at any rate at present.

Nemertina (Fig. 157, p. 235).—In this class of the *Vermes* for the first time in the animal kingdom we meet with a blood-vascular system. In the *Paleonemertina* (excepting *Valenciniidæ* and *Polliidæ*) it consists of 2 lateral vascular trunks, uniting posteriorly above the intestine, and anteriorly entering a lacunar system, which likewise establishes communication between them. In the *Schizonemertina* (with the *Polliidæ* and *Valenciniidæ*) there are 3 longitudinal vessels, 2 lateral, and 1 medio-dorsal which lies above the intestine, in the proboscidal region between the proboscis and the intestine. The 3 vessels become lacunar anteriorly, and communicate above and below the proboscis sheath. In the rest of the body they are connected together by transverse vessels. The same is the case in the *Hoplonemertina*, only a lacunar system is here wanting, and the vascular system is completely closed. The blood is colourless or contains red blood corpuscles. The vessels are lined with endothelium and occasionally have muscular walls.

Nemathelminthes.—The *Nematoda* have no vessels. In the *Acanthocephala*, throughout the whole subcuticle, a peculiar network of canals extends, whose morphological and physiological significance is still little understood. The system of canals, which are hollow spaces without walls of their own, running in the very much thickened subcuticle, consists of 2 completely separate parts—the canal system of the trunk and the canal system of the neck, the proboscis, and the lemnisci. In the trunk canal system we find 2 specially distinct longitudinal trunks which run either laterally, or dorsally and ventrally. The neck, head, and lemniscal canal system enters a circular canal situated at the base of the neck. The **lemnisci** (Fig. 172, *l*, p. 258) are two pouches, generally of a brown colour, which hang from the base of the neck into the body cavity and are processes or appendages of the subcuticle of the neck. A canal enters each lemniscus from the circular canal, and divides into two branches directly after entering; these branches run longitudinally through the lemniscus. Besides these, narrower canals also occur in the lemnisci.

Annulata.—The *Hirudinea* and the *Chætopoda* are separated by sharp and radical differences in the blood-vascular system. In the *Myzostomidæ* blood-vessels are altogether wanting.

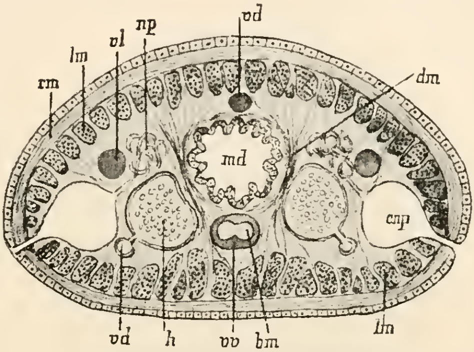


Fig. 163.—**Transverse section through Hirudo,** diagrammatic. *rm*, Circular musculature ; *lm*, longitudinal muscular layer ; *vl*, lateral vessels ; *np*, looped canals (nephridia) ; *vd*, dorsal vessel ; *dm*, dorso-ventral musculature ; *enp*, terminal vesicle of the nephridia ; *bm*, ventral chord ; *vv*, ventral vessel ; *h*, testes ; *vd*, vas deferens ; *md*, mid-gut.

Hirudinea.—In describing the body cavity we have already drawn attention to the difficulty of distinguishing it from the blood-vascular system. We are, besides, not certain that these are two originally separate systems, and it seems almost necessary to consider the whole together. There occur almost universally 4 longitudinal vessels (Fig. 163)—1 dorsal, lying over the intestine, 1 ventral, in which the ventral chord lies, and 2 lateral, which in many cases pulsate. Of these 4 vessels the ventral one (ventral sinus) may best be considered as the principal part of a reduced body cavity. The dorsal vessel is wanting in *Nephelis* and some land leeches. The longitudinal vessels are connected together, chiefly at the anterior and posterior ends of the body, by fine vascular branchings. Such a connection also takes place in various ways in other parts of the body. The peripheral vascular system consists principally of 2 well-developed systems of branched and often anastomosing capillaries, one of which lies in the integument and penetrates into the body epithelium, the other spreading out over the intestine. The excretory and sexual organs are richly supplied with blood-vessels. In *Nephelis* (Fig. 164) and land leeches there are, in connection with the anastomoses between the lateral and ventral vessels, ampullæ or blood vesicles in segmental arrangement, one on each side (*land leech*) or two together (*Nephelis*). In *Branchellion* on each side, at the base of every third gill, there is a blood sinus, widened into a vesicle. The blood everywhere contains colourless amœboid corpuscles, and often free nuclei. In the *Gnathobdellidæ* the blood is red. Hæmoglobin is found dissolved in the blood plasm.

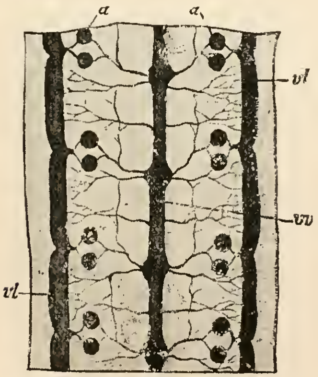


Fig. 164.—**Vascular system in 4 segments of the middle part of the body of Nephelis,** after **Jaquet.** *vv*, Ventral vessel ; *vl*, lateral vessels ; *a*, ampullæ.

By the presence of one dorsal and two lateral vessels, the blood-vascular system of the *Hirudinea* recalls that of the *Nemertina*. They also agree in the possession of blood sinuses.

The vascular system of the *Chætopoda* is strikingly different from that of the *Hirudinea*. It is entirely separate from the body cavity. Both the lateral vessels of the *Hirudinea* are wanting. The most important and constant parts of the *Chætopodan* circulatory apparatus are: (1) a medio-dorsal longitudinal vessel and (2) a medio-ventral longitudinal vessel (Fig. 165). The first is mostly contractile; in it the blood streams from behind forwards; it lies over the intestine, sometimes nearer the latter, sometimes nearer the body wall. The second is not contractile; in it the blood streams from before backward. It lies in the body cavity, below the intestine and above the ventral chord, approaching sometimes the one, sometimes the other. In the details of the arrangement, development, and course of the vessels there is extraordinary variety, which makes it impossible to describe them briefly and comprehensively. In a very simple case the ventral vessel divides at the anterior end of the body into 2 branches, which, surrounding the fore-gut, enter the anterior end of the dorsal vessel. The dorsal and ventral vessels are further connected in each segment by lateral vascular loops; it is from these especially that branches proceed to the body wall. Vessels coming from a vascular network surrounding the intestine also enter the dorsal vessel; this network in many cases may be replaced by a blood sinus lying between the epithelial and the muscular walls of the intestine. The blood in the vessels of the *Chætopoda* is generally red, and contains colourless corpuscles.

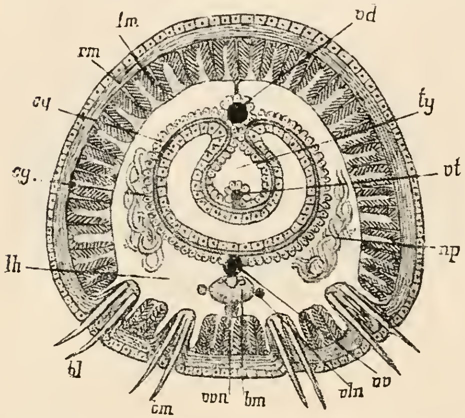


Fig. 165.—**Transverse section through a Lumbricus,** diagrammatic. *lh*, Body cavity; *cg*, chloragogen cells; *rm*, circular musculature; *lm*, longitudinal musculature; *dv*, dorsal vessel; *ty*, typhlosolis; *vt*, typhlosolis vessel; *np*, nephridia; *vv*, ventral vessel; *vln*, lateral vessel of the ventral chord; *bm*, ventral chord with the neurochord tubes; *vvn*, sub-neural vessel; *bm*, 2 setæ of the ventral row; *bl*, 2 of the lateral row.

The following are brief descriptions of the blood-vascular systems of an *Oligochætan* and of a *Polychætan* (arbitrarily selected).

Lumbricus (Fig. 166) (as an example of the *Oligochæta*).—There are 5 longitudinal vessels; first a medio-dorsal vessel;—second and third 2 medio-ventral vessels, one of which lies under the intestine and above the ventral chord, and represents the ventral vessel which is always found in the *Chætopoda*, while the other is much finer and runs under the ventral chord, the former is known as the **ventral vessel,** and the latter as the **sub-neural vessel**;—fourth and fifth, 2 delicate vessels which accompany the ventral chord throughout its whole length, running to the right and left of it; these are the **lateral vessels of the ventral chord.** The sub-neural vessel is connected with the lateral vessels of the ventral chord at intervals by transverse anastomoses. The dorsal vessel, near the mid-gut, has segmental swellings, so that it here assumes the form of a string of beads. In the genital segments it is connected with the ventral vessel by 5 pairs of wider pouch-like **contractile vascular loops,** the so-called **hearts.** In the region of the mid-gut the dorsal vessel gives rise in each segment to 3 pairs of vessels. The first pair run laterally in the body cavity and enter the sub-neural vessel. They give off in their course vessels to the body wall and the integument, and further, in the lower part of their course, anastomoses to the ventral vessel and the lateral vessels of the ventral chord. The two posterior pairs run on the intestine where they break up into an extremely rich and close network. The typhlosolis and the muscular stomach are also supplied from the dorsal vessel. Anteriorly, between the third and fourth pairs of hearts, there arises from the dorsal vessel on each side a vascular trunk, whose complicated branches supply the anterior part of the body, the intestine, the body wall, the first pair of Morren's glands, the pharynx, the œsophagus, etc.; these are also connected with the ventral and sub-neural vessels. In each segment the ventral vessel gives rise to a lateral pair of vessels, which branch in the body wall and the integument. These branches anastomose in that part of the body which contains the stomach intestine with the branches arising in each segment from the first pair of lateral vessels of the dorsal vessel, which latter maintain a communication between the dorsal vessel and the sub-neural vessel. The ventral and dorsal vessels give off branches to the extreme anterior end of the body, which ramify in the body wall and pharynx. The ventral vessel further divides at its anterior end into 2 branches, which penetrate to the brain and so form an œsophageal ring. The contractile part of the blood-vascular system possesses muscular walls.

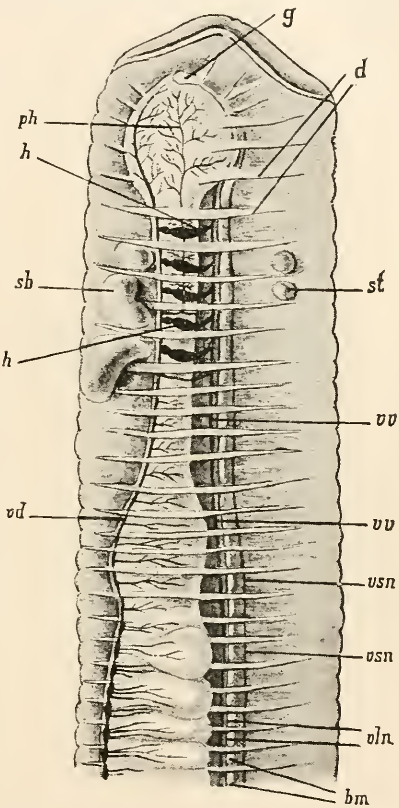


Fig. 166.—**Anterior portion of the body of Lumbricus terrestris, opened, to show the vascular system.** The intestine is seen from the right side (after **Jaquet**). *g*, Brain; *d*, dissepiments; *st*, sperm sacs; *ph*, pharynx; *sb*, seminal vesicles; *vd*, dorsal vessel; *vv*, ventral vessel; *vsn*, subneural vessel; *vln*, lateral vessels of the ventral chord; *bm*, ventral chord; *h*, contractile vascular loops (hearts) between the dorsal and ventral vessels.

Nephthys scolopendroides (Fig. 167) may be taken as an example of a *Polychætan* with homonomous segmentation of the body. We find here the two most important typical vessels, the **dorsal** and the **ventral.** Both lie close to the wall of the intestine. From the posterior end of the pharynx to the end of the body the dorsal vessel gives rise in each segment to a pair of lateral vessels, which run to the body wall and especially to the dorsal branch of the parapodia and there ramify. Soon after its rise out of the dorsal vessel each lateral vessel gives off a branch to the enteric wall, this branch there forming a rich vascular network. At the foremost end of the mid-gut the dorsal vessel shows a slight swelling; it then leaves the intestine and runs along the inner side of the body wall in the region where the pharynx lies to the extreme anterior end of the body. It here divides into 2 branches, which run backwards, to pass into the anterior end of the ventral vessel at the posterior end of the pharyngeal region. The departure from the general plan of the principal vessels in the pharyngeal region is evidently caused by the great development of the pharynx. If they lay as close to the pharynx as they do to the intestine in the rest of the body, they would be broken by its protrusion. The ventral vessel gives rise in each segment to a pair of lateral vessels, which run along to the base of the ventral branches of the parapodia, passing into the latter and there ramifying. A connection between the lateral branches of the dorsal vessel and the lateral branches of the ventral vessel takes place in the following way. Between the dorsal and ventral branches of a parapodium there runs on each side a vessel which ramifies on one side in the dorsal branch, on the other in the ventral branch. These ramifications of the connecting vessels anastomose with the ramifications of the dorsal or ventral lateral vessels. On the ventral side of each dorsal parapodial branch a sickle-shaped gill is inserted. Two vessels from the vascular system of the dorsal parapodial branch enter the gill, and with many windings and anastomoses run through its whole length. Besides the dorsal and ventral vessels, *Nephthys* possesses also two extremely delicate lateral vessels of the ventral chord, which are connected by fine branches with the lateral branches of the ventral vessel.

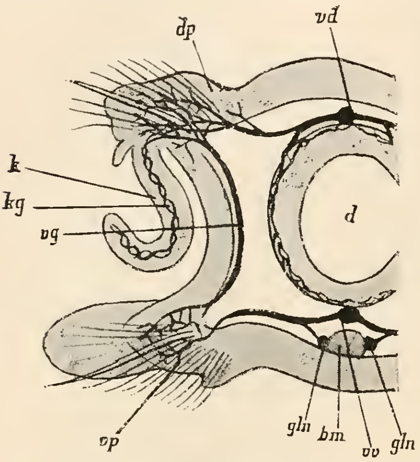


FIG. 167.—**Part of a transverse section through a segment of the body of Nephthys,** diagrammatic, to demonstrate the arrangement of the **blood-vessels** (partly after **Jaquet**). *dp*, Dorsal; *vp*, ventral parapodium, with bundles of setæ and supporting seta; *vd*, dorsal vessel; *vv*, ventral vessel; *gln*, lateral vessels of the ventral chord; *vg*, connecting vessel between the dorsal and ventral parapodia; *d*, intestine; *bm*, ventral chord; *k*, gills; *kg*, branchial vessels.

This arrangement of the blood-vascular system can, however, only to a very limited extent be considered typical of the *Polychæta*. In the different families, indeed, very great variations are to be found. The blood-vascular system is extraordinarily plastic. It follows the smallest modifications in the structure and arrangement of the other organs of the body. Its special form is above all dependent on the arrangement and development of the gills. In the *Terebellidæ* the dorsal vessel forms in the anterior part of the body a tubular pulsating heart, which is narrowed anteriorly, and which supplies the gills lying on the most anterior body segments with blood-vessels. At its posterior end it splits into two branches, which encircle the intestine. These branches unite below the intestine to form a sub-intestinal vessel which runs a certain distance backwards over the ventral vessel. Then the sub-intestinal vessel again divides into two branches, which encircle the intestine and again unite in the dorsal middle line to form a dorsal vessel running to the extreme posterior end of the body. In the *Cirratulidæ* (*Chætozone*), at the posterior region of the body where there are no gills, a separate dorsal vessel and an enteric vascular plexus are both wanting. They are here replaced by a blood sinus which continuously surrounds the intestine inside its muscular wall. This sinus is continued anteriorly into a strong pulsating dorsal vessel (heart) which runs through the whole branchial region and gives off vessels to the gills directly or indirectly. In the *Serpulidæ* the enteric canal is generally embedded along its whole length in a blood sinus, and a dorsal vessel is wanting. Lateral vessels frequently run along the sides of the intestine, and are connected by segmentally arranged transverse loops with the ventral vessel, and in the case of *Serpulidæ* provided with a thoracic membrane these lateral vessels give off branches segmentally to this membrane which break up in it into extraordinarily numerous and fine ramifications. In the *Serpulidæ*, where the gills are developed exclusively in the head segment, each branchial filament is penetrated by a single vessel, and the afferent and efferent blood passages first separate at the bases of the gills. In nearly all other *Polychæta* we can distinguish afferent and efferent vessels (branchial arteries and branchial veins) which pass into each other at the ends of the branchial filaments. In the *Capitellidæ* and *Glyceridæ* a blood-vascular system separate from the body cavity is wanting. The blood mingles with the cœlomic fluid (hæmolymph). In *Mastobranchus* alone there are still found rudiments of a blood sinus surrounding the intestine. In many *Polychæta* there is found, in that broader part of the dorsal vessel which is called the heart, a strand, generally of a brown colour, lying freely in its lumen. This is called the **heart body.** Its function is not yet clear. In *Chætozone* 3 such bodies are found.

The blood-vascular system of the *Echiuridæ* (Fig. 137, p. 207) is very simple. It consists of a ventral vessel running through the whole body and lying above the ventral chord. Behind the mouth this vessel divides (like the ventral chord) into 2 branches which, embracing the mouth between them, pass along the 2 sides of the prostomium to its extreme anterior end, where they unite (like the 2 limbs of the œsophageal ring). A dorsal vessel arises from the point of junction, which, running backwards, traverses the prostomium and then runs along the fore-gut to the posterior end of the crop. Here it divides into 2 limbs, embracing the intestine, and these enter the ventral vessel together. The dorsal vessel is thus connected with the ventral vessel by 2 pairs of loops—one anterior, represented by the lateral vessels of the prostomium, and one posterior, at the limit between the fore-gut and the mid-gut. The dorsal vessel is not continued back over the fore-gut.

Prosopygia.—A vascular system is wanting in the *Priapulidæ* among the *Sipunculacea*, and in all *Bryozoa*. In *Sipunculus* there are two vessels, one dorsal and the other ventral, which accompany the fore-gut. Both end posteriorly near the place where the proboscis retractors are attached to the body wall. Anteriorly they enter a sinus which lies in front of the brain at the base of the tentacle crown, encircles the oral cavity, and is in communication with the inner cavities of the tentacles. By the contraction of the dorsal and ventral vessels the fluid they contain is forced into the circular sinus, and from it into the tentacles, which consequently extend and expand. The elements which float in the cœlomic fluid are met with in the vascular fluid, so that an open communication between the body cavity and the vascular system probably exists. In *Phoronis* there is a closed blood-vascular system with red blood corpuscles. A dorsal blood-vessel conducts the blood into a vessel which runs along the base of the tentacle crown and gives off branches to the tentacles. Other branches conduct the blood back into a second vascular ring which runs on the outer side of the former. A vessel rises from each side of the external vascular ring, which unites with that from the other side under the œsophagus, and runs back as ventral vessel asymmetrically in the left chamber of the body cavity; this vessel has numerous lateral cæca. Besides these vessels there is a blood sinus around the stomach intestine. All the vessels are contractile.

The opinions of the most recent investigators as to the blood-vascular system of the *Brachiopoda* vary greatly. Some deny the existence of any circulatory apparatus. There is only, they say, a system of sinuses belonging to the body cavity. Other investigations confirm the old view according to which, in some *Brachiopoda* a contractile tubular heart lies above the stomach, and a vein arising from the heart over the fore-gut. There are also said to be vessels in the arms, and also vessels called genital arteries.

A blood-vascular system is wanting in the *Rotatoria*, *Dinophilus*, and the *Chætognatha*.

XII. Genital Organs.

Division of the sexes generally prevails among the worms. The exceptions to this rule, apart from single cases, are the *Hirudinea*, *Oligochæta*, *Myzostomidæ*, *Chætognatha*, *Phoronis*, and many *Bryozoa*.

Nemertina.—The genital apparatus (Fig. 135, p. 205) is here very simple. The ovaries in the female and the testes in the male are present in large numbers, and are found in the shape of small sacs in adult animals throughout that region of the body through which the mid-gut runs. They lie in the parenchyma (jelly) under the musculature. Each ovary and each testis, at the time of sexual maturity, becomes directly connected with the exterior by means of a special duct. The genital glands on each side generally lie in a longitudinal row in such a way that between two consecutive diverticula of the intestine there always lies an ovary or a testicle. They are therefore more or less regularly metameric in their arrangement, in correspondence with the more or less regular metameric arrangement of the enteric diverticula themselves. In some *Nemertina* there are also genital glands scattered about the parenchyma, each gland, however, has an independent external aperture. In this arrangement we find great agreement with the *Turbellaria* (especially the *Polyclada* and *Triclada*). In the latter, however, the oviducts and sperm ducts arising from the genital glands unite to form common channels of exit.

Nemathelminths.—1. **Nematoda.**—The male genital apparatus is unpaired, and emerges at the posterior end of the body in the cloaca; the female apparatus is paired, and emerges externally on the ventral side in front of the anus, generally near the middle of the body. The male genital apparatus (Fig. 168) is a single continuous tube, lying in the body cavity, which falls into several divisions between its blind inner end and its external aperture. The **testicle division** forms a thin much twisted tube into which a solid axis (rachis) projects from the blind end; attached to this rachis the sperm cells are found at different stages of development. The germ layer lies at the blind solid end of the testicle tube. The nearer we approach to the efferent duct the more advanced are the stages of development and ripeness of the spermatozoa. The testicle division passes into a shorter, wider, pouch-shaped division, the **sperm vesicle,**

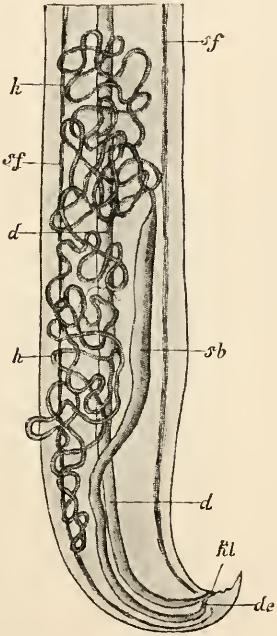


Fig. 168.—**Ascaris lumbricoides, male genital apparatus,** after **Vogt** and **Yung.** *sf*, Lateral lines; *h*, testes; *d*, intestine; *sb*, sperm vesicle; *kl*, cloaca; *de*, ductus ejaculatorius.

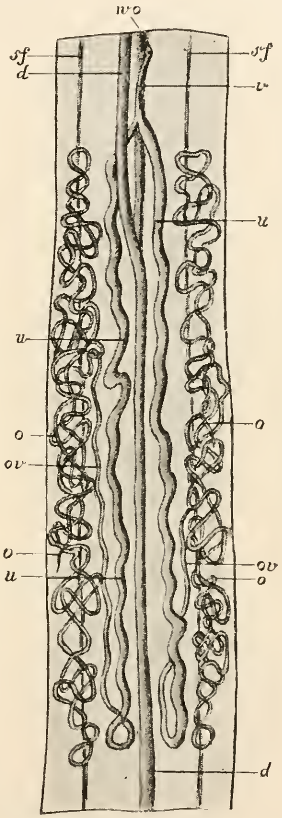


Fig. 169.—**Ascaris lumbricoides, female genital apparatus,** after **Vogt** and **Yung.** *wo*, Female aperture; *v*, vagina; *sf*, lateral lines; *d*, intestine; *u*, uterus; *o*, ovaries; *ov*, oviducts.

and this emerges by a short and narrow terminal piece, the **ductus ejaculatorius**, into the cloaca. Above the ductus ejaculatorius there often lie two elongated sacs, invaginations of the cloaca. Each sac contains a chitinous spiculum. In copulation the spicula may be protruded from the cloacal aperture by special muscles attached to the spicular sacs. In the female genital apparatus (Fig. 169) each of the paired genital tubes repeats in essentials the divisions of the male apparatus. The extraordinarily long **ovarial tube** lies in numerous windings in the body cavity. In its axis there also lies a rachis, to which the young eggs are attached. The ovarial tube is continued into a wider part, the **uterus**, at whose commencement fertilisation generally takes place, that is if the eggs have not already been fertilised in that terminal portion of the ovarian tube into which the rachis does not reach. The uterus contains fertilised eggs in the first stages of their segmentation, and even young embryos. The two uteri unite at their ends and pass into a short common terminal division, the **vagina**, which is often muscular, and opens outwardly in the ventral middle line through the female genital aperture.

2. **Gordiidæ.**—The genital apparatus of the *Gordiidæ* is quite different from that of the *Nematoda*. The male apparatus also is paired. The male and female genital apertures emerge into the last division of the intestine (cloaca). The female genital glands (Fig. 170) are lobed **ovaries** which lie in large numbers in pairs one behind the other on both sides of the dorsal mesentery. They are developed very late at the expense of the mesodermal cells, which in the young Gordiidæ almost entirely fill the body cavity. Some of the eggs which ripen in the ovaries reach the body cavity, entirely filling its lateral chambers and so forming those masses of eggs which were formerly erroneously considered to be ovaries. The further fate of these eggs is not known. Another portion of the eggs, however, pass out of the ovaries into two tubes lined with epithelium which lie in the dorsal mesentery. These tubes, which might be called **uteri**, run backwards, and when approaching the posterior end of the body become narrow and bend round as oviducts to the ventral side, where they enter a pear-shaped glandular accessory organ of the small degenerating **cloaca**, the **atrium**. There is further an unpaired vesicle, the **receptaculum seminis**, placed under

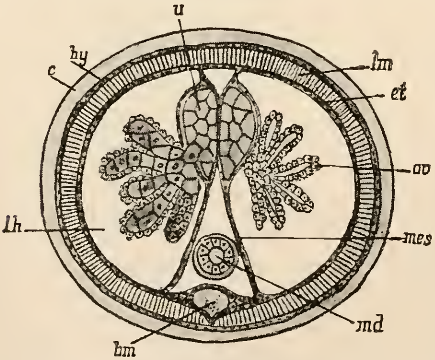


FIG. 170.—**Transverse section through Gordius, after Vejdovsky.** *lh*, Body cavity; *c*, cuticle; *hy*, hypodermis; *u*, uterus; *lm*, longitudinal musculature; *et*, endothelium of the body cavity; *ov*, ovarium; *mes*, mesenteries; *md*, mid-gut; *bm*, ventral chord.

the posterior part of the uterus; this is connected with the atrium, and during copulation becomes filled with spermatozoa. In the **male genital apparatus** the actual testes have not yet been found. The other parts correspond with the various divisions of the female apparatus. We can distinguish **sperm sacs** (corresponding with the uteri of the female), **sperm ducts**, and the well-developed **cloaca**, a flask-shaped organ whose terminal part can be evaginated. There is no organ corresponding with the receptaculum of the female.

3. **Acanthocephala; Female Apparatus** (Fig. 171).—In quite young animals the ovaries are enclosed in the ligament by means of which the genital apparatus is suspended from the base of the proboscis sheath. Masses of eggs (swimming ovaries) early reach the body cavity, probably by the bursting of the ligament, and in sexually mature animals are there present in great numbers together with single detached eggs. From the body cavity they are transmitted to the exterior by a muscular apparatus which is of very complicated structure, although consisting of a limited, but for each species definite and constant, number of muscle cells. We distinguish in it first an apparatus for swallowing the ova, the **uterus bell**, to the bottom of which the posterior end of the ligament is attached. It is in open communication with the body cavity by means of a large anterior and a small posterior aperture. It alternately expands and contracts, and thus draws in the eggs which float in the cœlomic fluid. From the uterus bell the eggs pass into the anterior apertures of two short canals which are called **oviducts**. The oviducts emerge into a tubular unpaired division, the **uterus**, and this opens externally at the posterior end of the body by a short terminal piece, the **vagina**. Through the posterior aperture of the uterus bell the unripe eggs which have been drawn in with the others are returned to the body cavity.

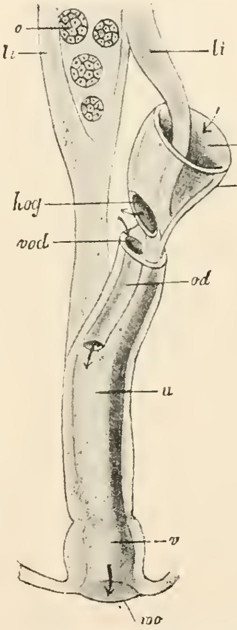


Fig. 171.—**Female genital apparatus of an Echinorhynchus**, diagrammatic. *ug*, Uterus bell. *vog*, anterior aperture of the same; *hog*, posterior ditto; *vod*, anterior aperture of one of the two oviducts (*od*); *u*, uterus; *v*, vagina; *wo*, female aperture; *o*, ovaries; *li*, ligament. The arrows indicate the course taken by the eggs in passing from the body cavity to the exterior.

Male Apparatus (Fig. 172, p. 258).—Two, or less frequently three, **testes** lie in the ligament. Each is continued in the form of a **sperm duct**. Each of these sperm ducts has three pouch-like invaginations along its course (**sperm vesicles**). Posteriorly they unite to form one common muscular **vas deferens**, which enters the **bursa** at the point of a conical muscular projecting

penis. The bursa is a spacious sac-like invagination of the posterior end of the body which can be evaginated in copulation. Three pairs of cement glands are generally connected with the male apparatus, their ducts entering the terminal division of the vas deferens (ductus ejaculatorius).

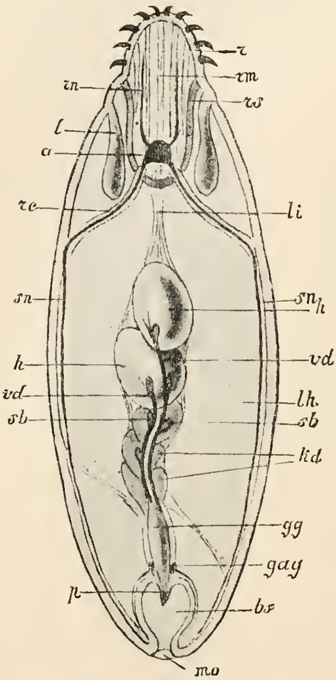


Fig. 172.—**Representation, partly diagrammatic, of the organisation of a male Echinorhynchus.** *r*, Proboscis with barbed hooks, protruded; *rm*, retractor muscles of the proboscis; *rs*, proboscis sheath; *rn*, proboscis nerves; *g*, cerebral ganglion; *re*, retinacula; *li*, ligament; *sn*, longitudinal nerves; *h*, testes; *vd*, vas deferens; *sb*, vesiculæ seminales; *kd*, cement glands; *gg*, common vas deferens; *gag*, genital ganglion; *bs*, bursa; *mo*, male genital aperture; *lh*, body cavity; *p*, penis; *l*, lemnisci.

Annulata.—The *Hirudinea* are hermaphrodite. Their **male genital apparatus** (Fig. 173) has the following general structure. Several testes lie in pairs segmentally arranged in the middle region of the body, generally between the consecutive lateral diverticula of the mid-gut, within the muscular septa separating these diverticula; the testes thus divide these septa into anterior and posterior lamellæ. A short efferent duct arises from each testis. The ducts of all the consecutive testes of one side emerge into a **vas deferens** which runs through the whole length of the testicle region. In front of the most anterior testis the two vasa deferentia converge towards the middle line, here to open outwardly by a common aperture, or in some cases by a common unpaired copulatory apparatus (penis).

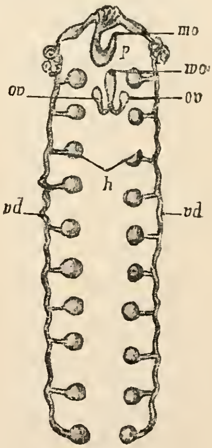


Fig. 173.—**Genital organs of Hirudo.** *p*, Penis; *mo*, male; *wo*, female genital aperture; *ov*, ovaries; *h*, testicles; *vd*, vas deferens.

The number of testes may in some cases be greatly increased (*Nephelis*, *Lumbricobdella*), and this probably results from the subdivision of each testis into several vesicles. Complications often occur in the last portion of the vasa deferentia. For example, in *Hirudo*, the vas deferens, before entering the penis through a short terminal passage, forms a tangled coil on each side. Glands are often connected with the penis. The male genital aperture in *Hirudo* is in the 10th segment, between the 30th and 31st rings.

The female genital apparatus (Fig. 173) lies behind the male aperture, and generally between the vasa deferentia. It consists of

two ovaries. From each ovary an **oviduct** arises, which, joining that of the other side, passes into a sac-like muscular terminal division, the **vagina** (*Gnathobdellidæ*), or opens outwardly direct (*Rhynchobdellidæ*).

In the land leeches (*Lumbricobdella*, *Cylicobdella*) the oviducts remain separate until they enter the vagina. The ovaries here occur in numbers as swellings of the oviducts. In the *Rhynchobdellidæ* the ovaries are elongated sacs; in the aquatic *Gnathobdellidæ* they are short and lobed, and usually contained in a round sac. In *Hirudo* the ducts unite, some distance before entering the vagina, to form a common oviduct, into which numerous glands (albumen glands) enter. The female aperture of *Hirudo* lies in the 11th segment, between the 35th and 36th rings.

The arrangement of the hermaphrodite genital apparatus of the *Hirudinea* vividly recalls the conditions which prevail in the *Turbellaria* (*Polyclada* and *Triclada*).

Oligochæta.—The sexual, but more especially the transmitting, organs of the *Oligochæta* are so completely different from those of the *Hirudinea*, that it is not possible at present to refer the two to one common type. Testes and ovaries are always very few in number; the former occur in one or two pairs, the latter in a single pair. The former always lie in front of the latter. The collective male and female genital apparatus occupies a limited number of segments in the anterior part of the body. The segments lying between the 9th and 14th generally form the genital zone. Less frequently (*Aphanoneura*, *Chætogastridæ*) the genital organs lie farther to the front. While in the *Hirudinea*, *Nemertina*, and *Nematoda* the egg and sperm passages are, as in the *Platodes*, direct canal-like continuations of the ovaries and testes, they are, in the *Oligochæta*, separated from the first from the germ glands, and show much agreement with nephridia in their structure. They are therefore pretty generally regarded as nephridia which have assumed the function of conducting the genital products out of the body. We must not, nevertheless, forget that the sperm ducts and oviducts, even if they really are transformed nephridia, must in the segments referred to represent supernumerary nephridia, since, in the adult *Lumbricidæ* and in the young stages of other *Oligochæta*, besides the oviducts and sperm ducts, typical nephridia occur in the genital segments as well as in the rest of the body. In the **male genital apparatus** we must distinguish three parts, viz. the testes, the sperm sacs, and the sperm ducts. In the *Lumbricidæ* there are almost always two pairs of testes, while the rest of the *Oligochæta* only possess one pair. The testes seem everywhere to break up at an early stage into the formative cells of the spermatozoa, so that in adult sexually mature animals they are retained at the best as rudiments. The sperm formative cells are early gathered into special **sperm sacs**, in which they develop further and produce the ripe spermatozoa. These sperm sacs, formerly regarded as testes, are large vesicles which develop on the dissepiments of the testicle segments as sac-like outgrowths of their posterior lamellæ. They are divided internally by lamellæ into numerous compartments and chambers, in which the developing spermatozoa lie, and are in open communication with the body cavity. The manner in which the sperm formative cells pass out of the testes into the sperm sacs is not known. The sperm sacs, even in nearly related genera and species, differ considerably in their number and special arrangement. In some *Lumbricidæ* a middle unpaired portion is formed, a **sperm capsule**, and the sperm sacs then appear merely as paired appendages to this capsule. In the *Chætogastridæ* alone no sperm sacs are developed.

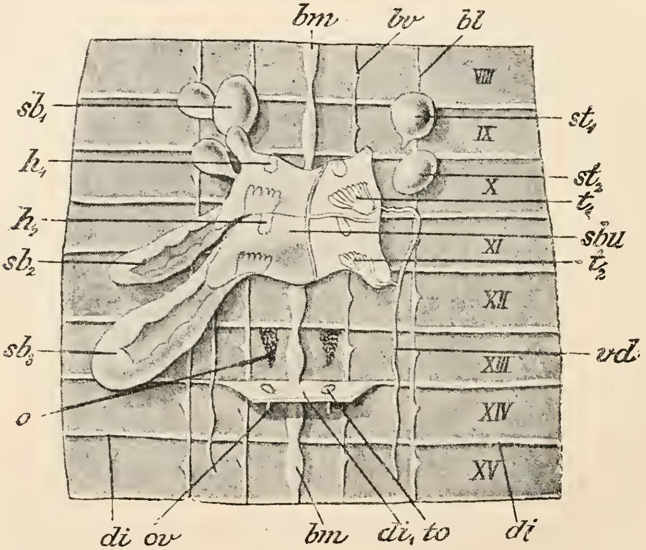


FIG. 174.—**Lumbricus agricola. Genital organs**, after **Vogt** and **Yung.** To the right the sperm sacs and a part of the unpaired sperm capsule are removed. *bm*, Ventral chord ; st_1, st_2, receptacula seminis ; t_1, t_2, sperm funnels ; *sbu*, unpaired sperm capsule ; *di*, dissepiments cut off at their bases ; *vd*, vas deferens ; *to*, funnels of the oviducts ; *o*, ovaries ; *ov*, oviduct ; di_1, part of the dissepiment between the 13th and 14th segments ; sb_1, sb_2, sb_3, paired sperm sacs ; h_1, h_2, testes ; VIII-XV, 8th to 15th segments.

The sperm formative cells in this family develop fully in the body cavity, and the ripe spermatozoa are collected direct out of the cœlomic fluid by the funnels of the sperm ducts. Each **sperm duct** consists of a preseptal funnel, and of a duct which penetrates the septum and opens externally through a widened terminal division, the atrium (arising by an invagination of the outer integument). Where only one pair of testes is present there is generally only one pair of sperm ducts. This is the case in the *Naidomorpha*, *Chætogastridæ*, *Tubificidæ*, and *Enchitraeidæ*. In other *Oligochæta*, however, especially those which live on land, and in most *Lumbriculidæ*, there are two pairs of sperm ducts. In this case all the four ducts are either entirely distinct from each other, or else the anterior and posterior ducts on each side enter a common atrium (many *Lumbriculidæ*), or the ducts of each side unite to form a common duct, which opens outwardly without the formation of an atrium (*Lumbricidæ*). The sperm funnels lie in the same segments as the testes. In those *Lumbricidæ* which have a median sperm capsule they lie in it.

Female Genital Apparatus.—This consists of the two **ovaries,** the two **oviducts** and **receptacula seminis.** The eggs either ripen in the ovaries, or the ovaries fall into a few groups of egg cells. Only one cell in each group then develops into an egg. The eggs occasionally pass out of the ovaries into special egg sacs corresponding to the sperm sacs, and pass out from these through the oviducts. In many of the lower *Oligochæta* there are no special oviducts. It is not really understood in what way the eggs are here transmitted to the exterior. The receptacula seminis are paired sacs which open outwardly in special segments of the genital zone. They arise as invaginations of the integument, and occur in most *Oligochæta* in one pair, in the *Lumbricidæ*, however, in two (less often three) pairs. They are closed towards the body cavity, are in no way connected with the rest of the genital apparatus, and are during copulation filled with sperm from without.

Fig. 174, which depicts the genital apparatus of *Lumbricus agricola*, will help to elucidate the above. In the 9th and 10th segments we see the 2 receptacula seminis, in the 10th and 11th the sperm capsule divided by a transverse partition wall into an anterior and a posterior part, with its 3 appendages (the sperm sacs) to the left; to the right the 3 sperm sacs and the cover of the sperm capsule are removed. We see the anterior and posterior testes of the right side of the body, and further the 2 right-hand sperm funnels and their ducts, which in the 12th segment unite to form the unpaired vas deferens emerging in the 15th segment. In the 13th segment the 2 ovaries lie at the 2 sides of the ventral chord. Behind these, on the anterior side of the dissepiment between the 13th and 14th segments are the funnels of the oviducts which open outwardly in the 14th segment.

Polychæta.—The description here may be brief. With isolated exceptions, the sexes are separate. The matrix from which, generally only at certain periods, the ovaries or testes are developed, is the endothelium of the body cavity. The position of the germ glands varies greatly. They are sometimes found on the so-called genital plates, sometimes on the dissepiments, or on the mesenteries, or they may be outgrowths of the endothelial covering of the ventral vessel, etc. The ovaries or testes are generally repeated in many, or at any rate in several, segments. Their form varies as much as their position; they are sometimes cellular thickenings, sometimes massive knobs, or tufts of strands, etc. The egg or sperm cells sever themselves sooner or later from the ovaries and testes, and ripen when floating freely in the cœlomic fluid. From this they are discharged through nephridia which are more or less strongly modified at the time of sexual maturity, or through nephridia which are permanently transformed into genital tubes.

In *Sternaspis*, in the female one ovary is found, and in the male one testis. The genital gland in both sexes has the form of a four-lobed pouch, which lies between the loops of the intestinal tube, and passes into 2 efferent ducts opening outwards, between the 7th and 8th segments. The genital products do not enter the body cavity, but pass from the cavity of the genital gland to the exterior through the efferent ducts. The question as to whether these ducts represent modified nephridia must be decided by further research.

The *Myzostomidæ* (Figs. 175 and 176) are hermaphrodite. Their sexual apparatus does not easily admit of comparison with that of the other *Annulata*, but rather recalls in many points that of the *Platodes*. It is, however, probable that this is more a case of analogy than of homology. In the sexually mature animals the parenchyma is filled with numerous egg cells which lie in

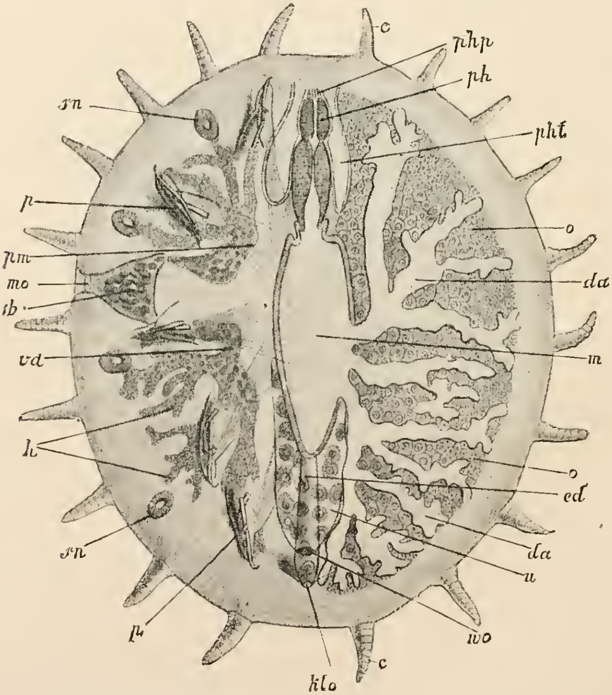


FIG. 175.—**Organisation of Myzostoma cirriferum,** after **v. Graff.** To the left the parapodia (*p*), the suckers (*sn*), and the male genital apparatus are represented. To the right the enteric branches (*da*) and ovaries (*o*). *c*, Cirri; *php*, pharyngeal tentacles; *ph*, pharynx; *pht*, pharyngeal pouch; *m*, stomach (mid-gut); *ed*, hind-gut; *u*, uterus; *wo*, female genital aperture, which enters the cloaca; *klo*, aperture of cloaca; *pm*, muscles for moving the parapodia; *mo*, male genital aperture; *sb*, sperm vesicle; *vd*, vas deferens; *h*, testes; *p*, parapodia with hooks and supporting rod.

masses between the branches of the intestine, especially on the dorsal side. These masses of eggs are regarded as ovaries. It is, however, possible that they consist of eggs which have left the real ovaria.

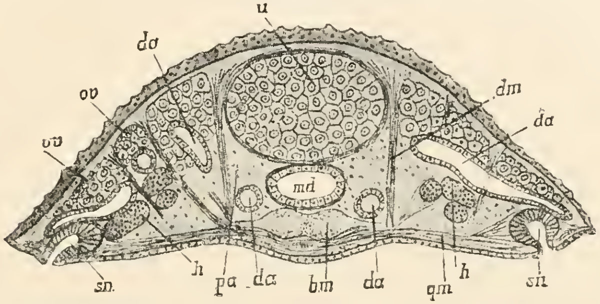


FIG. 176.—**Section through Myzostoma,** after v. Graff. *ov*, Ovaries; *da*, intestinal branches; *u*, uterus; *dm*, dorso-ventral muscle fibres; *sn*, suckers; *h*, testes; *qm*, transverse muscles; *bm*, ventral ganglionic masses; *pa*, parenchyma; *md*, intestine.

The origin and places of formation of the eggs are not known with any certainty. The ripe eggs pass into a spacious **uterus** which lies on the dorsal side of the stomach-intestine. One dorsal and two lateral **oviducts** connect the uterus with the cloaca. The male genital apparatus is paired. On each side branched solid **testicle strands** lie in the parenchyma below the intestine and its branchings. On each side an anterior and a posterior **vas deferens** collect the sperm from the testes. Both vasa deferentia enter a muscular lateral **sperm vesicle**, which lies between the 3d and 4th suckers, and which opens outwardly at the edge of the body.

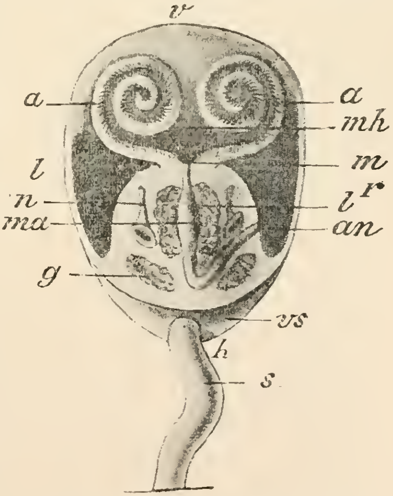


FIG. 177.—**Diagrammatic representation of the organisation of a Brachiopod,** from the dorsal side; the dorsal halves of shell and mantle are removed. *a*, Arms; *mh*, mantle cavity; *m*, mouth; *l*, liver; *ma*, stomach; *n*, nephridia; *an*, anus; *g*, genital glands; *vs*, part of the ventral shell which projects backwards over the dorsal shell; *v*, anterior; *h*, posterior; *r*, right; *l*, left.

Prosopygia.—The places of formation for the eggs and spermatozoa of the *Sipunculidæ*, *Phoronidæ*, and *Brachiopoda* are definite points of the endothelium of the body cavity. The sexual products fall into the cœlomic fluid, and are emptied out thence by the nephridia, as was the case in the Polychæta.

In the *Sipunculidæ* the formation of the germs takes place for the most part at the base of the ventral proboscis retractors. *Phoronis* is hermaphrodite. The male and female sexual products arise on the asymmetrical ventral vessel. According to recent research it is probable that in most, perhaps in all, *Brachiopoda* the sexes are separate. The germ glands are outgrowths of the endothelium of the body cavity, and lie as branched or reticulated strands, in the *Testicardines* in pairs in the body cavity of both mantle folds, in the *Ecardines* in the mantle folds and in the body cavity of the trunk, or in the latter alone (Fig. 150, p. 226; Fig. 177, p. 263).

In the *Priapulidæ* the anal tubes, which in early stages act as excretory organs, become later the places of formation of the genital products. They are then at the same time germ glands and efferent ducts.

In the *Bryozoa* there seems to be no definite rule; separation of the sexes is sometimes found, and at other times hermaphroditism. The ovaries and the testes arise, in the *Ectoprocta*, as cell outgrowths on the inside of the body wall or on the funiculus. The first position is most characteristic of the ovaries, the second of the testes. In the fresh-water *Bryozoa*, however (Fig. 139, p. 208), there also arise on the funiculus the **statoblasts**, which are to be regarded as parthenogenetic eggs. Special efferent ducts are wanting. The eggs and spermatozoa fall into the body cavity. We do not yet know for certain how they reach the exterior. Many observers maintain that in hermaphrodite *Bryozoa* self-fertilisation takes place in the body cavity. In many marine *Ectoprocta* (*Chilostomata* and some *Cyclostomata*) the ripe (fertilised) eggs are taken up into special capsule-like foldings of the body wall, the so-called **ooecia** or **ovicells**, and these are regarded as modified individuals which have arisen by gemmation. This view does not as yet rest on sufficient foundation. The sexes seem to be separate in the *Endoprocta*, but it may perhaps be the case that the ovaries and testes do not develop at the same time. Two testes lie between the stomach and body wall, and pass into 2 sperm ducts, which emerge into a sperm vesicle, the latter opening by a pore into the vestibulum (the depression between the tentacles at the bottom of which the mouth lies). The female genital apparatus shows a similar arrangement: 2 ovaries, 2 oviducts, and an unpaired terminal division which also opens into the vestibulum by a pore. The genital apparatus of the *Pterobranchia* is not yet sufficiently known; under the 2 eyes of *Cephalodiscus* lie 2 ovaries.

Rotatoria (Fig. 161, p. 245).—Separation of the sexes here prevails. The usually unpaired, seldom paired, female germ gland lies near, generally below, the intestine, and consists of two parts—a germarium, which yields the egg germs, and a vitellarium, which richly supplies the young cells with yolk. The germ gland, which we may call the germ-vitellarium, is surrounded by a membrane which passes into a fine oviduct opening into the cloaca. The last part of the oviduct, where the eggs often remain for some time, may be called the uterus. In the male a testis with a vas deferens and protrusible penis are found, which latter lies at the posterior end of the body; through it also the contractile terminal vesicles of the nephridia open outwardly.

In *Dinophilus* (Fig. 162, p. 246) the sexes are separate. An ovary lies on the outer surface of the intestinal wall, ventrally on the boundary between the mid-gut and the hind-gut. It may perhaps be developed out of an endothelium, which, however, has not yet been proved to exist. The ripe eggs fall into the body cavity and are emptied out through a pore which forms temporarily in the body wall in front of the anus. The male sexual organs are not yet sufficiently known.

In the male of *D. apatris*, at the posterior end, a conical organ (penis) is found, which lies in a sac out of which it can be protruded and into which it can be withdrawn.

The *Chætognatha* (Fig. 152, p. 227) are hermaphrodite. The ovaries are two long tubes which lie in the posterior part of the two lateral chambers of the trunk cavity. Throughout their whole length they are attached laterally by a mesentery to the body wall, this mesentery enclosing them all round like a sac. On the outer side of each ovary, and enclosed in its mesentery, lies a long **oviduct,** ending blindly to the front, and opening outwardly behind near the septum which separates the trunk and the tail cavities. It is not yet known how the eggs reach the oviduct and are discharged. The two **testes** lie as lateral cell thickenings or germ masses projecting into the body cavity from the body wall of the tail cavity. Groups of young sperm formative cells sever themselves and fall into the two lateral chambers of the tail cavity. The ripe spermatozoa are discharged through the **sperm ducts.** In each sperm duct we can distinguish an inner ciliated funnel, a duct, and a vesicle; these open externally at the sides of the caudal segment. Thus in the arrangement of the reproductive organs, especially in that of the male genital apparatus, we find great similarity between these animals and the *Chætopoda*, *Sipunculidæ*, *Phoronis*, and the *Brachiopoda*.

Sexual Dimorphism in Worms.—Apart from the difference between the sexual organs and outer copulatory organs, there are, in many worms in which the sexes are separate, insignificant external differences between the male and the female. In some worms, however, the differences in inner organisation cause a remarkable sexual dimorphism in outer appearance and in size between the two. This is especially the case in the *Rotatoria*, *Dinophilus*, and *Bonellia*. It is always the male which, in comparison with the female, appears reduced and generally dwarfed. The *Rotatorian* male is smaller than the female, with degenerated enteric canal and simplified wheel apparatus. The males are known only in the minority of genera and species, and are much rarer than the females. In *Seison* alone the males and females are alike. The fertilisation of the Rotatorian eggs has till now not been observed. The females usually produce two sorts of eggs—delicate-skinned summer eggs, and hard-shelled eggs which last through the winter. In *Dinophilus vorticoides* the two sexes are not different; in *D. apatris* the male is smaller, with ciliated rings. Mouth, intestine, and anus are wanting. The males of *Bonellia*, which are ciliated all over, and are in appearance not unlike the *Rhabdocœlan Turbellaria*, are minute in comparison with the females; these males live parasitically on the female in varying numbers on the proboscis, in the œsophagus, or in the nephridium which serves as uterus and oviduct. The intestinal canal is without mouth or anus, a vascular system is wanting, nor have they the prostomium which in the female is strongly developed as a proboscis. In short, apart from the sexual organs, they remain on the larval level. In some *Myzostomidæ* there are so called complementary males, which are considerably smaller than the hermaphrodite individuals on which they live. Their organisation is like that of the hermaphrodites. As rudiments of ovaries and oviducts have been discovered in their bodies, we can only consider these complementary males as originally hermaphrodites with one-sided development of the male genital apparatus, or as young hermaphrodites with the female genital apparatus not yet developed.

XIII. Parthenogenesis.

Reproduction by means of unfertilised eggs certainly takes place in the *Rotatoria* and *Bryozoa*. It was formerly thought that only the summer eggs of the wheel animalculæ could develop without fertilisation, while the winter eggs must be fertilised, but the act of fertilisation has not yet been observed in connection with these latter. The statoblasts of the fresh-water *Bryozoa* are parthenogenetic eggs, and such eggs are also found in some marine *Bryozoa*. These eggs are enclosed in hard cases provided with many arrangements (air rings, processes, etc.) serving to disperse them in the air or water.

XIV. Asexual Reproduction by Gemmation and Fission.

Many worms, especially the *Nemertina*, *Chætopoda*, *Sipunculidæ*, *Phoronis*, and the *Bryozoa*, are distinguished by a highly developed capacity of regeneration, which is of the greatest use for the maintenance of the individual and of the race. Such portions of the body as have been lost through adverse external circumstances, broken off, bitten off, etc., are quickly regenerated, even such as contain the most important organs, *e.g.* the anterior part with the brain. Isolated broken off pieces may occasionally be regenerated into whole animals. As already indicated, we may perhaps some day be able to refer back the capacity shown throughout the animal kingdom for asexual reproduction by gemmation and fission to such an accidental multiplication by voluntary or enforced falling to pieces of the body with subsequent regeneration.

Among the *Vermes* this form of reproduction occurs in the *Polychæta*, *Oligochæta*, and *Bryozoa*.

Polychæta.—One of the *Capitellidæ*, *Clistomastus*, constricts off (most probably periodically) the posterior part of the body, which contains the sexual products, reforming it again by regeneration. In a *Syllis*, *Haplosyllis spongicola*, which lurks in holes at the bottom of the sea, the parapodia and setæ of a number of the posterior segments become more strongly developed as sexual maturity approaches. The group of segments thus modified, containing the sexual products, severs itself, and swims about freely in the sea as a sexual swimming bud, dispersing the sexual products. In other *Syllidæ* (*Syllis*, *Autolytus*) at the anterior end of the swimming bud a new head is formed with highly developed eyes, and this takes place even before it is severed. The detached swimming bud then represents a complete individual (person), in which the sexual products ripen. The individual from which the swimming bud has severed itself forms no sexual products, but is able at its posterior end to produce new swimming buds. The detached swimming buds or sexual animals may, apart from the fact that they contain the sexual organs, be distinguished from the mother animal by other, chiefly external, points of their organisation. We thus have before us an alternation of generations. A mother animal which remains asexual produces asexually successive daughter animals which differ from the mother animal externally; these detach themselves and reproduce sexually by means of fertilised eggs; we thus have alternating asexual and sexual generations. In *Myrianida* (also a *Syllis*) new buds arise on the mother animal even before the hindermost has detached itself. There thus arises a chain of buds of which the hindermost is the oldest and the foremost the youngest. This is a case of axial gemmation which is very similar to strobilation.

Oligochæta.—In autumn *Lumbriculus* falls into pieces which are all able to regenerate into complete animals. In the genera *Æolosoma* and *Ctenodrilus* no sexual organs and no sexual reproduction have as yet been observed, only asexual reproduction. In *Ctenodrilus monostylos* the body becomes constricted in the middle, and finally separates into two pieces, each of which may again divide. These pieces regenerate into normal animals after detachment. It is otherwise in *Ct. pardalis*. Here, in each segment (except the foremost) behind the dissepiment of the preceding segment, a budding zone appears, in which brain, œsophagus, etc., form. The development of these budding zones takes place from before backward. The segments thus transformed finally separate. In each of them the fore-gut and hind-gut become connected with the mid-gut and the typical segmentation is developed, so that each becomes a complete individual. In *Æolosoma*, as in the *Syllidæ*, several posterior segments are included in the first bud. While the head forms anteriorly in this bud, it as well as the mother body increases in length, and the latter develops other buds posteriorly before the first and oldest, *i.e.* the hindermost bud detaches itself. The processes of gemmation are most complicated in *Nais* and *Chætogaster*, since here in the (anterior) mother individual as well as in the daughter individual new phenomena of gemmation appear before they become detached from each other. Chains of several individuals varying in age and stage of development thus arise. The age and degree of development may be given in a formula. *A* indicates the foremost and oldest individual, in which at first the daughter individual *B* appeared; then the bud *C* began to form in the individual *B*, and so on. An order of development of buds which has been observed in *Nais barbata* (from before backward) is as follows: *A*, *F*, *D*, *B*, *E*, *C*. Finally, the chain breaks up into its separate parts, which no longer multiply asexually, but increase the number of their segments, and as sexual individuals can develop sexual products. There is therefore here also a kind of alternation of generations, since sexual and asexual reproduction mutually exclude one another.

XV. Stock Formation.

The peculiar *Syllis ramosa*, which lives in deep-sea sponges, forms by means of lateral gemmation much-branched stocks, in which, as in most other *Syllidæ*, special sexual individuals develop and detach themselves. This is the only case of lateral gemmation in the *Chætopoda*. Among the *Bryozoa*, animal stocks of the most various shapes arise by lateral gemmation. They are sometimes tree-like, sometimes tufts, or they may be spread out like webs or crusts; sometimes many single animals rise from a creeping stem. We thus find repeated in the *Bryozoa* the forms assumed by the *Hydroida*. In *Loxosoma* alone the buds detach themselves, so that a permanent stock is never formed. On the stocks of many *Chilostoman Bryozoa* peculiar appendages, so-called **vibracularia** and **avicularia**, are found. The former are prominences on the wall of the ordinary individuals (zooecia), each of which carries a long seta, by means of whose free movement particles of food are brought within reach, and the water surrounding the colony is kept in motion. The stalked avicularia are catching apparati which hold small animals fast till they die. The mechanism is similar to that of a crab's forceps or a bird's beak; a movable mandible is hinged upon an immovable beak, and is worked by special muscles, so that the forceps can open and shut. Avicularia and vibracularia are, like the above-mentioned ooecia and ovicells, regarded as metamorphosed individuals without intestine. This assumed polymorphism of *Chilostoman* stocks is, however, as yet weakly supported. In marine *Bryozoa* all the individuals of a stock are connected together by a network of nerve threads, forming what has been called a colonial nervous system.

XVI. **Ontogeny of the Worms.**

The eggs of worms are either holoblastic alecithal, or holoblastic telolecithal. In the latter case the yolk may vary very much in quantity. The course of segmentation and gastrulation varies in correspondence with the constitution of the egg. There is sometimes (in the holoblastic alecithal egg, example *Sagitta*) a total and tolerably equal furrowing, forming a cœloblastula, and then by invagination a cœlogastrula. Sometimes the furrowing is more or less unequal, and often connected with the formation of micromeres (*cf.* p. 124, segmentation of *Bonellia*). We find, always according to the quantity of yolk stored in the egg, all the stages from a cœloblastula to a sterroblastula, from an invagination to an epibole, and from a cœlogastrula to a sterrogastrula. Alecithal eggs or telolecithal eggs with little nutritive yolk, cœloblastulæ and cœlogastrulæ, are found in those groups of worms in which a free-swimming and independently feeding larva develops very early. This is the case in very many marine worms, especially in *Nemertina*, *Polychæta*, *Sipunculidæ*, *Bryozoa*, *Phoronis*, *Brachiopoda*, and *Chætognatha*. Telolecithal eggs with much nutritive yolk. sterroblastulæ and sterrogastrulæ, are found in those cases where the developing animal only begins to move and to feed very late, *i.e.* in an almost adult condition, and especially where a so-called direct embryonic development takes place, *e.g.* *Oligochæta*, *Hirudinea*, *Rotatoria*.

Before passing on to describe the more important larval forms among the Vermes, we will briefly describe the development of Eupomatus uncinatus (Serpulidæ) (Fig. 178, cf. also Fig. 92, p. 123). The blastula has a small blastocœl. The cells of the upper (animal) half are smaller and more numerous than those of the lower (vegetative) half. The former form the ectoderm, the latter the endoderm. At an early stage, at one side of the blastula, which we may call the anal side, 2 round cells appear with remarkable distinctness at the limit between the ectoderm and the endoderm. By the rise of these **primitive mesoderm cells** the blastula becomes bilaterally symmetrical. Besides an aboral or animal side and an oral or vegetative side, we can also distinguish an anterior and posterior (where the 2 primitive mesoderm cells lie), and likewise a right and a left, and a median plane. The two primitive mesoderm cells lie to the right and left of the median plane. The vegetative or endodermal wall of the blastula then becomes invaginated into the segmentation cavity to form the archenteron while at the same time the ectoderm grows out over the invaginated part. The process thus stands half way between invagination and epibole. The primitive mesoderm cells, lying at the posterior edge of the blastopore, sink between endoderm and ectoderm, *i.e.* deeper into the segmentation cavity. This gastrula formation takes place in such a way that the blastopore is a median ventral longitudinal slit. This closes from back to front, until anteriorly, *i.e.* excentrically, only a small aperture remains. An equatorial ciliated ring, the **preoral ciliated ring**, appears early in the gastrula larva. In the cell thickening which carries this ring of cilia a circular nerve is developed. At the aboral pole the ectoderm thickens to form the neural plate, which carries a tuft of cilia. Directly round the narrowed blastopore the ectoderm becomes invaginated like a funnel, and forms the larval œsophagus or the **stomodæum**, which gradually approaches the anterior ventral edge of the preoral ciliated ring. The archenteron elongates downwards and backwards. Several smaller cells are severed by fission from the primitive or pole cells of the mesoderm, and these are spread out in the segmentation cavity (primary body cavity) and form various larval organs, *e.g.* muscle fibres and the larval **head nephridia.** The primary body cavity lengthens. That half of the body which lies behind and below the preoral ciliated ring assumes a conical form. The point of the cone is the posterior end. From the posterior end to the mouth the body becomes flattened. On the dorsal surface the posterior end of the intestine opens by means of a small invagination of the ectoderm, the **proctodæum** with an **anus**; this occurs not far from the posterior end of the larva. Diametrically opposite to this, at the neural area, which is surrounded by the preoral ciliated ring, lies the neural plate, which represents a part at any rate of the rudiment of the brain. A **pigment spot** (eye) arises asymmetrically in a cell of the neural area. Behind the mouth a slighter postoral ciliated ring appears. The whole ectoderm between the preoral and postoral ciliated rings is covered with short cilia, and thus forms an **adoral ciliated zone.** A narrow medio-ventral ciliated band forms from the mouth to the posterior end. Two auditory vesicles are developed out of two ectodermal cells immediately behind the postoral ciliated ring, and sink beneath the surface later. Two cell streaks or bands are developed from the two pole cells of

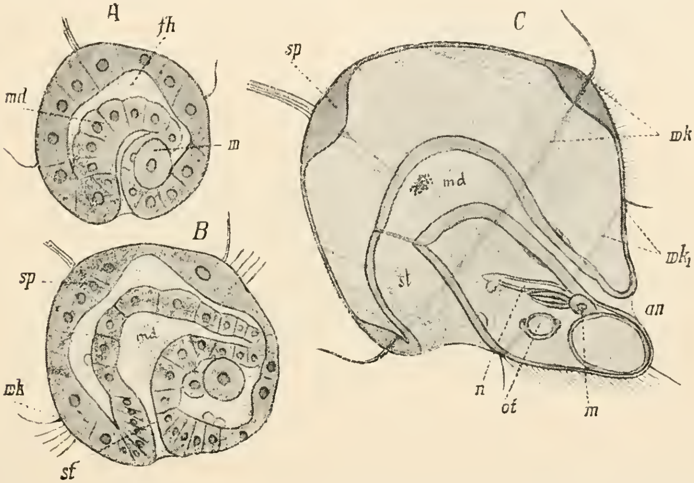


FIG. 178.—*A*, *B*, *C*, **Three stages of development of the larva** (Trochophora) **of Eupomatus**, from the side. *m*, Polar cells of the mesoderm; *md*, mid-gut; *fh*, segmentation cavity; *sp*, neural plate; *wk*, preoral ciliated ring; *st*, stomodæum; wk_1, postoral ciliated ring; *n*, larval head nephridium; *ot*, otolith; *an*, anus (after **Hatschek**).

the mesoblast which lie near the posterior end; these lie close to the ectoderm ventrally on each side, and develop anteriorly by constricting off smaller cells and by the continuous division of the same; they are the two **mesoderm streaks.** The larva has now reached what is known as the *Trochophora* stage. It swims about freely by means of its ciliated rings. The hindermost smaller portion of the body with the intestine, proctodæum, and the posterior part of the mesoderm streaks, represents the rudiment of the afterwards segmented trunk plus the anal segment; the whole of the larger anterior portion contains the rudiment of the head or oral segment.

Larvæ of the *Trochophora* type occur not only in worms, but are also common among *Molluscs.*

In addition to the *Trochophora* the following are some of the most important kinds of worm larvæ.

The free-swimming larva of the *Sipunculidæ* (Fig. 179) is already much further developed when hatched than the *Polychætan Trochophora*, with which, however, it has much general similarity. In the *Sipunculus* larva the characteristic preoral ciliated ring of the *Trochophora* larva is wanting, but such a ring, weakly developed, is said to occur in the *Phascolosoma* larva. A postoral ciliated ring, on the other hand, is strongly developed. The intestine consists, as in the *Trochophora* larva, of stomodæum, mid-gut, and proctodæum. The latter is moved somewhat from the posterior end on to the back, and the postanal part of the body growing faster than the preanal part, the anterior position of the anus which is characteristic of the adult animal comes about. The neural plate with 2, and later 4, larval eye-spots is found in the same place as in the *Polychætan Trochophora.* A larval head kidney is not formed. The mesoderm, on the contrary, is far more developed than in the *Polychætan Trochophora.* The retractors of the anterior body (proboscis), and the two trunk nephridia, have already begun to form. There is a spacious body cavity, but this does not correspond with the primary body cavity of the *Trochophora*, but rather with the secondary body cavity of the *Annulata* which appears within the mesodermal streaks, so that under the integument and around the intestine there is already a layer of mesoderm cells answering to the parietal and visceral layers of the mesoderm of the *Annulata.* While, however, in the *Annulata* the mesodermal streaks become segmented and the body cavity is thereby divided into consecutive pairs of chambers, in the *Sipunculidæ* there is neither segmentation of the mesoderm nor of the body cavity.

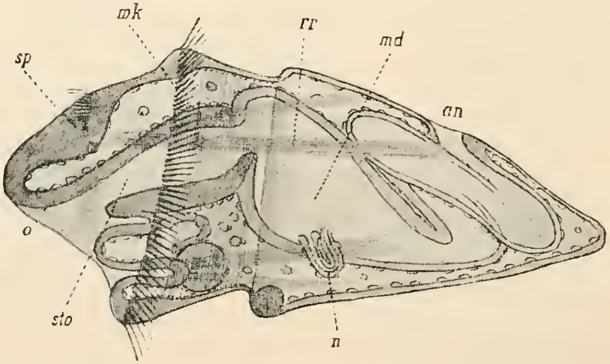


FIG. 179.—**Larva of Sipunculus, after Hatschek.** *o*, Mouth; *sp*, neural-plate; *sto*, stomodæum *wk*, post-oral ciliated ring; *rr*, retractors of the anterior body (proboscis); *md*, mid-gut; *n* nephridium; *an*, anus.

Bryozoa.—It is very difficult to describe the different, and for the most part still insufficiently known, larval forms of the *Bryozoa*, and to establish their relations to the adult animals. We must confine ourselves to a description of the larva of *Pedicellina* (*Endoprocta*) (Fig. 180). A ciliated ring on a circular elevation divides the larval body into two regions. In the oral region, which is ciliated all over, lie the mouth and anus, the latter on a conical prominence. Behind the mouth lies a prominence with a tuft of cilia. Between the mouth and anus there is a depression, the vestibular pit. The whole oral region can be withdrawn into the aboral, so that the mouth and anus come to lie at the base of a depression whose edge is formed by the ciliated ring, and which is called the vestibulum. In the middle of the aboral region rises a ciliated tuft. From the base of this ciliated tuft an organ consisting of long ectodermal cells, the so-called cement gland, projects into the interior of the larva. There is also in the aboral region another organ projecting inwards like a sac, into which a short canal enters from outside, this is the so-called dorsal organ. Both these organs are said to disappear in later metamorphosis. In examining the inner organisation we find a stomodæum, a sac-like mid-gut, and a hind-gut rising up to the anus. The wall of the intestine turned towards the vestibulum is much thickened and is called the liver. Muscles arranged in various ways serve for retracting the oral region. Between the stomach-intestine and the body epithelium of the oral region lies a mass of mesoderm cells, and connected with this on each side a small ciliated canal (nephridia of the adult animal ?). If we wish to compare these *Endoproctan* larvæ, which show considerable resemblance with the *Ectoproctan* larva of *Membranipora* known as *Cyphonautes*, with a *Polychætan Trochophora*, we must consider the ciliated ring as equivalent to the preoral ciliated ring of the latter. Then the so-called cement gland

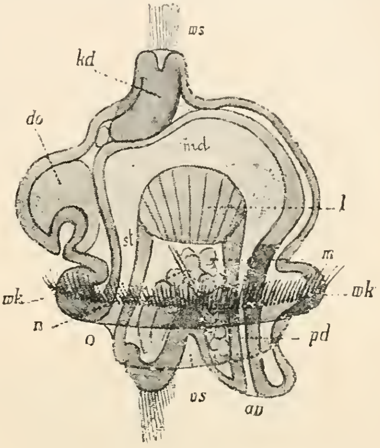


FIG. 180.—**Larva of Pedicellina** (after **Hatschek**), from the side. *o*, Mouth ; *n*, nephridium ; *wk*, ciliated ring ; *do*, dorsal organ ; *kd*, "cement gland" ; *ws*, ciliated tuft ; *l*, "liver" ; *m*, mesoderm cells ; *pd*, proctodæum ; *an*, anus ; *vs*, vestibular pit ; *st*, stomodæum ; *md*, mid-gut.

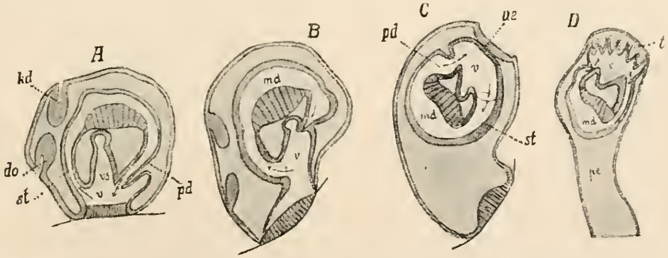


FIG. 181.—*A*, *B*, *C*, *D*, **Four stages of the metamorphosis of the attached larva of Pedicellina.** *do*, Dorsal organ ; *kd*, "cement gland" ; *st*, stomodæum ; *md*, mid-gut ; *pd*, proctodæum ; *v*, vestibulum ; *vs*, vestibular pit ; *t*, rudiment of tentacles ; *pe*, peduncle. The arrows indicate the direction from mouth to anus. *ve*, Invagination of the body wall towards the vestibulum (after **Barrois**).

with the ciliated tuft would answer in position to the neural plate of the *Trochophora.* The further development of the *Pedicellina* larva involves a peculiar metamorphosis (Fig. 181, *A-D*). The larva attaches itself by the oral region, while at the same time the vestibulum closes by the growing together of its free edges over the mouth and the anus. Thereupon the whole enteric canal, with the altered vestibulum turns round, inside the sac-like ectoderm which encloses them, so that later, reversing the larval order, the vestibulum, with the stomodæum and proctodæum entering it, is turned to the free end, *i.e.* the original aboral region of the larva. The vestibulum becomes connected with the exterior by means of a new invagination of the ectoderm ; at the point of junction the tentacles appear. According to this ontogenetic observation the anus would lie, not dorsally, but ventrally, behind the mouth, and so would the ganglionic mass, which would thus not be homologous with the brain of other worms. Further investigations, however, especially as to the development of the nervous system, are needed to elucidate these points.

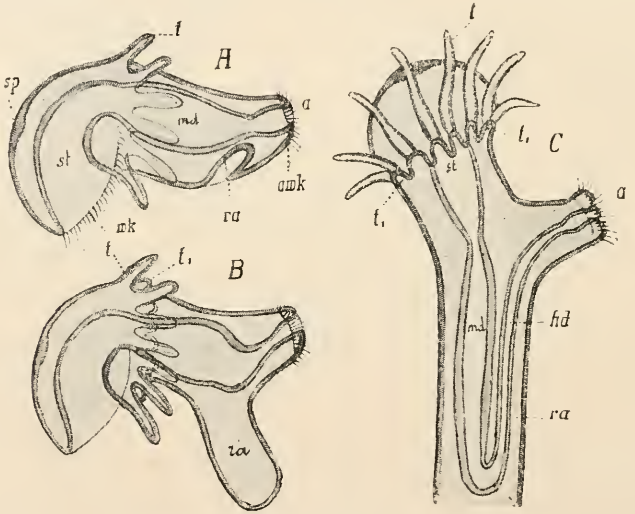


FIG. 182.—*A*, *B*, *C*, Three stages of the development of the larva of Phoronis (Actinotrocha), from the side. *sp*, Neural plate ; *wk*, ciliated organ ; *st*, stomodæum ; *t*, larval tentacles ; t_1, definitive tentacles ; *md*, mid-gut ; *ra*, rudiment of the trunk (stalk), invaginated in the larva *A*, protruded in *B*, developed into the trunk in *C* ; *a*, anus ; *awk*, anal ciliated ring ; *hd*, hind-gut (partly after Metschnikoff).

The larva of *Phoronis* (Fig. 182) is known by the name of **Actinotrocha.** The mouth and anus lie at opposite ends of the ciliated larval body. Over the mouth a large **prostomium** hangs down, whose edge carries stronger cilia which probably correspond with the preoral ciliated ring of the *Trochophora.* A larval ganglion (neural plate) lies in the ectoderm of the prostomium, and is in one species provided with 4 eye-spots. Behind the mouth lies a ring of larval tentacles, and immediately behind this the rudiments of the definitive tentacles, at whose bases the nerve ring of the adult *Phoronis* begins to form. Around the anus we find a strongly ciliated ring. Behind the definitive tentacles on the ventral side lies the rudiment of the trunk, invaginated into the larval body. The secondary body cavity is well developed. In front of the invaginated rudiment of the trunk a nephridium like the head nephridia of the *Trochophora* lies on each side. These become the permanent nephridia of the adult *Phoronis*. The *Actinotrocha* thus formed sinks to the bottom of the sea; the invaginated trunk protrudes and grows quickly, the mid-gut at the same time entering it and forming a loop with ascending and descending limbs. The whole prostomium, with the neural plate and the larval tentacles, are thrown off and devoured by the young *Phoronis*. Through all these processes the body has approached the adult stage; it is quite evident that by the protrusion and rapid growth of the trunk, and the comparatively slight growth of the rest of the original larval body, the anus comes to lie dorsally near the mouth. This process readily allows of being referred back to the similar process in *Sipunculus*, only there the rudiment of the trunk is never invaginated into the larval body.

Brachiopoda.—The free-swimming larva of *Argiope* (Fig. 183) consists of three consecutive divisions, which are called the anterior, middle, and posterior segments.

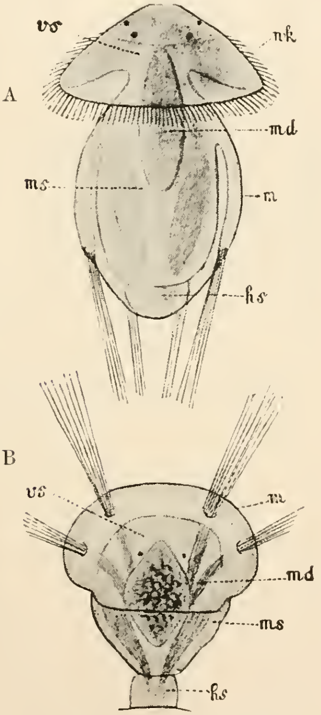


Fig. 183.—*A*, free-swimming, *B*, attached larva of **Argiope**, from above (after **Kowalewsky**). *vs*, Anterior segment; *ms*, middle segment; *hs*, posterior segment; *m*, mantle; *md*, mid-gut; *wk*, ciliated organ.

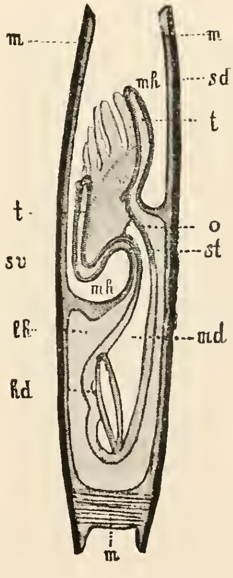


Fig. 184.—**Vertical median longitudinal section through an advanced embryo of Lingula**, after **Brooks**. *m*, Mantle folds; *sd*, dorsal, *sv*, ventral shell; *t*, tentacles; *mh*, mantle cavity; *lh*, body cavity; *st*, stomodæum; *o*, mouth; *md*, mid-gut; *hd*, hind-gut; *m* (below), shell muscles.

The anterior segment is umbrella-shaped, and carries anteriorly 4 eyes. The margin of the umbrella has longer cilia than the rest of the body. The middle segment has dorsal and ventral folds directed posteriorly, and covering the posterior segment. At each side of the free edge of the ventral fold two bundles of setæ are found. The mid-gut is the only part of the intestine which is developed. Between the intestine and the outer integument of the larva are found the paired secondary body cavity, mesenteries, and muscles. The larva attaches itself by the end of the posterior segment which grows out into a stalk. The two folds of the middle segment bend forward like valves and form the mantle, the reduced anterior segment coming to lie in the mantle cavity. The bundles of setæ are thrown off. The stomodæum is formed by an invagination of the body wall of the anterior segment, whose base breaks through into the anterior end of the mid-gut. It lies a little below the eyes which afterwards degenerate. The rudiments of the nervous system and of the nephridia have not been observed. In *Terebratulina* tentacles develop as buds on the circular edge of a disc which projects from the dorsal mantle fold. The tentacles increase in number and are grouped in the shape of a horse-shoe. The tentacular disc is then anteriorly prolonged into two processes, the arms, on which the double row of tentacles become the arm cirri. We here recognise great agreement with the *Bryozoa* and *Phoronis*. Assuming that the point where the eyes lie on the umbrella-shaped anterior segment in the *Brachiopod* larva corresponds with the neural plate of *Actinotrocha*, the agreement between their courses of development is considerable. The posterior segment of the *Brachiopod* larva perhaps answers to the evaginating trunk part (stalk) in *Actinotrocha*. The oral nerve rings in the *Brachiopoda* and in *Phoronis* must be homologous.

A free-swimming larva which occurs among the *Nemertina* is called *Pilidium* (Fig. 185). It is helmet-shaped. We can distinguish in it a convex aboral region and a somewhat concave oral region. The ciliated ring is found on the boundary between these two, which corresponds with the edge of the helmet. Along the base of the ciliated ring runs a nerve. The ciliated ring, which answers to the *Trochophoran* preoral ciliated ring, is produced to the right and left into two pendent lobes, which are comparable with the ear-flaps of many helmets. At the highest point of the aboral region is a depression; in it the ectoderm is thickened, and carries a ciliated tuft. This answers in position to the neural plate of the *Trochophora*. The mouth lies in the middle of the oral region. It leads into the stomodæum, and this into a sac-like mid-gut which lies excentrically (behind). A proctodæum is wanting, and does not attain development during larval life. The space between the intestine and the ectoderm is a spacious segmentation cavity or primary body cavity. In it lie muscle fibres, and generally branched star-like mesoderm cells. The ectoderm of the oral region is invaginated into the primary body cavity at 4 points, forming 2 pairs of sacs. One pair of these sacs lies in front of and the other behind the stomodæum. The further development of these sacs is as follows (Fig. 186, *A*, *B*, *C*, *D*): They sever themselves from the ectoderm of the larva. They then become connected in pairs, then the anterior fused pair unites with the posterior pair, so that now, on the oral side of the *Pilidium*, in its body cavity, a hollow plate arises with inner and outer walls. The inner wall grows round the enteric canal on all sides,

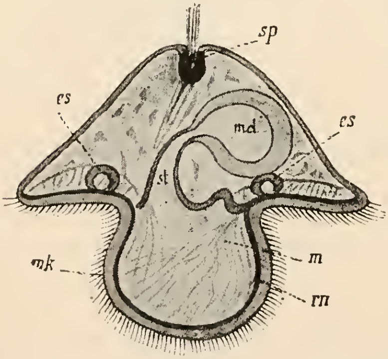


FIG. 185.—**Pilidium-Larva of a Nemertian** from the side (after **Salensky**). *sp*, Neural thickening with ciliated tuft; *wk*, ciliated ring; *rn*, nerve of the same; *m*, muscles; *st*, stomodæum; *md*, mid-gut; *es*, ectoderm sacs.

and forms the permanent outer integument of the young *Nemertian*. The outer, thinner, wall then forms inside the *Pilidium* integument a sac-like covering for the young *Nemertian*, the **amnion.** This integument with ciliated ridge and neural plate, *i.e.* the primary ectoderm, falls away together with the amnion when the young *Nemertian* issues from the *Pilidium*. At an early stage we find on the inner side of the ectoderm sac a layer of cells, which in the *Pilidium* arise out of the ectodermal wall of the sac itself, but in the related *Desor's larva* are said to be derived from the mesoderm cells which lie in the primary body cavity. The 4 layers of cells thus arising represent the rudiment of the definitive mesoderm. The central nervous system arises out of 2 ectodermal outgrowths which unite to form the brain in the young *Nemertian*. They grow out posteriorly into two strands, the lateral nerves. The proboscidal apparatus rises firstly out of an invagination of the ectoderm above the brain, and secondly out of parts of the mesoderm which surround this invagination.

The *Pilidium* larva takes up a position intermediate between the young *Turbellarian* larva of the *Polyclada* (*cf.* p. 167, *Müller's larva*) and the typical *Trochophoran* larva. It agrees with the former in the absence of a proctodæum. The 4 rudiments of the mesoderm probably answer to the 4 mesoderm masses of the young *Polyclad* larvæ or embryos.

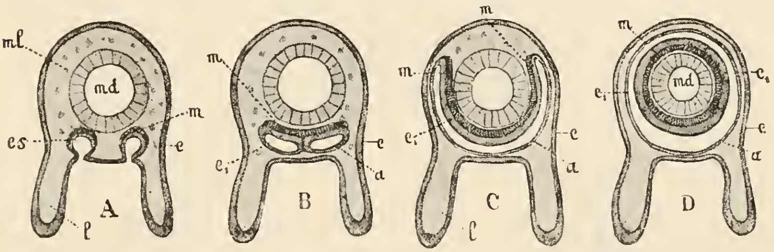


Fig. 186.—*A*, *B*, *C*, *D*, **Four diagrammatic transverse sections behind the mouth through a Pilidium larva during metamorphosis,** to illustrate the method of formation of the mesoderm and secondary (definitive) ectoderm. *e*, Larval ectoderm; e_1, definitive ectoderm; *a*, amnion ectoderm; *es*, ectoderm sac; *m*, mesoderm; *l*, lateral lobes of the larva; *md*, mid-gut; *ml*, larval mesoderm.

A *Nemertian* larva related to the *Pilidium*, **Desor's larva,** shows the larval characteristics less developed. The ciliated ring and the ectodermal thickening with the ciliated tuft which corresponds with the neural plate are wanting. But the definitive ectoderm is formed, as in *Pilidium*, of discs which detach themselves from the primary ectoderm. Many *Nemertina* develop without metamorphosis.

If we glance over the larval forms of worms we see that all are distinguished by peculiarities of structure which are explained by the circumstance that the animals feed independently and swim about freely at a very early stage of development. The simplest organs of locomotion which can be developed early are the cilia. They appear in all larvæ. Ciliated rings are universally present; the most constant is the preoral, which is provided with a special nervous system (nerve ring). Almost everywhere we find a spacious larval body cavity filled with fluid. The larvæ are hydropic, their specific gravity being nearly that of water. They are provided with a functional hollow enteron and other functional parts—nervous system, sensory organs, muscles, excretory organs. It is pretty generally found that those parts of the larval body which function at an early stage are thrown off or reabsorbed at the end of larval life, and that the organs of the adult animal consist of cell material which is present in the larva as undifferentiated germ material performing no specific functions. A comparison of the larva with the adult animal shows that the body of the former corresponds with the anterior portion of the body of the latter, *i.e.*, in segmented animals with the head segment. The smaller portion of the larva corresponds with the posterior end of the adult animal, while the trunk, with the exception of the mid-gut, remains in its embryonic condition in the larva. This is again to be explained by the fact that the embryo, which is provided with little or no nutritive yolk, must early develop organs necessary for independent feeding and locomotion, and these most indispensable organs lie chiefly at the anterior end of the body. This also explains why the locomotory organs of the larva, the ciliated rings, lie near the mouth, mostly somewhat in front of it; and why, besides this, there sometimes appears a preanal ciliated ring; why also, in certain (*Polytrochan*) *Annelid* larvæ, other segmental ciliated rings appear as the segments of the trunk develop.

Direct Embryonic Development.—This is chiefly found in fresh-water worms. The embryo is provided with enough nutritive yolk, generally stored in the endoderm cells, to enable it to develop direct (usually within an egg shell). Hence it follows that the organs necessary for free independent locomotion and feeding as an embryo are unnecessary. The comparison of the direct development of the embryo, say of Lumbricus, with that of a pelagic larva, *e.g.* a *Trochophora*, is very instructive.

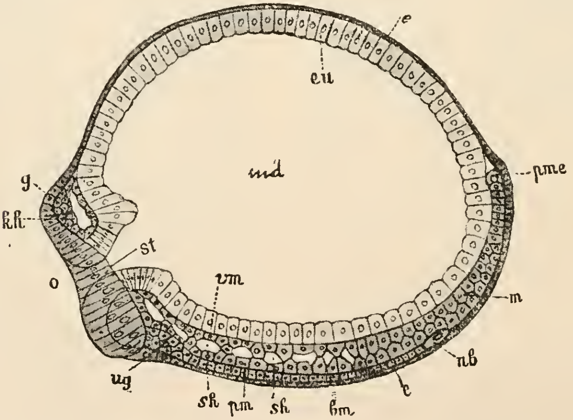


FIG. 187.—**Embryo of Lumbricus** (after **Wilson**). Optical median longitudinal section. *e*, Ectoderm; *pme*, pole cells of the mesoderm; *m*, mesodermal streaks; *sh*, rudiments of the segmental body cavities in the mesoderm; *nb*, neuroblast cells; *bm*, rudiment of the ventral chord; *vm*, visceral layer; *pm*, parietal layer of the mesoderm somites; *ug*, rudiment of the infra-œsophageal ganglion; *g*, rudiment of the brain; *kh*, head cavity; *o*, mouth; *st*, stomodæum; *md*, mid-gut; *en*, endoderm.

The egg of **Lumbricus** is supplied with little yolk. The egg and the embryo which develop out of it are nourished in another manner. In every capsule there are several eggs in the midst of a mass of albumen which nourishes them. The embryo (Fig. 187) is at a certain stage egg-shaped, and surrounded on all sides by a thin unciliated ectodermal epithelium. The mouth lies anteriorly, somewhat near the ventral side; it is surrounded by an epithelial thickening, and leads into a short stomodæum. This again opens into a very spacious mid-gut, whose epithelial wall lies close to the body wall all round. On the ventral side only, masses of cells, the two germ streaks, to be described later, are intercalated between the intestine and the body epithelium. A proctodæum is wanting, it develops only at a later stage. Anteriorly, above the mouth and directly under the ectoderm from which it is derived, lies a mass of cells—the rudiment of the brain. In many other worms with direct development the mid-gut is solid and not hollow, in consequence of the large masses of yolk contained in the endoderm cells (primitive macromeres).

Since embryonic head nephridia have been observed in some *Oligochæta*, the chief differences between them and the *Polychætan Trochophora* are the following: Cilia are wanting in the former, and especially a pre-oral ciliated ring. Sensory organs (eyes, ciliated tufts) are wanting. A body cavity is wanting, and also a proctodæum. On the other hand, as we shall see later, the mesoderm is much more developed than in the *Polychætan Trochophora* above described. The parts of the body present in the embryo represent the rudiments of the definitive organs, they do not, as in a free-swimming larva, fulfil specific functions, and therefore seldom disappear in the course of further development. The *Gnathobdellidæ* form an exception, for in them a metamorphosis takes place, and, according to recent research, the larval integument with its muscular and nervous systems, and further the provisional trunk nephridia and the œsophagus, are said to disappear.

Development of the Outer Integument.—We may say, generally, that the outer integument or body epithelium of the worms is derived from the embryonic or larval ectoderm. The ectoderm either changes, without suffering any loss worth mentioning, into the body epithelium; or some parts of the larval ectoderm which perform specific functions are thrown off; or else certain portions of the larval ectoderm sever themselves, and unite on all sides of the body within the larval ectoderm to form the permanent ectoderm or body integument (*e.g. Sipunculidæ*, *Nemertina*). We consider these processes as a kind of ecdysis. In the *Gnathobdellidæ* (*Hirudinea*) alone it is said that the secondary ectoderm is not formed from the larval ectoderm, and that the latter is quite lost. The larval and definitive sensory organs, the larval and definitive nervous systems, and the larval and definitive setiparous sacs (of the *Chætopoda*) are products of differentiation of the ectoderm. The last mentioned are groups of glandular hypodermis cells, which sink under the integument, the setæ arising in them as secretions. The ectodermal setiparous glands are enveloped by mesodermal elements which supply their musculature.

Development of the Mesoderm and the Mesodermal Organs.—The mesoderm is for us a topographical conception. All that lies in the adult animal between the outer integument and the intestinal epithelium belongs to the mesoderm. The relations of the various mesodermal organs and systems of organs to the outer integument are very varied. These relations are closest in the nervous system in consequence of its dependence on the (ectodermal) sensory organs. As already described (*cf.* p. 223), in many worms the central nervous system remains in the integument, even in the adult animal, and is thus not mesodermal. The mesodermal position of the nervous system is, however, the general rule, as it is even as early as in the Platodes. As, however, it nearly always develops entirely separate from the rest of the mesoderm, we shall describe its development first.

The **Brain.**—In some cases the brain, or a part of it at any rate, develops out of the ectodermal neural plate (many *Annelids*, *Sipunculidæ*). The elements of the neural plate probably arise in connection with the provisional or definitive sensory organs of the head (eyes, neural tuft, tentacles), though this cannot be established in detail. There are thus different parts which unite together to constitute it a sensory nervous centre. The neural plate must thus represent an organ similar to the sensory body of the *Ctenophora* or the marginal centres of the *Medusæ*. It is often thrown off with the larval integument (*e.g.* in *Phoronis*, *Pilidium*), and the oral nerve ring or the brain arises anew out of the secondary ectoderm.

Ventral Chord of the Annulata.—The ventral chord seems always to begin to form separately from the neural plate. It arises either as a continuous thickening of the ectoderm in the ventral middle line, or as a pair of thickenings one on each side of this middle line. The differentiation of the rudiment of the ventral chord into the definitive ventral chord goes hand in hand with the development of the rest of the trunk, and proceeds from before backward. It either remains, like the brain, connected during life with the ectoderm, or it becomes constricted off from it and takes up a position either in the musculature of the body wall or still deeper in the body cavity. At the posterior end of the body it almost always retains its embryonic condition, as it here remains throughout life in its place of formation, the integument. The *Hirudinea* and *Lumbricus* among the *Oligochæta* differ very much from other *Annulata* and *Sipunculidæ*. The ventral chord here does not arise *in situ* in the ectodermal integument; but two ectodermal segmentation spheres (micromeres) appear very early near the posterior end, and take up a position under the ectoderm, lying symmetrically on each side near the middle line. New cells are continually constricted off anteriorly from these **neuroblasts** (Fig. 188, *nb*), which again divide, and a cell strand thus arises on each side of the ventral middle line, immediately beneath the integument. The two cell strands, which form part of the germ streaks of the *Hirudinea* and of *Lumbricus*, represent the rudiment of the ventral chord, which, beginning behind the mouth, becomes continuously differentiated from before backward. It is evident from this that the rudiment of the ventral chord is unusually localised, and at the same time is to be referred to a very early stage of development. The connection of the ventral chord with the brain through the œsophageal commissure seems everywhere to take place secondarily. It may perhaps in time be proved that the central nervous system in the *Worms* and *Platodes* proceeds ontogenetically and phylogenetically from two chief parts, viz. first from the sensory part of the brain, *i.e.* from the united sensory centres or sensory ganglia of the anterior end of the body, and second from the motor central nervous system, *i.e.* the ventral chord, the œsophageal commissure, and the motor part of the brain of the *Annulata*, the longitudinal trunks and the motor part of the brain of the other worms and *Platodes*. In the *Nemertina*, however, the lateral nerves are said to grow out from the brain posteriorly. This may perhaps here, and also in the *Turbellaria*, point to a concentration of the whole central nervous system into one single rudiment.

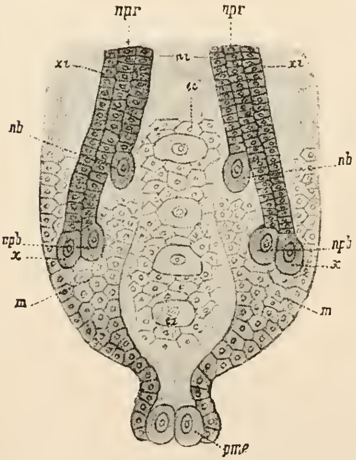


FIG. 188.—**Superficial aspect of the germ streaks in a Lumbricus embryo** (after **Wilson**). *pme*, Pole cells of the mesoderm (mesoblasts); *nb*, pole cells of the ventral chord (neuroblasts); *npb*, pole cells of the nephridial rows (nephroblasts); *x*, pole cells of the cell rows (*xr*) of unknown significance; *ec*, ectoderm; *ez*, large ectoderm cells; *npr*, nephridial cell rows; *nr*, neural cell rows; *m*, mesoblast streaks.

In the development of the other component parts of the mesoderm, we find that, just as the rudiment of the ventral chord in the *Hirudinea* and *Lumbricus* is shifted back to an early stage, and is condensed into two germ cells (the neuroblasts), so the rudiment of all other mesodermal organs in worms are extremely condensed and localised and shifted back to early stages, so that generally a few germ cells or a limited germ zone represents the condensed rudiment of all mesodermal organs, with the exception of the nervous system.

We accordingly find in the *Hirudinea* (*Clepsine*) and in *Lumbricus*, in early stages of development, even during segmentation, on each side of what morphologically corresponds with the posterior end of the embryo, 4 or 5 micromeres, which soon sink down under the ectoderm-micromeres, or are grown round by them. The 2 which lie posteriorly are the largest; they lie close to each other, and in front of them 3 or 4 lie on each side of the ventral median line (Fig. 188). The 2 inner micromeres we already know; they are the neuroblasts. Just as 2 rows of cells develop anteriorly from the neuroblasts, forming the rudiment of the ventral chord, rows of cells also develop anteriorly from the remaining **polar cells.** The single or double cell rows which lie near the neural rows are the **nephridial rows**; the polar cells from which they develop are the **nephroblasts.** They yield the material for the nephridia, which become differentiated from before backward. The most anterior nephridia are temporary; they are the larval or embryonic nephridia. It is not yet known what part of the mesoderm is formed by the lateral rows of cells with their posterior polar cells. The cell rows which proceed from the most posterior largest polar cells represent the rudiments of the body musculature, the endothelium, septa, and mesenteries. We shall return to their further development.

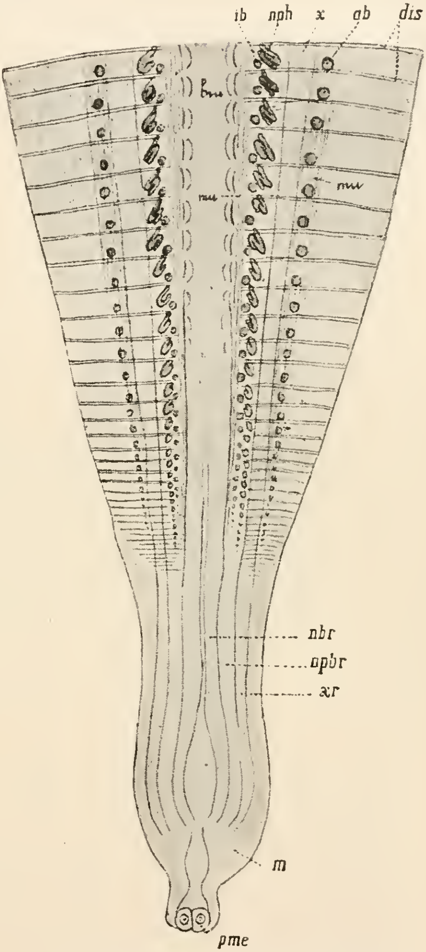


Fig. 189.—**Surface view of the germ streaks of a somewhat older Lumbricus-embryo**, after the disappearance of the anterior polar cells (after **Wilson**). *pme*, Polar cells of the mesoderm (*m*); *x*, *xr*, cell rows of unknown significance; *nphr*, nephridial cell streaks; *nbr*, neural cell streaks, rudiment of the ventral chord (*bm*); *dis*, dissepiments; *ib*, inner; *ab*, outer rows of setiparous glands; *nph*, rudiments of the nephridia; *mu*, longitudinal musculature.

All these cell rows taken together are known as the paired germ streaks. They lie at the two sides of the ventral middle line between the intestine and the integument. The germ streaks thus yield all the mesodermal organs, nervous system, nephridia, muscles, endothelium, etc. In the *Gnathobdellidæ*, where the whole larval ectoderm is lost, the germ streaks are said even to produce the definitive body epithelium as well. This statement, however, requires confirmation.

There are germ streaks in many worms similar to those in the *Hirudinea* and *Lumbricus.* But it appears that these do not consist of contiguous rows of cells, but that each germ streak is the product of a single polar cell at the end of the embryo or young larva. We have described these two polar cells in *Eupomatus* as primitive mesoderm cells. The germ streaks which proceed from them are called mesoderm streaks; they seem to yield the whole mesoderm with the exception of the nervous system. Here, therefore, the rudiments of almost all the mesodermal organs are localised and condensed into two blastomeres which appear at an early stage at the posterior edge of the blastopore.

In the larva of *Lopadorhynchus* (*Polychæta*), as the trunk grows, what is called the postoral ventral plate of the ectoderm is said to split from front to back into an inner muscular plate and an outer neural plate, the ventral chord being principally formed from the latter.

Further Development of the Germ Streaks (Figs. 187-189).—In Lumbricus the two cell rows of the germ streaks, which are formed from the two large posterior polar cells, soon begin to be differentiated from before backward. Their cells divide. The simple cell rows thus become solid plates or strands. They extend forwards on both sides and meet dorsally above the mouth. In this cephalic portion of the germ streaks a central cavity appears which enlarges and becomes the cavity of the head. The outer layer of cells attaches itself to the outer integument of the head, and becomes the outer musculature and endothelium of the head segment. The inner layer forms the musculature of the pharynx and its endothelial covering. Behind the head on each side clefts also occur in the above-mentioned cell strands, and these, forming in segmental order from before backward and increasing in size, form the rudiments of the paired segmental chambers of the cœlome. They separate the cell strands in each segment into a parietal layer contiguous to the integument and a visceral layer contiguous to the intestine. The cell strands are thus divided into paired segmentally consecutive portions. In each segment on each side both the parietal and the visceral layers grow up between integument and intestine till they meet in the dorsal middle line. The partition wall which is here formed in this way, and which divides the two lateral chambers of the body cavity, is the rudiment of the dorsal mesentery which is often temporary. A ventral mesentery arises in a similar manner. The cell material, which separates the consecutive chambers of the body cavity forms the dissepiments. The parietal layer forms the musculature of the body wall and the parietal endothelium; the visceral layer forms the muscular layer of the intestine and the visceral endothelium.

Development of the Blood-vascular System.—This system arises (*Terebella*, *Psygmobranchus*) as a cavity filled with fluid between the epithelial intestinal wall and the contiguous visceral layer of the mesoderm. The chief vessels arise as longitudinal bulgings of the mesodermal walls of this enteric sinus, which finally become constricted off from it, passing from the form of grooves to that of closed canals. In *Lumbricus* and other *Oligochæta* the dorsal vessels arise in a similar way as clefts between the enteric epithelium and the enteric muscle layer. They are at first paired, but generally unite to form the unpaired dorsal vessel. In a few *Lumbricidæ*, however, even in adult animals, over a larger or smaller region of the body, they may remain double.

Development of the Nephridia.—In the anatomical section we distinguished three parts in each nephridium: (1) the funnel; (2) the nephridial duct; and (3) the terminal portion which opens outwardly, which in the *Hirudinea* and *Oligochæta* is often widened out into a vesicle. It appears that in *Lumbricus* the nephridia develop in the following way. The nephridial ducts develop in pairs in each segment as outgrowths of the nephridial cell rows. Each duct consists at first of one cell or of a few cells, and later of a row of cells bent in the shape of the letter U, which projects into the body cavity and is thus provided with an outer endothelium. One limb of the cell row remains in contact with the integument, the end of the other attaches itself to the posterior wall of the dissepiment which lies in front of it. At this point an inner canal first appears in the solid row of cells. The terminal portion arises by an invagination of the integument. The funnel begins to form from one cell on the anterior wall of the dissepiment at the point where, on the posterior wall, the end of the nephridial duct lies. This cell only secondarily becomes a hollow ciliated funnel, which then unites with the nephridial canal through the dissepiment. The funnel thus arises separately from the nephridial canal out of the epithelium of the body cavity, and not out of the nephridial rows of cells. In the *Polychæta* also the funnel and the nephridial duct of each nephridium are said to arise separately.

Development of the Sexual Glands.—It may be considered certain that in the *Annulata* and *Prosopygia* the ovaries and testes are developed from special parts of the endothelium of the body cavity.

The Development of the Mesoderm in the Chætognatha (Fig. 190).—The nervous system here lies in the integument of the body and does not belong to the mesoderm.

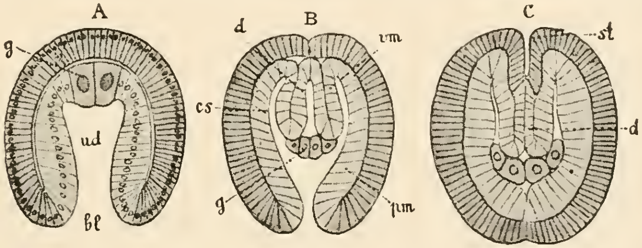


Fig. 190.—*A*, *B*, *C*, **Three early stages of development of Sagitta** (after **O. Hertwig**). *a*, Gastrula; *bl*, blastopore; *ud*, arch-enteron; *g*, primitive cells of the sexual organs; *vm*, visceral layer; *pm*, parietal layer of the mesoderm; *d*, rudiment of mid-gut; *cs*, cœlome sacs; *st*, stomodæum; *d*, intestine.

In this case the mesoderm develops in a manner different from that in the worms as yet described. A cœlogastrula forms whose principal axis answers pretty accurately to the longitudinal axis of the adult *Sagitta*. The aboral pole of the gastrula corresponds with the future anterior end of the body. Two large cells which soon divide enter the base of the archenteron from the endoderm at an early stage. These 4 cells are the rudiment of the testes and ovaries. Then on each side there arises out of the base of the archenteron a fold of the endoderm, which grows into the archenteric cavity towards the blastopore. These 2 folds divide the archenteric cavity into a central cavity and two lateral cavities, which communicate at the free edges of the folds. The central cavity is the definitive enteric cavity; its epithelial walls, *i.e.* the inner epithelial lamellæ of the folds, represent the rudiment of the definitive enteric epithelium. The folds close dorsally and ventrally to form the enteric tube, the latter carrying the 4 sexual cells at its freely projecting end. The two lateral cavities, which may almost be looked upon as 2 sac-like invaginations of the archenteron (cœlomic sacs), form the commencement of the body cavity. Each sac has an outer epithelial wall in contact with the ectoderm, and an inner wall in contact with the enteric tube. The former is the parietal, the later the visceral layer of the mesoderm. The former probably forms the musculature and the endothelium of the body wall, the latter the enteric endothelium. At the aboral pole of the larva a small depression of the ectoderm becomes connected with the enteric tube. The permanent mouth and the stomodæum thus arise. The primitive mouth closes. The enteric tube becomes a solid strand, which continues to grow till it reaches the closed primitive mouth, *i.e.* the posterior end of the body. An enteric cavity does not again appear till a later stage. On the ventral side, a little in front of the posterior end of the body, an anus forms. The postanal intestine degenerates, its 2 visceral layers of the mesoderm forming the septum of the caudal segment. From the 4 genital cells the testes and ovaries develop. We thus see that in *Sagitta* the mesodermal organs have a double origin: first, 2 (afterwards 4) large endoderm cells lying at the base of the archenteron, which form the rudiments of the sexual glands; secondly, the whole middle and oral epithelial wall of the archenteron of the cœlogastrula; this represents a germ zone, continued at the edge of the blastopore into the ectoderm, and at the aboral portion of the larva into that part of the wall of the archenteron from which the definitive intestine is produced. This germ zone forms at an early stage two lateral cœlome sacs as a consequence of the formation of the folds above mentioned; the cavities of these sacs produce the body cavity, and their walls the endothelium of the body cavity, and probably also the musculature of the body wall.

Two hollow lateral cœlome sacs of the archenteron appear at an early stage in one of the *Brachiopoda*, *Argiope*, much in the same way as do those in *Sagitta*; these, constricting themselves off from the intestine, are said to form the body cavity and the mesoderm. The development of the mesodermal organs has, however, up to the present time been insufficiently observed.

Various theories have been put forward as to the phylogenetic significance of the different processes of development to which the mesodermal organs owe their rise ontogenetically, all these theories resting upon the assumption that the ontogenetic process exactly repeats, sometimes in one point sometimes in another, the phylogenetic development. These theories rest upon weak foundations as long as comparative anatomy knows of no series of animal forms which shows us the gradual rise of the mesodermal organs in a manner similar to that seen in the successive ontogenetic stages of development. It is very doubtful whether the whole mesoderm, except the nervous system, can be derived phylogenetically from such simple organs as the cœlome sacs, or from cell groups such as the polar cells of the mesoblast, once present in simple gastrula-like racial forms. Observations are increasing in number which tend to show that ontogenetically also there is no single rudiment of the whole mesoderm, but rather several rudiments for the different mesodermal organs. Our review of the history of development of the worms supports this latter view. It may perhaps in time be established that the manner in which the various mesodermal organs appear in the *Cnidaria* moving from their places of formation, the ectodermal body epithelium and the endodermal enteric epithelium, into the deeper parts of the body wall, is essentially the same as that in which the mesodermal organs originally arose in the ancestors of the *Platodes* and the *Vermes*. The ontogenetic development of the mesoderm would then represent this process very much abbreviated and localised, pushed back to very early stages. If, in the *Hirudinea* (in *Clepsine* at least) and in *Lumbricus* as opposed to the other *Annulata*, the ventral chord does not arise *in situ* in the ectoderm but is formed by two blastomeres, the neuroblasts, which arise at an early stage, it is difficult to see why the polar cells of the other mesodermal organs (nephroblasts, mesoblasts, etc.) should not represent similar early developing condensed and localised rudiments. And why should not these different rudiments themselves be pushed back to, and localised and condensed in, a rudiment such as the early developed primitive mesoderm cells or zones? In the *Polyclada* we see at an 8-micromere stage (Fig. 94, p. 125) the rudiment of the whole ectoderm, with the nervous system localised and condensed in 4 micromeres, the rudiment of the mesoderm in 4 other micromeres, and the rudiment of the whole endodermal enteric system in the 4 macromeres.

Development of the Intestine.—The intestine of the worms consists as a rule of three parts of different origin—the fore-gut, the mid-gut, and the hind-gut. From the endodermal archenteron of the gastrula only the mid-gut is derived. At an early stage in larval life an anterior ectodermal invagination, the embryonic or larval œsophagus or the stomodæum, becomes connected with it, while a similar invagination at the posterior end yields the proctodæum. While the proctodæum becomes in a direct manner the hind-gut, which is often very short, the fore-gut does not always proceed direct from the stomodæum. Sometimes, *e.g.* in the *Hirudinea*, the stomodæum disappears and a new œsophagus arises independently in its place. Sometimes the definitive œsophagus begins to form out of the stomodæum which as such disappears. This is the case in many *Polychæta*. The musculature of the fore-gut, which is often very strongly developed as the pharynx, seems everywhere to be formed from the cephalic portion of the mesodermal or germ streaks. The origin of the muscular wall of the mid-gut and its endothelium, where this is present, from the visceral layer of the mesodermal streaks has already been described.

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CHAPTER V

The first division of the Arthropoda—The organisation and development of the Crustacea.

THE FIFTH RACE OR PHYLUM OF THE ANIMAL KINGDOM.

ARTHROPODA—ARTICULATA.

Bilaterally symmetrical animals with chitinous exoskeleton, segmented body, and paired jointed extremities on all or some of the segments. With brain, œsophageal commissures, and segmented ventral chord. With heart lying above the intestine. Sexes separate, with one pair of sexual glands and originally paired ducts from these glands.

First Sub-race or Sub-phylum.

Branchiata.—Aquatic animals. With the exception of the anterior antennæ all the appendages are morphologically biramose. Respiration cutaneous or by means of gills, which are almost always appendages of the basal joints of the limbs.

Single Class. **Crustacea.**

First appendage to the Sub-race Branchiata : The Trilobites, Gigantostraca, Hemiaspidæ, and Xiphosura.

Second appendage to the Sub-race Branchiata : The Pantopoda or Pycnogonidæ.

Second Sub-race or Sub-phylum.

Tracheata.—Land animals. Limbs not biramose, consisting of a single row of joints. Respiration by means of tracheæ (tubular or book-leaf tracheæ).

Class I. **Protracheata.**

Class II. **Antennata (Myriapoda and Hexapoda).**

Class III. **Chelicerota sive Arachnoidea.**

Appendage to the Phylum of the Arthropoda.

The Tardigrada or Bear animalcules.

THE CRUSTACEA.

Systematic Review.

Sub-Class I. Entomostraca.

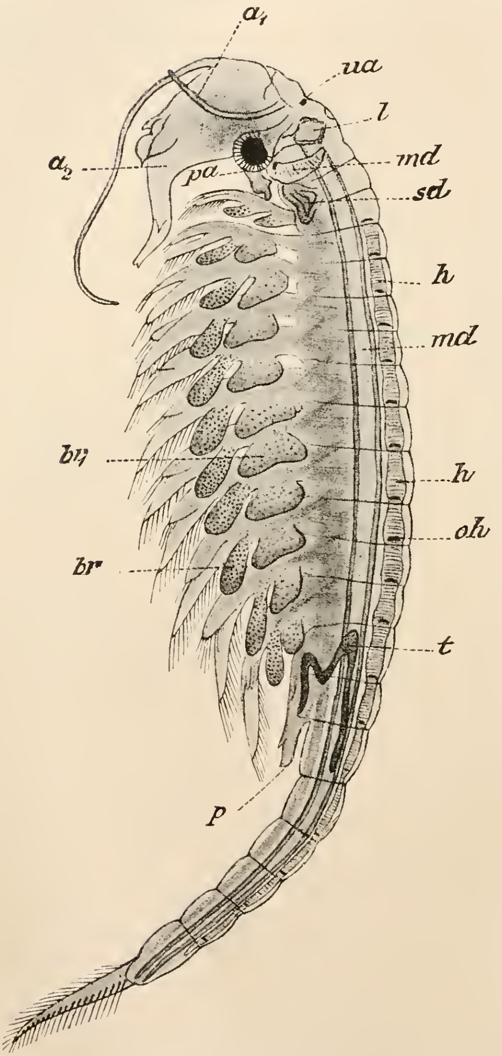

Fig. 191.—**Branchipus stagnalis**, male. a_1, Anterior antennæ; a_2, posterior antennæ, seizing antennæ with accessory appendages; *ua*, unpaired eye; *l*, liver; *md* (above), mandible; *sd*, shell gland; *h*, heart or dorsal vessel; *oh*, slit-like apertures (ostia) of the heart; *md* (below), intestine; *p*, penis; *br*, branchial sac; br_1, branchial leaflet; *pa*, paired stalked eyes (after **Claus**).

The trunk consists of a varying number of segments. We can here often distinguish an anterior division bearing limbs from a posterior division which has no such appendages. Each division, however, consists of a varying number of segments. The genital apertures usually lie between the two divisions of the trunk. A dorsal shield is often present, and is developed in various ways. The limbs are very variously shaped. Besides the usual lateral eyes, the unpaired frontal eye of the *Nauplius* larva is retained by the adult animal. A masticatory stomach is wanting. A *Nauplius* larva is hatched from the egg. Mostly small animals.

Order I. Phyllopoda.

With swimming feet which carry branchial sacs, mandibles without feelers, and reduced maxillæ.

Sub-Order 1. Branchiopoda.

Body distinctly segmented with numerous trunk segments, and numerous pairs of swimming feet. Carapace seldom wanting, either flat and shield-shaped or in the form of a bivalve shell. Heart an elongated dorsal vessel with numerous pairs of ostia. In fresh water. *Branchipus* (Fig. 191) (without shell), *Apus* (with flat carapace), *Estheria*, *Limnadia* (with bivalve shell).

Sub-Order 2. **Cladocera** (**Daphnidæ**), **Water Fleas.**

Body small, with few indistinct segments and 4 to 6 pairs of swimming feet. The posterior antennæ are large rowing feet.

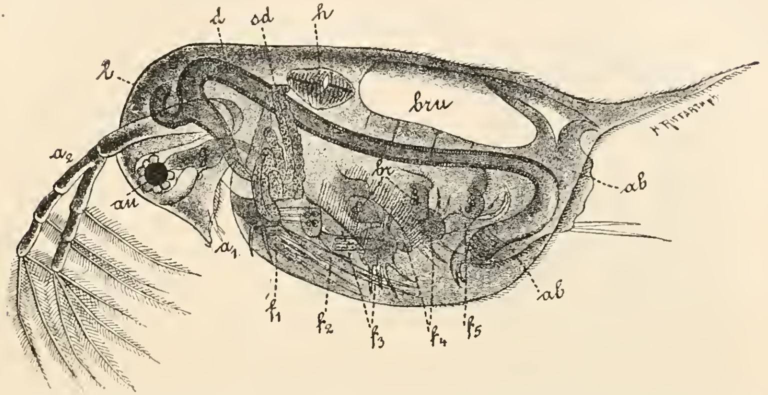

Fig. 192.—**Daphnia similis,** young female (after **Claus**). a_1, Antennule; a_2, second (rowing) antenna; *l*, hepatic cæcum; *au*, eye; *d*, intestine; *sd*, shell gland; *h*, heart; *bru*, brood cavity; *ab*, abdomen; *br*, branchial sac; f_1-f_5, trunk feet; *g*, brain.

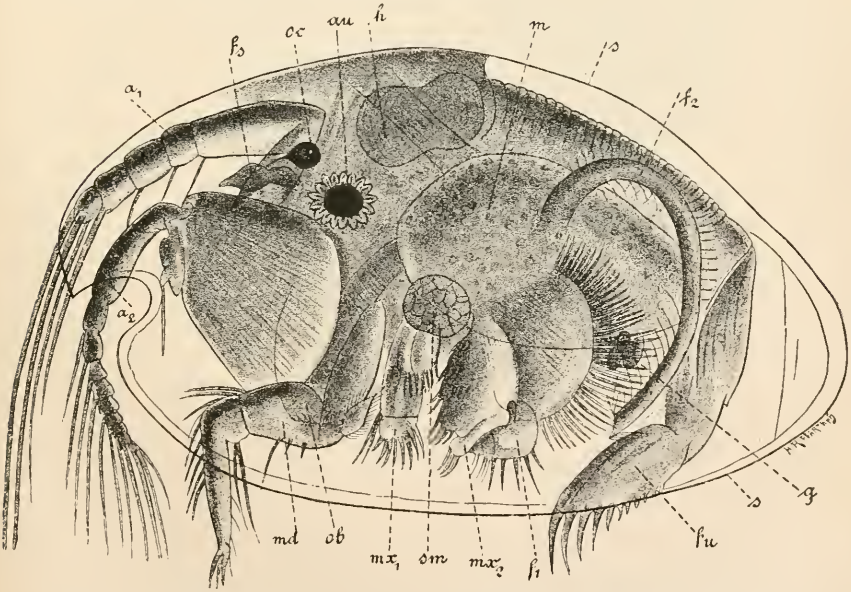

Fig. 193.—**Cypridina mediterranea,** female, from the side (after **Claus**). a_1, Anterior, a_2, posterior antennæ; *fs*, frontal organ; *oc*, unpaired eye; *au*, paired eye; *h*, heart; *m*, stomach; *s*, shell; f_2, cleaning foot; *g*, sexual organs (?); f_1, first foot; mx_2, second maxilla; *sm*, shell muscle, mx_1, first maxilla; *ob*, upper lip; *md*, mandible.

Branchial sacs may be wanting. With bivalve shell. Head freely projecting. Female with dorsal brood cavity between shell and trunk. Heart sac-shaped with one pair of ostia. Mostly in fresh water. *Daphnia* (Fig. 192), *Sida, Moina, Lynceus, Polyphemus, Leptodora, Evadne* (marine).

Order 2. **Ostracoda.**

Body small, consisting of few segments indistinctly segmented, with bivalve shell. Besides the 5 pairs of well-developed limbs to be attributed to the head, viz. the antennæ, mandibles, and maxillæ, all or some of which may be developed as creeping or swimming feet, we find only 2 pairs of trunk limbs. The heart may be present or wanting. Fresh-water form: *Cypris.* Marine forms: *Cythere, Halocypris, Cypridina* (Fig. 193).

Order 3. **Copepoda** (with biramose or rowing feet).

Sub-Order 1. **Eucopepoda.**

Body small, mostly distinctly segmented, without shell fold. The trunk consists of 10 segments, the 5 anterior carrying 5 pairs of biramose rowing feet, while the 5 posterior are limbless. The foremost trunk segment is fused with the head. Antennæ, mandibles, and maxillæ (the two branches of the posterior maxillæ separated from one another) are well developed, at any rate in the free-living forms. The mouth parts in the parasitic forms either suck or pierce. Heart sometimes wanting; when present it is

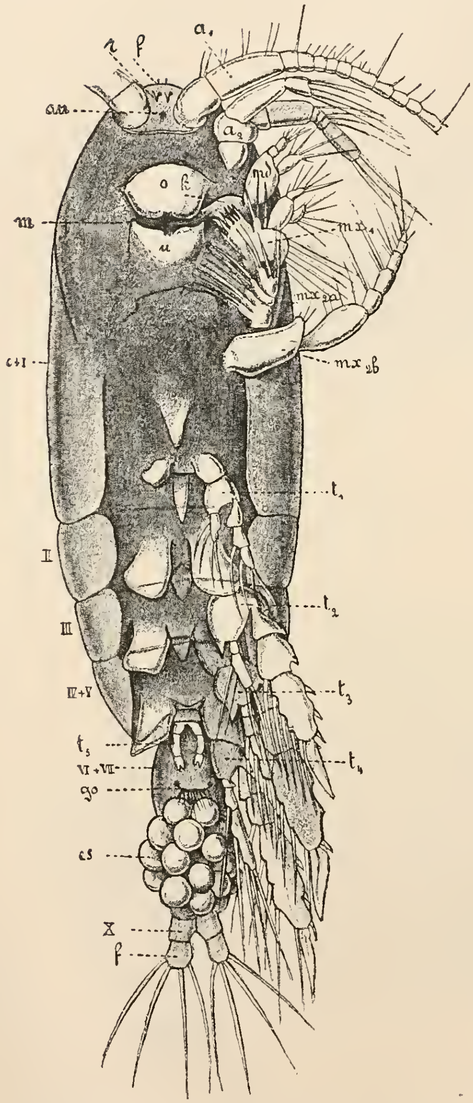

Fig. 194.—**Clausocalanus mastigophorus (Claus),** female, from the ventral side (after an original drawing by **W. Giesbrecht).** Only the extremities of the left side of the body are depicted. a_1, Anterior, a_2, posterior antennæ; *md*, mandible with masticatory ridge *k*; mx_1, anterior maxilla; mx_2a, mx_2b, anterior and posterior maxillipedes = endopodite and exopodite of the second maxilla; t_1-t_5, rowing feet (biramose), t_5, rudimentary; *f*, frontal organ; *r*, rostrum; *au*, eye; *o*, upper lip; *m*, mouth; *u*, under lip; *c+I*, head and 1st trunk segment; *II-X*, 2d-10th trunk segments; *I-V*, limb-bearing segments (thoracic segments); *VI-X*, limbless segments (abdominal segments); *VI+VII*, genital double segment; *go*, genital aperture; *es*, ovisac (unpaired); *f*, furcæ.

sac-shaped. The females carry about the fertilised eggs in a paired or unpaired ovisac. Gills are wanting. **Free-living** or **commensal Copepoda**: *Cyclops, Canthocamptus*, in fresh water; *Cetochilus, Clausocalanus* (Fig. 194), marine; *Notodelphys*, commensal in the branchial cavity of the *Ascidians*. **Parasitic Copepoda**: *Corycæus, Sapphirina* (some of which are only occasionally or temporarily parasitic), *Chondracanthus, Caligus, Lernæa, Lernæocera, Penella, Lernanthropus, Lernæaseus, Achtheres, Anchorella*.

Sub-Order 2. **Branchiura (Argulidæ), Carp Lice.**

Body consists of the flattened shield-shaped cephalo-thorax and the small flat abdomen (caudal fin) divided longitudinally. In front of the oral suctorial tube a long protrusible stylet. Four pairs of long cirrus-like biramose swimming feet. Two large compound lateral eyes. Testes in the caudal fin. Heart present. Females without ovisacs, attach the eggs to foreign objects. *Argulus* (Fig. 195), on the carp.

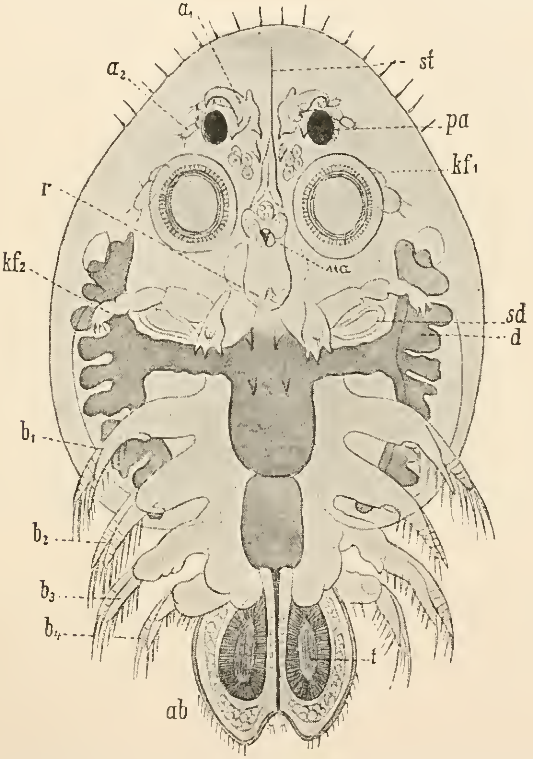

FIG. 195.—**Argulus foliaceus** young male (after **Claus**). a_1, Anterior, a_2, posterior antenna; *pa*, paired eye; *ua*, unpaired eye; *r*, beak or suctorial tube enclosing the mandibles and maxillæ; kf_1, anterior maxillipede with the adhering disc; kf_2, posterior maxillipede; *sd*, shell glands; *d*, intestine with its lateral branched diverticula; b_1, b_2, b_3, b_4, thoracic feet; *ab*, abdomen; *t*, testes.

Order 4. **Cirripedia.**

Characteristics of the attached forms: body indistinctly segmented, attached by the head end, surrounded by a mantle which generally calcifies and then forms a shell or case. Anterior antennæ (adhering antennæ) minute, posterior antennæ reduced. Oral limbs small, partly reduced. Six (less frequently 4) pairs of long biramose tendril-like feet. Without heart. Hermaphrodite, occasionally with dwarf males, less frequently sexes separate and dimorphic. Live in the sea.

Family 1. **Lepadidæ** (**Pedunculata**).

Head end elongated into an attached peduncle. *Lepas* (Figs. 204 and 205), *Conchoderma*, *Scalpellum*, *Pollicipes*, *Ibla*.

Family 2. **Balanidæ**.

Peduncle wanting. Body surrounded by a ring of calcareous plates. *Balanus* (Figs. 206 and 207), *Tubicinella*, *Coronula*.

Family 3. **Alcippidæ** (**Abdominalia**).

Body surrounded by a flask-shaped integumental mantle, with 3 or 4 pairs of feet, corresponding with the last 3 or 4 pairs of other *Cirripedes*. Live in the calcareous shells of other *Cirripedes* and *Molluscs*. *Alcippe*, *Cryptophyalus*.

Family 4. **Proteolepadidæ** (**Apoda**).

Body maggot-like, without tendril-like feet. Anterior (adhering) antennæ ribbon-shaped. Mouth a sucker. Enteric canal rudimentary. Parasitic in the mantle of other *Cirripedes*. *Proteolepas*.

Family 5. **Rhizocephala** (**Kentrogonidæ**), perhaps to be separated as a special sub-order or order from the other *Cirripedes*.

Body pouch-shaped, answers to the cephalic portion only of related Crustaceans. Integument split into 2 lamellæ; between them is a brood cavity which opens outwardly by means of an aperture in the outer lamella. Enteric canal wanting. Limbs wanting. Hermaphrodites, with dwarf males. Parasitic on the abdomen of *Decapoda*. The pouch-shaped body has an adhering peduncle from which spring the branched "roots" which penetrate everywhere between the viscera of the host and convey nourishment into the body of the parasite. The larval stages (*Nauplius*- and *Cypris*-like larvæ) are like those of other *Cirripedes*. *Sacculina* (Fig. 208), *Peltogaster*.

Sub-Class II. **Malacostraca**.

The body consists of 3 regions with constant number of segments. (1) The head, originally formed of 5 segments; (2) the thorax, consisting of 8 segments, of which the anterior segment or segments, or all the segments, may fuse with the head to form an incomplete or a complete cephalo-thorax; (3) the abdomen, which (reckoning the telson) consists of 7 segments, (in *Nebalia* alone, including the terminal segment, of 8). All the segments of the body except the last (and in *Nebalia* the last but one) carry limbs. The most anterior thoracic feet often move into the neighbourhood of the mouth to serve as foot-jaws and to assist in taking in food. The sixth pair of pleopoda (abdominal limbs) almost always differs in shape from the rest, and often forms with the telson a caudal fin. A shell fold springing from the posterior cephalic region is very common. A pair of compound lateral eyes is always found, as is also a masticatory stomach. The female genital apertures lie in the 6th thoracic segment, the male in the last. Development sometimes with, sometimes without, metamorphosis. The larva hatched from the egg is rarely a *Nauplius*. In many *Thoracostraca* the larvæ pass through the *Zoœa* stage.

Legion I. **Leptostraca**.

An extremely important group, which of all living Crustaceans stands the nearest to the racial form of the *Malacostraca*, and is often placed as a special sub-class between the *Entomostraca* and the *Malacostraca*. Body slender, covered with a bivalve shell, which extends back, leaving only the last 4 abdominal segments free. Besides this there is a movable cephalic plate. Head, with the 5 typical pairs of appendages, distinct from the thorax. All the 8 segments of the short thorax are distinct, with 8 pairs of similar biramose lamellate feet. On the basal joint of the protopodites of these segments there is a large epipodial lamella functioning as a gill. The 4 anterior pairs of pleopoda are strong biramose rowing feet, the 2 posterior pairs are short and uniramose. The last segment of the abdomen carries two furcal processes. On the head are 2 stalked compound lateral eyes. Heart elongated, with 7 pairs of ostia, stretches through the thorax and the abdomen as far as into the 4th abdominal segment. Masticatory stomach present.

Single **order** and **family**, *Nebalidæ*: *Nebalia* (Fig. 196), *Paranebalia*, *Nebaliopsis*, marine forms.

The fossil Paleozoic forms *Ceratiocaridæ* (*Archæostraca*), *Hymenocaris*, *Ceratiocaris*, etc., are probably related to the *Leptostraca*.

Legion II. **Arthrostraca (Edriophthalmata).**

A shell fold is wanting, except in the division of the *Anisopoda*. The first thoracic segment (less frequently the second also) is fused with the head, and the foremost pair of thoracic feet are transformed into foot-jaws. The 2 lateral eyes are sessile.

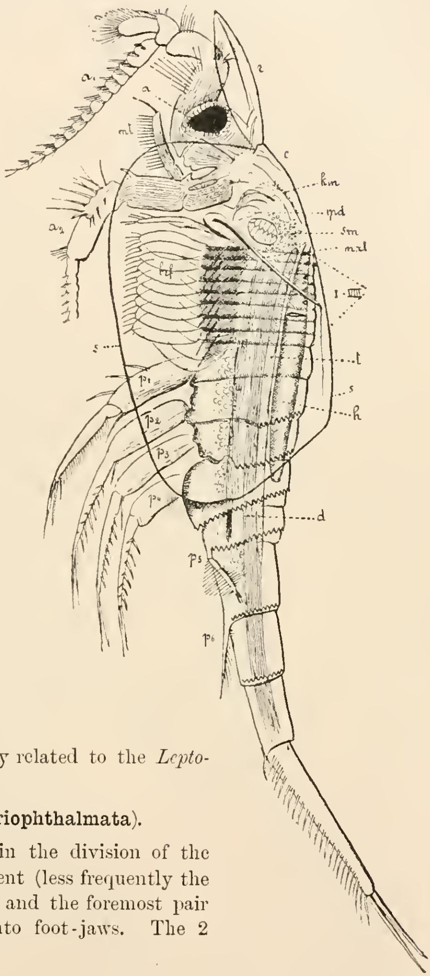

FIG. 196.—**Nebalia Geoffroyi**, male (after **Claus**). *r*, Rostral plate; *c*, cephalic region; *km*, masticatory stomach; *md*, mandible; *sm*, shell muscle; *mxt*, feeler of the anterior maxilla (cleaning foot); *I-VIII*, thoracic segments; *t*, testes; *s*, shell; *h*, heart; *d*, intestine; a_1, anterior, a_2, posterior antenna; *mt*, mandibular feeler; *brf*, thoracic feet; p_1-p_6, pleopoda; *a*, eye.

Order 1. **Anisopoda.**

First and second thoracic segments fused with the head. Cephalothorax with lateral shell fold, which on each side covers a respiratory cavity. Both the pairs of maxillæ have feelers. The feelers of the anterior pair project into the respiratory cavity as cleaning appendages. The maxillipede has an epipodial appendage functioning as gill. The pair of limbs belonging to the second thoracic segment, which is also fused with the head, are developed as powerful forceps. Abdomen with biramose swimming feet. Heart in the thorax, generally with 2 pairs of ostia (the heart of *Apseudes* has only 3 ostia). *Apseudes*, *Tanais*, *Leptochelia*.

Order 2. **Isopoda.**

Body broad, often flattened dorso-ventrally. Only the foremost thoracic segment is fused with the head, the other 7 are free. No freely projecting shell fold.

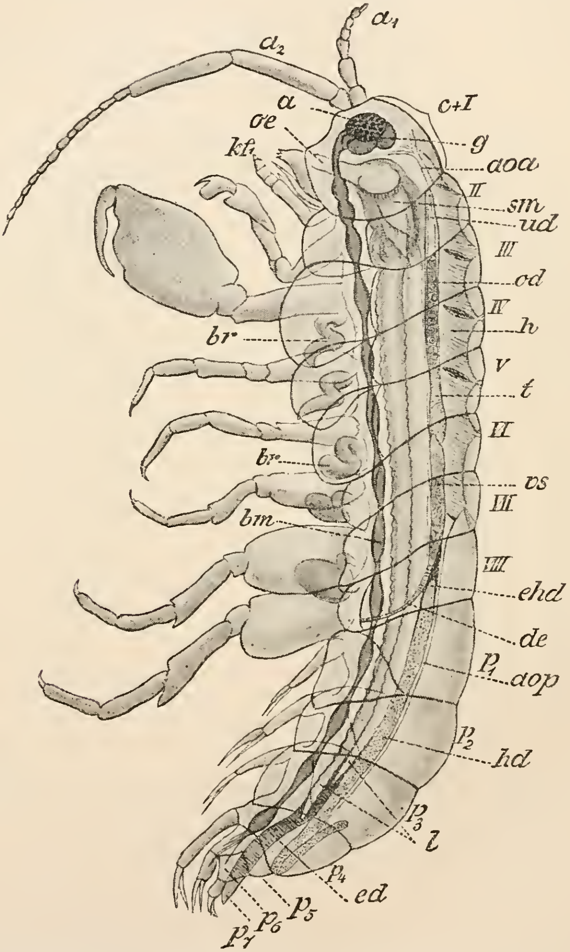

Fig. 197.—**Organisation of Orchestia cavimana**, male (after **Nebeski**). $c+I$, Head + 1st thoracic segment; *II-VIII*, free thoracic segments with their extremities; p_1-p_7, abdominal segments; a_1, anterior, a_2, posterior antenna; *a*, eye; *œ*, œsophagus; *kf*, foot-jaw; *br*, gills; *lm*, ventral chord; *g*, brain; *aoa*, anterior aorta; *sm*, œsophagal stomach; *ud*, unpaired intestinal cæcum; *od*, egg-bearing part of the germ glands; *h*, heart; *t*, testis; *vs*, vesica seminalis; *de*, ductus ejaculatorius; *ehd*, entrance of the urinary gland (*hd*) into the intestine; *aop*, posterior aorta; *l*, ends of the hepatic tubes; *ed*, posterior end of the intestine.

The 2 pairs of maxillæ without feelers. Abdomen generally short, often reduced, mostly consisting of 6 segments with biramose lamellated pleopoda, whose branches, especially the endopodites, function as gills. Heart in the abdomen, generally stretches as far as into the posterior thoracic region, with 1 to 2 pairs of ostia.

Cymothoidea, hermaphrodite, some living free, others parasitic on fishes: *Cymothoa*, *Aniloera*, *Cirolana*, *Neroeila*, *Aega*, almost exclusively marine forms. *Sphæromidæ*, free living, mostly marine, *Sphæroma*. *Pranizidæ*, free in the sea, the 3 anterior thoracic segments fused with the head. *Aneeidæ*, female parasitic, male free-living, *Anceus*. *Idotheidæ*, free living, principally marine, *Idothea*. *Asellidæ*: *Asellus*, fresh water. *Oniscidæ*, on land: *Oniscus*, *Porcellio*. The divisions of the *Bopyridæ*

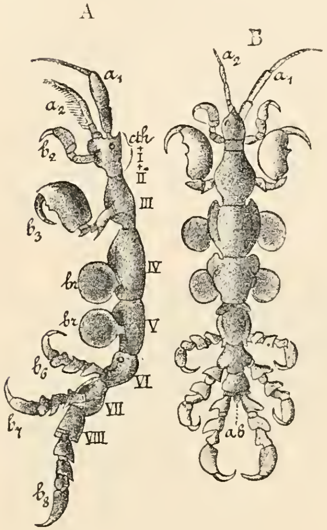

FIG. 198.—**Caprella acutifrons**, after **P. Mayer.** *A*, male from the side; *B*, from the back. a_1, Anterior, a_2, posterior antenna; b_2, b_3, b_6, b_7, b_8, 2d to 8th thoracic feet, the 2d moved on to the throat; *br*, gills in the place of the 4th and 5th thoracic feet; *cth*+*I*+*II*; cephalo-thorax=head +1st and 2d thoracic segments; *III-VIII*, free thoracic segments; *ab*, truncated abdomen.

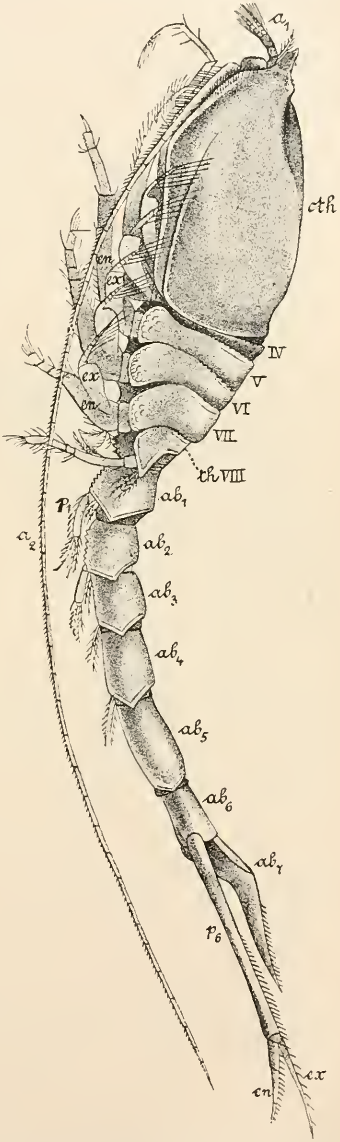

FIG. 199.—**Diastylis stygia**, male (after **G. O. Sars**). a_1, Anterior, a_2, posterior antenna; *cth*, cephalo-thoracic shield; *IV-VIII*, free thoracic segments; ab_1-ab_7, abdominal segments; p_1, 1st pleopod; p_6, 6th pleopod; *en*, endopodite; *ex*, exopodite.

and *Cryptoniscidæ* contain parasites which are chiefly hermaphrodite with dwarf males. Body of the female deformed. *Bopyrus* (sexes separate), *Gyge*, *Entoniscus*, *Cryptoniscus*.

Order 3. **Amphipoda.**

Body laterally compressed. In the typical *Amphipoda* only the foremost thoracic segment is fused with the head, in the *Caprellidæ* and *Cyamidæ* the two anterior segments. The gills are found on the thoracic feet as pouch-shaped epipodial appendages. Where the abdomen is well developed it carries 6 pairs of biramose feet, of which the 3 anterior, generally more strongly developed, serve as swimming feet, the posterior, directed backwards and often stylet-shaped, as springing feet. Heart in the thorax with 3, seldom 1 or 2 pairs of ostia.

Sub-Order 1. **Crevettina.**

Head and eyes small. Foot-jaws with their limb-like feelers form a large under lip. Marine forms: *Corophium*, *Talitrus*, *Orchestia* (Fig. 197), *Lysianassa*. In fresh water, *Gammarus*.

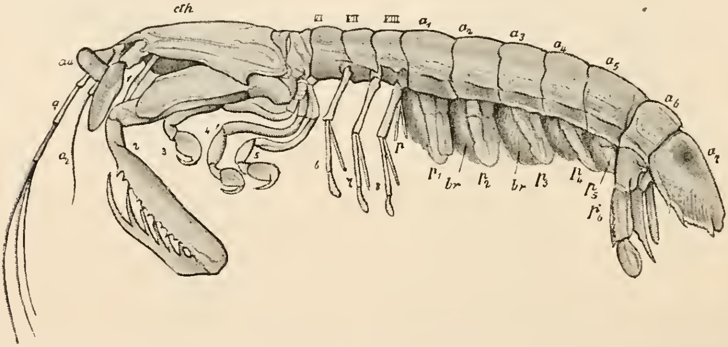

FIG. 200.—**Squilla**, from the side. *cth*, Cephalo-thoracic shield; *VI*, *VII*, *VIII*, the 3 posterior free thoracic segments; a_1-a_7, the segments of the abdomen; a_7, the telson; *au*, eye; a_1, anterior; a_2, posterior antenna; 1-8, the 8 thoracic feet, of which 1 is the 1st foot-jaw and 2 is the 2d foot-jaw or the large seizing foot, 3, 4, 5 are the posterior seizing feet, 1-5 are called oral feet, 6, 7, 8, the 3 biramose rowing feet of the 3 posterior thoracic segments; *p*, penis; p_1-p_6, the pleopoda (swimming feet), p_6 forming with the telson the powerful caudal fin; *br*, the branchial tufts on the exopodites of the pleopoda.

Sub-Order 2. **Hyperina.**

Head and eyes large, the latter often divided into frontal and lateral eyes. Foot jaws form a small lower lip without feelers. Marine forms: *Hyperia* (eyes not divided), *Phronima*, *Platyscelus*, *Oxycephalus*.

Sub-Order 3. **Lämodipoda.**

Abdomen truncated. The 2 anterior thoracic segments fused with the head. Gills on the 2d and 3d free thoracic segments; limbs on these segments often reduced. Marine forms: *Caprellidæ*, body very slender and thin—*Caprella* (Fig. 198), *Proto*, *Protella*; *Cyamidæ*, body broad and flat, parasitic on the skin of whales, *Cyamus*.

Legion III. **Thoracostraca (Podophthalmata).**

With a shell fold which covers a larger or smaller part of the thorax and fuses with the dorsal integument of all or some of the anterior thoracic segments, always, however, projecting freely laterally and covering the respiratory cavity as branchiostegite. A varying number of anterior thoracic segments, or all the thoracic segments fused, at least dorsally, with the head to form an incomplete or a complete cephalo-thorax. The 2 lateral eyes stalked (except in the *Cumacea*).

Order 1. **Cumacea.**

Shell (cephalo-thoracic shield) small, leaving the 5 posterior free thoracic segments uncovered. Eyes sessile, close together or fused into one, weakly developed, occasionally wanting. Two pairs of foot-jaws. The first with a very large epipodite carrying a gill. Of the 6 subsequent pairs of thoracic feet, the first 2 always carry exopodites as well as endopodites, the next 3 also often have exopodites, but this is never the case with the last. Abdomen long and slender. In the female the pleopoda are wanting, excepting the last pair. Marine form, *Diastylis* (Fig. 199).

Order 2. **Stomatopoda.**

Cephalo-thoracic shield rather small, not covering the 3 distinct posterior thoracic segments. Body elongated, flattened dorso-ventrally. Abdomen large and strong. The 5 anterior pairs of thoracic feet (oral feet because moved to near the mouth), are holding or seizing feet with epipodial lamellæ, but without exopodites. The 3 posterior pairs of thoracic feet are biramose limbs without epipodial appendages. The 5 anterior pairs of pleopoda are strong lamellated swimming feet, whose exopodites carry branchial tufts. The 6th pair of pleopoda forms with the telson a powerful caudal fin. The heart with several pairs of ostia is elongated into a dorsal vessel running through the abdomen. Ovaries and testes in the abdomen. Marine, *Squilla* (Fig. 200).

Order 3. **Schizopoda.**

Cephalo-thoracic shield well developed, like a delicate integument covering the whole thorax. The dorsal integument of the last 5 thoracic segments, or of the last thoracic segment, is not united with it. The 8 pairs of thoracic feet are formed pretty much alike, and are biramose (with exopodite and endopodite); we can, however, generally describe the 2 anterior pairs of thoracic feet as foot-jaws, as they may have masticatory ridges. Abdomen strong, slender. Pleopoda very small in the female, strongly developed in the male. The last pair of pleopoda, well developed in both sexes, forms with the telson a rowing or swimming fin. Marine.

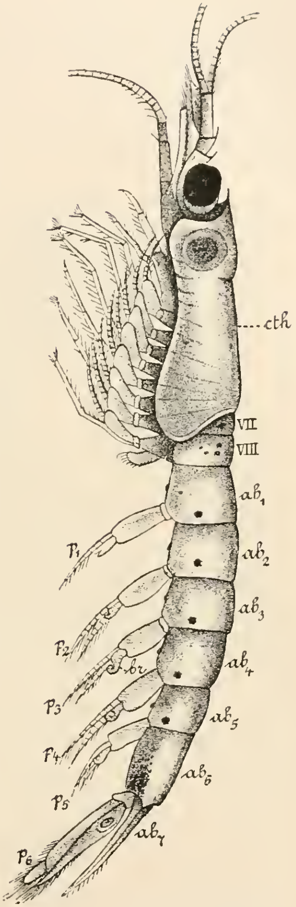

Fig. 201.—**Siriella Thompsonii**, male (after **G. O. Sars**). *cth*, Cephalo-thoracic shield; *VII*, *VIII*, 7th and 8th thoracic segments; ab_1-ab_7, abdominal segments; p_1-p_6, pleopoda; *br*, gills.

Family 1. **Mysidæ.**

Thoracic feet without gills, the first pair with large vibratile epipodial lamellæ. Last 5 thoracic segments free under the dorsal shield. Auditory organs in the endopodites of the 6th pair of pleopoda. *Mysis*, *Siriella* (Fig. 201); in the male, gills on the pleopoda.

Family 2. **Lophogastridæ.**

With branchial tufts on the thoracic feet; last 5 thoracic segments as in the *Mysidæ*. *Lophogaster.*

Family 3. **Euphausidæ.**

With branchial tufts on the thoracic feet. Only the last thoracic segment is free under the dorsal shield. *Euphausia*, *Thysanopoda.*

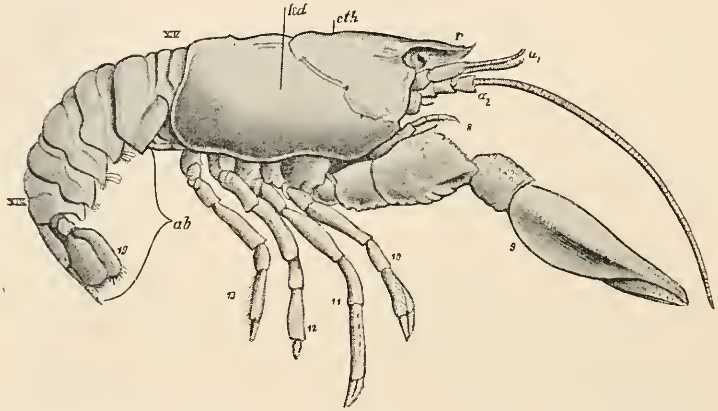

Fig. 202.—**Astacus fluviatilis,** male, from the side. *cth*, Cephalo-thorax; *ab*, abdomen; *kd*, branchiostegite of the cephalo-thoracic shield; *XIV*, first, *XIX*, last but one abdominal segment; *r*, rostrum; a_1-a_2, 1st and 2d antennæ; 8, third foot-jaw or maxillipede; 9, chelate foot; 10, 11, 12, 13, the 4 remaining ambulatory feet; 19, the pleopoda of the 6th abdominal segment, which with the telson or terminal segment form the caudal fin (after **Huxley**).

Order 4. **Decapoda.**

Cephalo-thoracic shield large, generally firm and hard, calcareous, covering the whole thorax, and fused with the dorsal integument of all the thoracic segments. Exopodite of the 2d maxilla forms a vibratile plate which regulates the streaming of the water in the branchial cavity. The 3 anterior pairs of thoracic feet developed as foot-jaws or maxillipedes, the 5 posterior, some of which are armed with pincers, as ambulatory feet (hence "Decapoda"). In the adult these ambulatory feet consist only of protopodite and endopodite, while the exopodite is almost always wanting; auditory organs on the basal joints of the inner antennæ. Development direct or with metamorphosis. In the latter case a *Nauplius* is seldom (*Carididæ*) hatched from the egg; the larvæ hatched are generally further developed, and pass through a *Zoœa* and a *Mysis* stage. This order is very rich in forms.

Sub-Order 1. **Macrura.**

With well-developed abdomen, which is at least as long as the cephalo-thorax. Mostly with the full number of pleopoda, the last pair of which forms with the telson a powerful caudal fin. *Carididæ* (shrimps): *Penæus, Palæmon, Crangon, Pontonia, Alpheus, Sergestes, Lucifer*, in the sea. *Astacidæ: Astacus fluviatilis* (Crayfish, freshwater; Figs. 202 and 203), *Homarus* (lobster), *Nephrops, Callianassa, Gebia*, marine. *Palinuridæ: Palinurus, Scyllarus*, in the sea.

Sub-Order 2. **Anomura** (this division cannot be sharply demarcated).

Abdomen moderately large; caudal fin mostly reduced. The hindermost pair of ambulatory feet or the two posterior pairs reduced. Third foot-jaws limb-like. *Paguridæ*, hermit-crabs, marine, in empty shells of *Molluscs*; abdomen soft skinned, asymmetrical, with degenerated pleopoda serving as clinging organs. *Pagurus, Eupa-*

gurus, *Birgus* (in holes in the ground). *Hippidæ*, marine, live in mud; posterior body hard skinned, the half of it bent forwards. The *Galateidæ* (*Galatea*) approach the *Macrura*, and the *Porcellanidæ* (*Porcellana*) the *Brachyura*.

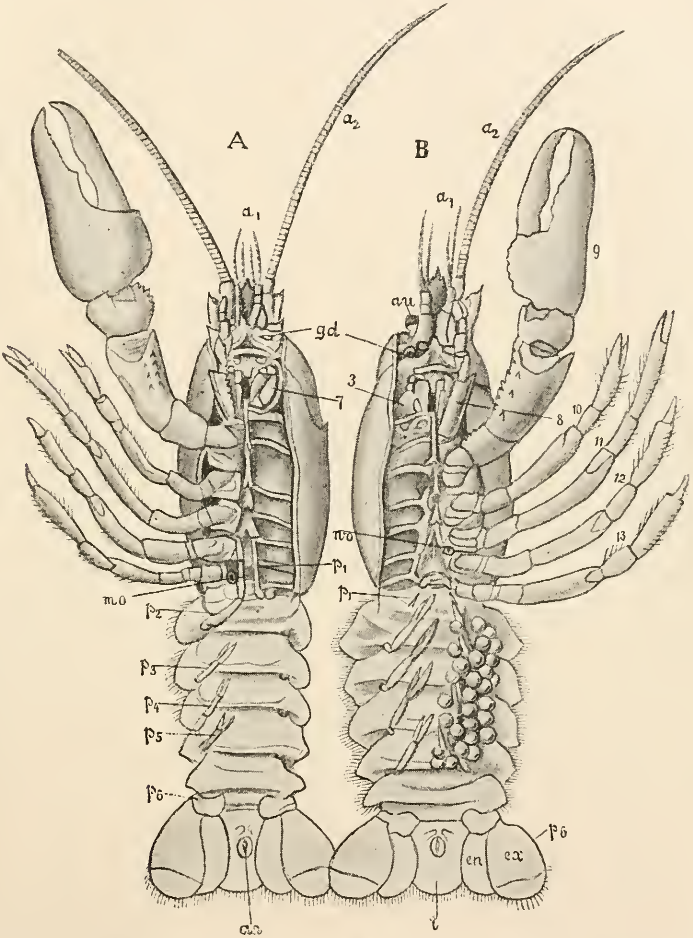

FIG. 203.—**Astacus fluviatilis**, from the ventral side. *A*, male; *B*, female. In the male the 8th to 13th and 15th to 18th extremities of the left side of the body are removed; in the female the 2d and 4th to 13th of the right side. 3-13, Extremities of the cephalo-thorax; a_1-a_2, anterior and posterior antennæ; *gd*, aperture of the antennal glands; *wo*, female; *mo*, male genital aperture; p_1-p_6, pleopoda; *en*, endopodite; *ex*, exopodite of the last pair of pleopoda; *an*, anus; *t*, telson (after **Huxley**).

Sub-Order 3. **Brachyura (Crabs)**.

Body flattened. Posterior body without anal fin, reduced, bent round on the ventral side of the cephalo-thorax. In the male only the two anterior pairs of pleopoda are usually retained. *Notopoda*, in the sea: *Dromia*, *Dorippe*, *Lithodes*. *Oxystomata*, round crabs: *Calappa*, *Ilia*, in the sea. *Oxyrhyncha*, triangular crabs: *Maja*, *Pisa*, *Stenorhynchus*, *Inachus*, *Lambrus*, in the sea. *Cyclometopa*: *Telphusa* (fresh water), *Cancer, Xantho, Pilumnus, Eriphia, Portunus, Carcinus,* in the sea. *Catometopa,* square crabs: *Pinnoteres, Ocypoda, Grapsus,* in the sea, *Gecarcinus,* land-crabs.

I. Outer Organisation.[1]

Nowhere in the animal kingdom does the study of outer organisation afford so much of interest to the comparative anatomist as among the *Arthropoda.* The more or less hard chitinous envelope which outwardly covers the body and all its limbs not only serves as a protection to the inner organs, but also represents the skeleton to which the musculature is attached inside. Herein lies the chief cause of the specially close relations between inner and outer organisation in the *Arthropoda.*

In describing the outer organisation of the Crustacea we must take into consideration in turn (1) the body, (2) the extremities, and (3) the gills.

A. The Body.

We denote by this term the whole animal minus its appendages. It consists of a number of consecutive joints (segments, metameres, somites).

The consecutive segments are movably articulated together. The chitinous integument investing the whole animal remains thin and soft between adjoining segments and forms intersegmental membranes.

The study of comparative anatomy leads us to suppose that originally each segment except the last possessed a pair of limbs, so that the number of the limbs answered to the number of somites. We may diagrammatically represent the Crustacean body as consisting of a great number of segments, as is the case in the *Annulata.* The most anterior or head segment is distinguished by the possession of the eyes, the mouth, the brain, and a pair of extremities, which as feelers differ from all the other extremities; these latter resemble one another more or less closely; their special modifications will be described below. The anus lies in the hindermost segment, which has no limbs.

This diagrammatic representation of the segmentation of the Crustacean body is not exactly realised in any known Crustacean. In fact we everywhere find important deviations even in those which are considered to stand nearest the racial form.

We find first of all that in all Crustaceans the anterior region of the body is outwardly unsegmented, and, in opposition to our typical Crustacean, carries not one but **five pairs** of limbs. We are inclined to assume that this region has arisen by the fusing of a head segment with the four following segments, this assumption being supported by similar phenomena observed in various groups of Crustacea.

Thus the most anterior unsegmented region of the body, which

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[1] In order to emphasise the great morphological significance of the *Leptostracan* body, *Nebalia* is treated of in this division apart from the other *Malacostraca.*

carries 5 pairs of limbs, is known as the **head**, as apart from the **trunk**, *i.e.* the whole of the remaining segmented body.

The trunk of the *Entomostraca* consists of a **very varying number of segments**, which in different regions may differ greatly in many respects (heteronomous segmentation of the trunk). The trunk of the *Malacostraca* always consists of **a constant number of segments, viz. fifteen.** It always falls into two sharply distinguished regions, each with a constant number of segments, an **anterior thoracic region, consisting of 8 segments, and a posterior abdominal region (pleon) containing 7.**

The trunk of the *Leptostraca* (*Nebalia*), which in classification takes a place half way between the conjectural racial forms of the *Entomostraca* and those of the *Malacostraca*, though really more nearly related to the latter, also consists of (1) a **thorax of 8 segments** (which exactly answers to the thorax of the *Malacostraca*), and (2) an **abdomen of 8 segments.**

There is nothing to hinder us from assuming that in all Crustaceans the segments which are numbered alike correspond, for instance the 2d, 6th, and 10th trunk segments of an *Isopod* with the 2d, 6th, and 10th trunk segments of a *Phyllopod.*

As in the *Annulata*, so also in the *Crustacea*, the somites become differentiated ontogenetically in regular order from before backward, so that the youngest segment always appears posteriorly in front of the anal segment, this latter containing the formative material for the segments which are to appear in the course of development. There is therefore also nothing to hinder us from assuming that the anal segments of all Crustaceans correspond, of however many segments the trunk may consist.

Apart from the above-mentioned conjectural fusing of the 5 most anterior primary segments to form the unsegmented head of the Crustacean, the metamerism of the trunk, either of the whole trunk or of single regions of it, may be obscured or even entirely obliterated. Such obscuration or obliteration may in almost all cases be referred to one or more of the following causes:—

1. To the appearance of a shell or carapace as a fold arising from the dorsal side of the posterior head region, which spreads in varying form more or less far back over the body, covering or enveloping the same. Such a carapace serves for the greater protection of the body, and also is often closely connected with the respiratory functions. Since a shield-like integumental fold is formed in an essentially similar manner in the most various groups of Crustaceans and their larval forms, we have reason for assuming that it represents a primitive peculiarity of the Crustacean body. By the concrescence of the shield or shell with the integument of all or a portion of the trunk segments, the outer metamerism of the body is obliterated to a greater or less extent.

2. To the fusing of the anterior trunk segments with the head in

order to associate the limbs of these segments with the limbs already present on the head in the work of taking in food.

3. To the fact that the extremities in certain regions of the body give up their various functions (which are almost always associated with movement), and consequently become reduced or quite disappear. The independence of the segments which carry such reduced limbs is then more or less lost, that is if the said region does not in any other way gain a locomotory significance.

4. To the loss of the capacity for active locomotion by adaptation to the parasitic mode of life; this adaptation leads to the reduction of the extremities and the more or less complete obliteration of the metamerism of the whole body.

Having prefaced these remarks by way of elucidation, we proceed to sketch in outline the external morphology of the body in the principal groups of the Crustacea.

I. Entomostraca.

Phyllopoda.—In *Branchipus* (Fig. 191) the trunk appears distinctly segmented, and falls into an anterior and a posterior region which are called thorax and abdomen respectively. The 11 segments of the thorax carry 11 pairs of limbs; the abdomen, which consists of many segments, is limbless, and ends in 2 so-called furcal plates. A shield or shell fold is wanting. The head carries 2 stalked movable lateral eyes. In *Apus* the body is covered for the most part with a flat shell fold, not fusing with any of the anterior thoracic segments. The trunk consists of a large number of segments, the most posterior being limbless. In the *Estheridæ* the body is quite enveloped in a bivalve shell, which also covers the limbs laterally. The trunk consists of numerous segments. The posterior segments, which have no limbs, form a short abdomen, as opposed to the thorax of many segments. A bivalve shell also occurs in the *Cladocera*; here also the shell covers the limbs. In this case, however, it leaves the well-marked head uncovered. In the trunk the segmentation is obliterated. It carries 4 to 6 pairs of limbs, and ends in an unsegmented abdomen devoid of appendages.

Ostracoda.—The body is entirely enveloped in a bivalve shell, into which also the limbs can be withdrawn. The whole body is unsegmented. Besides the 5 pairs of cephalic limbs there are only 2 other pairs, so that the trunk appears extraordinarily reduced.

Copepoda.—A shield or shell-fold is here in all cases wanting. The manner of life of the animal leads to very various modifications of the body. In most free-living *gnathostomatous Copepoda* the trunk is distinctly segmented (Fig. 194). We can distinguish in it a thorax of 5 segments carrying appendages, and an abdominal region also of 5 segments, but without appendages. The most anterior thoracic segment is fused with the head to form an incomplete cephalo-thorax. The abdomen ends in 2 spine- or bristle-carrying processes which diverge in a fork (furcal processes). In certain female *Notodelphydæ* each of the 4 free limb-carrying segments has on the dorsal side an unpaired wing-like fold.

In the *siphonostomatous Copepoda* and *Argulidæ* we observe an advancing obliteration of the segmentation of the trunk and a reduction of the abdomen as the parasitic manner of life becomes more marked. The body, in a few of the parasitic *Siphonostomata* (*Lernæidæ*, *Lernæopodidæ*, *Chondracanthidæ*), assumes such various and extraordinary forms that no similarity to other Crustaceans can be recognised.

Cirripedia.—These, in an adult condition, are attached or parasitic animals.

The similarity to Crustaceans in outer appearance is only retained in the free-moving young stages, while in the adult forms this similarity is hardly recognisable. If we first consider the attached *Lepadidæ* (Figs. 204 and 205), we can distinguish outwardly an attached peduncle and a flattened shell, with a slit-like aperture on one side carried by the peduncle; this shell consists (in *Lepas*) of 5 calcareous plates. If we open the shell we find within it the indistinctly segmented body, which carries long tendril-like feet (Fig. 205) and is attached to the shell near the point of insertion of the peduncle. The tendril-like feet are found on that side of the body turned away from the peduncle. A thorough ontogenetic and anatomical study of *Lepas* has now proved that these parts are to be described as follows. The peduncle corresponds with the prolonged anterior portion of the Crustacean head, which has become attached, and which still carries on its anterior end the much-simplified anterior antennæ in the shape of very small adhering organs (Fig. 205, a^1). The shell is an integumental fold arising from the posterior head region. It answers to the shell or shield of other Crustaceans. In the chitinous integument of this fold in the *Cirrepedia*, however, there arise by calcification the various calcareous plates, to which we shall again refer. The part of the indistinctly segmented body enclosed by the shell which lies anteriorly next the peduncle corresponds with the posterior head region, while the remainder, which carries the tendril-like feet, answers to the thorax of an *Entomostracan*; and in addition to these parts there is a small truncated portion representing a reduced abdomen. The abdomen carries a long

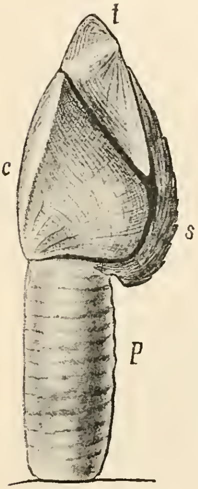

FIG. 204.—**Lepas anatifera after Darwin.** Seen somewhat diagonally from the carinal side. *c*, Carina; *t*, tergum; *s*, scutum; *p*, peduncle.

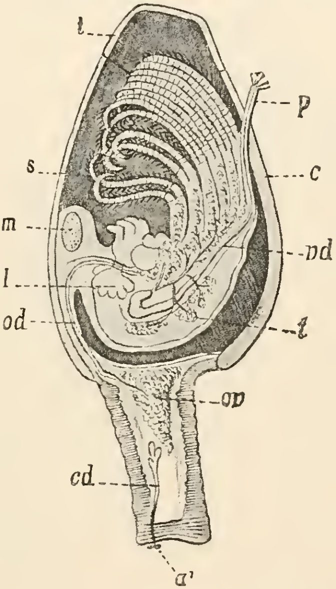

FIG. 205.—**Organisation of Lepas, after Claus.** The right half of the fold of the body integument with its calcareous plates removed. *t*, Tergum; *s*, scutum; *c*, carina; *m*, closing muscle of the scuta; *l*, liver; *od*, oviduct; *ov*, ovarium; *cd*, cement glands; a^1, anterior (adhering) antenna; *t*, testes; *vd*, vas deferens; *p*, cirrus-shaped penis.

appendage, the male copulatory organ (p). This is bent forwards on the ventral side, and lies between the tendril-like feet. The thorax consists of 6 indistinct segments.

In *Lepas* we find, as already mentioned, 5 shell pieces or calcareous plates of the integumental fold (mantle), one unpaired and four paired. The unpaired piece (c) lies on the dorsal side and is called the **carina.** The paired pieces (s, t) lie to the right and left; the anterior are called the **scuta,** the posterior the **terga.** The cleft in the mantle or shell lies posteriorly and ventrally. Accessory shell pieces, unpaired as well as paired, may be found in addition to the above.

In the *Balanidæ* (Figs. 206 and 207), in contradistinction to the *Lepadidæ*, the attached anterior portion of the body is not prolonged like a stalk. The mantle forms by calcification several strongly united shell pieces which surround the body like a rampart, to which the scuta and terga form a kind of movable lid.

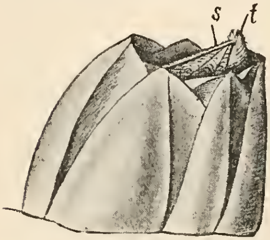

Fig. 206.—**Case of Balanus Hameri**, from the side (after **Darwin**). *s*, Scutum; *t*, tergum.

In the *Abdominalia*, which live in the shells of *Cirripedes* and *Molluscs*, the number of the thoracic segments is reduced, and the body is enclosed in a flask-shaped mantle which does not calcify, as the shell of the host affords sufficient protection. The *Apoda* live parasitically, like the *Abdominalia*, in the mantle of other *Cirripedes.* The mantle fold does not here attain development. The body of 11 segments assumes the form of a fly-maggot, having lost the tendril-like feet. The Crustacean body suffers the greatest degree of degradation in the *Rhizocephala*, which live parasitically on the abdomen of *Decapoda*. In this case we find only an unsegmented sac (Fig. 208), entirely devoid of limbs, containing the viscera (testes, germarium, cement glands, ganglion), and itself enveloped in another outer sac-like membrane. This outer membrane which surrounds the brood cavity has been considered, erroneously it appears, as the mantle. An aperture in it leading to the exterior is termed the cloaca. The body is attached to that of the host by means of a short peduncle. On this stalk of attachment arise long branched filaments which penetrate the body of the host and conduct nourishment from its body to the parasite in a manner similar to that in which the roots of a plant convey nourishment out of the earth.

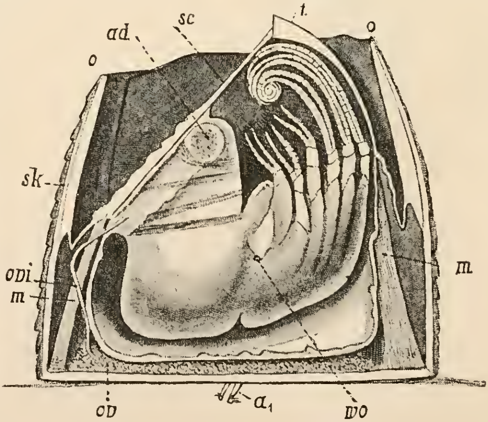

Fig. 207.—**Balanus tintinabulum**, after removal of the right half of the calcareous ring. *o-o*, Edges of the aperture of the ring *sk*; *sc*, scutum; *t*, tergum; a_1, anterior (adhering) antennæ; *ov*, ovarium; *ovi*, oviduct; *wo*, female genital aperture; *m*, muscles for moving the scuta and terga; *ad*, musculus adductor scutorum (after **Darwin**).

The *Rhizocephala* are classed as a special order of the Entomostraca (*Kentrogonidæ*). It is from their ontogeny alone that we learn that they are Crustaceans at all and nearly related to the *Cirripedes*. In the course of their development they pass through stages similar to those of the *Cirripedes*, free-swimming and provided with Crustacean limbs.

In many *Cirripedes* there are by the side of the ordinary hermaphrodite individuals, **complementary dwarf males** differently formed, which will be referred to later.

II. Leptostraca.

In the segmentation of the trunk, the **Leptostraca** (Fig. 196) take an intermediate place between *Entomostraca* (especially *Phyllopoda*) and *Malacostraca*. As in the latter, the **thorax** which follows the head consists of **eight** limb-bearing segments, here very short but distinct. After the thorax comes the well-developed powerful **abdomen** consisting of 8 segments, *i.e.* of one more segment than the typical *Malacostracan* abdomen of 7 segments. The abdomen is further followed by the 2 so-called furcal processes. Only the 6 anterior abdominal segments carry limbs. The 6 limb-bearing abdominal segments must correspond with the 6 anterior abdominal segments of the *Malacostraca*. On the dorsal side of the posterior head region an integumental fold arises, which in the shape of a delicate laterally compressed bivalve shell covers the thorax and the 4 anterior abdominal segments, but does not fuse with them. This shell also, like the corresponding shells of many *Entomostraca*, covers a large part of the limbs (Fig. 196). The head carries on each side a stalked compound (facet) eye.

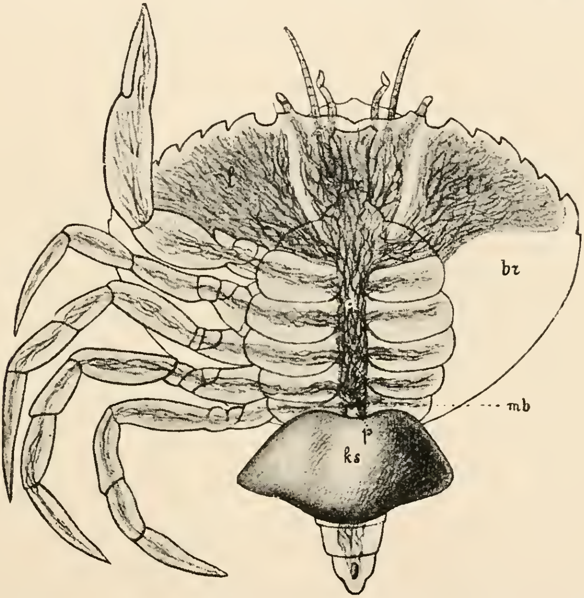

Fig. 208.—**Sacculina carcini** *in situ* on the host (after a somewhat diagrammatic original drawing by Professor **Delage**, Paris). *br*, Branchial region ; *l*, hepatic region ; *d*, intestinal region of the host (*Carcinus*) ; *ks*, body ; *p*, peduncle of the *Sacculina* ; *mb*, basilar membrane out of which the roots of the parasite proceed.

III. Malacostraca.

There are two peculiarities specially to be noticed in the segmentation of the body of this large division.

First.—Apart from the unsegmented head, which carries the typical number of limbs (5 pairs), the trunk always consists of two regions, the thorax and the abdomen. **They both have a constant number of segments, the former 8, the latter 7.** Each of these, with the exception of the last abdominal segment, is typically provided with a pair of limbs. The limbs of the 6th abdominal segment often form with the 7th or terminal segment a **caudal** or **rowing fin.**

Second.—The segments of the thorax show a tendency to fuse with the head. Either the first segment or several anterior segments fuse with the head to form an incomplete cephalo-thorax, or all the thoracic segments unite, and with the head form a complete cephalo-thorax, which then shows external signs of the original segmentation only on the ventral side.

Arthrostraca (*Amphipoda, Isopoda,* and *Anisopoda*).—The foremost thoracic segment is fused with the head. Seven thoracic segments thus remain free (Fig. 197). The eyes are sessile (*Edriophthalmata*). In the *Amphipoda* the body is laterally compressed. The *Caprellidæ* (*Amphipoda*) (Fig. 198) present many important peculiarities. The 2d thoracic segment is also fused with the head, so that only 6 thoracic segments are left free. The abdomen is reduced to a stump. The body of the *Isopoda* is dorso-ventrally flattened. In a few *Isopoda* even more thoracic segments become fused with the head. Thus in the *Pranizidæ* (*Anceus*) the 3d thoracic segment is comprised in the incomplete cephalo-thorax. A shell-fold, though as a rule wanting in the *Arthrostraea,* is found in the *Anisopoda,* although slightly developed. In these latter the 2 anterior thoracic segments are fused with the head. In parasitic *Isopoda* the metamerism of the body may be indistinct and obliterated, and the body itself become asymmetrical.

Thoracostraca.—A shell-fold is everywhere developed, proceeding from the head; this, as a cephalo-thoracic shield, fuses dorsally with the integument of a larger or smaller number of thoracic segments, but, unlike the corresponding integumental fold of the *Entomostraca* and *Leptostraca,* it only covers the thorax, never the extremities and the abdomen. On the head (except in the *Cumacea*) there are 2 stalked facet-eyes (*Podophthalmata*).

I. **Cumacea** (Fig. 199).—The cephalo-thoracic shield remains small; the cephalo-thorax includes the 3 or 4 anterior thoracic segments; the 4 or 5 posterior ones remain free and distinct from one another. The abdomen is long and slender, and distinctly segmented. In the female it carries no feet; the 6th segment only has on each side a pair of biramose stylet-like limbs. The two eyes (when present) are fused into one unpaired eye, or are very close to one another.

II. **Stomatopoda** (Fig. 200).—The cephalo-thoracic shield is fused with the most anterior thoracic segments and covers the thorax with the exception of its 3 posterior segments which remain free. The broad abdomen is very strongly developed, and longer than the cephalo-thorax. The strongly developed lamellate limbs of the 6th abdominal segment form with the limbless terminal segment (telson) an imposing caudal plate (swimming fin).

III. **Schizopoda** (Fig. 201).—The soft-skinned cephalo-thoracic shield generally covers the whole thorax, and fuses with the dorsal integument of a varying number of its segments. One or more segments, however, always remain unfused. In the *Mysidæ* the last 5, in the *Euphausidæ* only the last thoracic segment, remains unfused. Abdomen elongated and strong, ending in a swimming fin.

IV. **Decapoda** (Figs. 202 and 203).—The strong cephalo-thoracic shield, which occasionally becomes through calcification of its chitinous integument as hard as stone, generally covers the whole thorax, and is also fused with the dorsal integument of the thoracic segments. A complete cephalo-thorax is thus formed. The pleura of the cephalo-thorax, which project freely downwards at the sides, cover the two respiratory cavities, and are called **gill covers** or **branchiostegites.** The form and dimensions of the abdomen are very various. In the *Macrura* the abdomen is strongly developed. In the good swimmers (*e.g. Carididæ*) the whole body is laterally compressed, while in those *Macrura* which generally crawl, or only swim occasionally and not well (*Astacidæ, Palinuridæ, Galatheidæ, Thalassinidæ*), it is more or less flattened dorso-ventrally. The abdomen always ends in a strong caudal fin (terminal segment with the limbs of the 6th abdominal segment). In the *Paguridæ* (hermit crabs), which live in empty mollusc shells, the last thoracic segment is separate and not fused with the cephalo-thorax; the abdomen, which is covered by the mollusc shell, is soft-skinned, the caudal fin reduced and bent round forwards. The *Brachyura* are distinguished by the fact that the abdomen is reduced to a small plate, which is bent forward on the ventral side of the cephalo-thorax, so that in looking at these Crustaceans from above only the cephalo-thorax can be seen. The abdominal limbs are reduced in number and form. The caudal fin is atrophied.

B. The Extremities.

According to the scheme sketched above of the segmentation of the Crustacean body, every segment except the last is provided with a pair of jointed extremities which articulate ventrally and laterally with the body. In order to complete the scheme with reference to the limbs, we must distinguish between the limbs of the most anterior segment and the rest. The first pair are not biramose, but consist of a single row of consecutive joints. All the other pairs are biramose. In such a biramose limb we distinguish 3 parts; the **shaft** or **stem (protopodite)**, the **inner branch (endopodite)**, and the outer branch **(exopodite)**. The shaft consists of 2 joints, a proximal joint articulating with the body, and a distal joint carrying the 2 branches. The 2 branches themselves are again jointed; the inner branch is turned towards the median plane of the body, the outer branch away from it.

The limbs of the Crustacea undergo the most various transformations according to the special functions they perform. They can always, however, be referred back to the typical forms, the first pair to the unbranched (uniramose) form, and all the rest to the biramose form.

This typical arrangement is found in the **Nauplius**, which is the youngest Crustacean larva, universally found among the *Entomostraca* and occurring also in a few *Malacostraca*. The *Nauplius*, which hatches from the egg, is unsegmented, and always possesses 3 pairs of appendages, the first uniramose, the second and third biramose.

The limbs of the *Nauplius* become in all cases the three anterior pairs of limbs of the adult animal. The most anterior pair becomes the **anterior antennæ**, the second the **posterior antennæ**, and the third the **mandibles** of the adult. In the course of the metamorphoses of the *Nauplius*, which are accompanied by numerous moults, the larval body elongates into the adult animal, and behind the appendages of the *Nauplius* new appendages bud from the body as a rule in order from before backward. All these newly formed appendages originate as biramose limbs; the biramose character may, however, be more or less indistinct, or may even be lost as the limbs develop into the corresponding limbs of the adult.

In attempting a comparative review of the limbs throughout the class of the Crustacea, only the most important points can be touched upon. The setæ with which they are often provided, and whose form and arrangement are extremely important for classification, cannot here be taken into consideration.

1. The Limbs of the Head.

In all the Crustacea the head carries 5 pairs of limbs, which are called, following the order from before backward, the anterior antennæ, posterior antennæ, mandibles, anterior maxillæ, and posterior maxillæ. The 3 anterior pairs correspond with the 3 pairs of limbs of the *Nauplius.*

a. The Anterior Antennæ (Antennules) (Fig. 209).

These lie in front of the mouth, and consist typically of a single row of joints. As a rule they function as organs of touch, but usually also carry the olfactory organs, and occasionally the auditory organs.

Fig. 209.—**Anterior antennæ (antennules) of various Crustaceans.** *A,* Of *Astacus* (after **Huxley**); *o,* auditory sac. *B,* Of *Munnopsis typica, Isopod* ♂ (after **Sars**). *C,* Of *Nebalia Geoffroyi* ♂ (after **Claus**), without the setæ; *pl,* plate. *D,* Of *Cyclops serrulatus* ♂ (after **Claus**); *rf,* olfactory hairs. *E,* Of *Daphnia pulex* (after **Leydig**); *rf,* olfactory hairs; *g,* ganglion.

Entomostraca.—In all *Entomostraca* the antennules consist typically of a single row of joints. In the *Phyllopoda* (Fig. 209, *E*) they are small, carry numerous olfactory hairs, and are called feelers or olfactory antennæ. In the *Ostracoda* (Fig. 193) they are strongly developed and occasionally provided with olfactory hairs, but chiefly function as locomotory organs for crawling and swimming. The anterior antennæ of the *Copepoda* are strongly developed as swimming feet in the free-swimming forms, and are longer than any of the other limbs (Fig. 194). They carry olfactory hairs, and serve in the males as organs for seizing and holding the female during copulation (Fig. 209, *D*). In the parasitic forms they are usually much shortened. The anterior antennæ of the *Cirripedia* (Figs. 205 and 207) are very small, and can no longer be called limbs. The cement glands, whose secretion serves for fastening the body to the surface it rests on, open on them. These antennæ, as well as all other limbs, are wanting in the *Rhizocephala*. In all *Cirripedes*, however, even in the *Rhizocephala*, they are well developed in the free-swimming young forms (the *Nauplius* and the so-called *Cypris*-like larva).

Leptostraca.—In *Nebalia* (Fig. 209, *C*) the antennules are well developed. They consist of a 4-jointed shaft which carries two appendages, one in the form of a plate; the other, which is slender and flagellate, has many joints and carries olfactory filaments. These two appendages can in no wise be considered as the exopodite and endopodite of a biramose limb, as these latter always arise from the 2d (distal) joint of the shaft or protopodite. The shaft, with its many-jointed flagellum, corresponds with the undivided uniramose antenna. The plate is a new formation.

Malacostraca.—Here also the anterior antennæ are well developed and provided with olfactory filaments. They usually consist of a 3- or 4-jointed shaft and 2 flagella, one of which (accessory flagellum) is a secondary production of the antennule (Fig. 209, *A*). There are sometimes 2 accessory flagella, and sometimes they are altogether wanting (*Isopoda*), and in this latter case the antennule shows its typical uniramose form (Fig. 209, *B*). The form of the *Malacostracan* antennules varies very much in details; it shows more or less considerable variations in the two sexes. That the antennules of the *Malacostraca* also were originally uniramose as opposed to all the other biramose appendages, and that the accessory flagella are new formations, is principally proved by the *Nauplius* larva which occurs in some of the *Malacostraca*; its first pair of limbs (the later antennules) being always uniramose.

b. The Posterior Antennæ (Fig. 210).

These correspond with the 2d pair of limbs of the *Nauplius*, being its first pair of biramose limbs, and often serve as feelers. They consist typically of the 2-jointed shaft or protopodite, an outer branch (exopodite) and an inner branch (endopodite). They appear in this form in many *Entomostraca.*

Entomostraca.—Among the *Phyllopoda* the posterior antennæ appear in the *Cladocera* as strong biramose rowing antennæ (Fig. 192). In *Apus* they are reduced, and in *Branchipus* transformed into pincers. Among the *Ostracoda* in the *Halocypridæ* and *Cyprinidæ* they are biramose swimming feet. The exopodite is, however, considerably reduced, and in the male supplied with seizing hooks. In the *Cyprididæ* and *Cytheridæ*, however, they are uniramose, *i.e.* without exopodite. The posterior antennæ of most *Copepoda* are clinging organs. In a few free-living forms they are typically biramose (Fig. 210, *D*), in others uniramose, consisting of several joints (Fig. 210, *C*). In the parasitic *Copepoda*, however, they appear degenerated into short simple clinging hooks (Fig. 210, *E*). The posterior antennæ are always wanting in adult *Cirripedes.*

Leptostraca (Nebalia) (Fig. 196).—The posterior antennæ consist of a 3-jointed shaft and a many-jointed flagellum, which is unusually long in the male. The exopodite is wanting.

Malacostraca.—In this division the posterior antennæ is very commonly a 5-jointed shaft and a thin (ringed) many-jointed flagellum, the 2d joint of the shaft carrying a scale (squame). This structure of the posterior antennæ is to be explained as follows. The first 2 joints of the shaft answer to the protopodite, the 3 other joints together with the flagellum to the endopodite, and the scale to the exopodite, of a typical biramose limb. This is clear from the fact that the 2d antennæ of the *Malacostracan* larvæ (*Nauplius*, *Protozoœa*) show the typical biramose structure, the exopodite (which is often still jointed) being transformed in the course of development into the squame of the antenna in the adult. The 3 distal joints of the shaft are thus only the 3 proximal joints of the endopodite enlarged.

Arthrostraca.—*Amphipoda*, the squame (exopodite) is wanting. In the female *Hyperidæ* the antennæ are rudimentary. *Isopoda*, squame wanting. In *Bopyridæ* and *Entoniscidæ* the antennæ rudimentary. *Anisopoda*, squame present in *Apseudes*.

Fig. 210.—**Second or posterior antennæ of various Crustaceans.** *A*, **Iolanthe acanthonotus**, *Isopod* (after **Beddard**). *B*, **Eulimnadia texana**, larva (after **Packard**). *C*, **Cyclops signatus** (after **Uljanin**). *D*, **Pseudocalanus elongatus** (after **Brady**). *E*, **Trebius caudatus**, parasitic *Copepod* (after **Kroyer**). *F*, **Eulimnadia Agassizii**, adult *Phyllopod* (after **Packard**). *G-I*, **Euphausia pellucida** (after **Sars**). *G*, Last *Furcilia* stage; *H*, first *Cyrtopia* stage; *I*, young *Euphausia*. *K*, **Astacus fluviatilis** (after **Huxley**); *go*, aperture of the green gland (antennal gland); *ex*, exopodite (squame); *en*, endopodite with flagellum; *I*, proximal; *II*, distal joint of the protopodite.

Thoracostraca.—*Cumacea*, antennæ without squame, in the male with unusually long flagellum, in the female rudimentary. *Stomatopoda*, with large squame. *Schizopoda*, with well-developed squame (Fig. 210, *G-I*). *Decapoda*, except the *Brachyura*, with squame (Fig. 210, *K*), the outer being the posterior antennæ.

The antennal glands which have been observed both in the *Entomostraca* and the *Malacostraca* show a constant relation to the 2d antennæ. That is to say, they always open on the basal joint of their protopodites.

c. The Mandibles (Fig. 211).

The mandibles correspond with the 3d pair of extremities (the 2d pair of biramose feet) of the *Nauplius*. They lie to the front at the side of the mouth and serve for mastication. They are originally typically biramose, but appear in various ways transformed in consequence of having undertaken the function of mastication. It is always the basal joint of the protopodite, as that lying nearest the mouth, which changes into a variously formed, hard, masticatory portion (corpus mandibulare), and is often toothed on the side turned towards the mouth; the rest of the limb is more or less degenerated.

Entomostraca.—In the *Phyllopoda* (Fig. 211, *G*) the mandible is reduced to the horny masticatory portion. The mandibles of the *Ostracoda* (*H*) have retained the typical form. The strongly developed masticatory joint is followed by a segmented "feeler," whose first joint (corresponding with the distal joint of the protopodite) may carry a little fan-like plate. This represents the exopodite, while the feeler, with the exception of its first joint, represents the endopodite. The mandibles in the free-living *Copepoda* (*E*, *F*) are toothed masticators (hence Gnathostomata) and carry feelers. The first joint of the feeler (2d joint of the protopodite) may carry a segmented exopodite. In most parasitic forms the mandibles are changed into stylet-shaped organs for sucking and piercing (Siphonostomata). Among the *Cirripedes* the mandibles are wanting in the *Rhizocephala*, and in other groups are developed as masticatory portions without feelers.

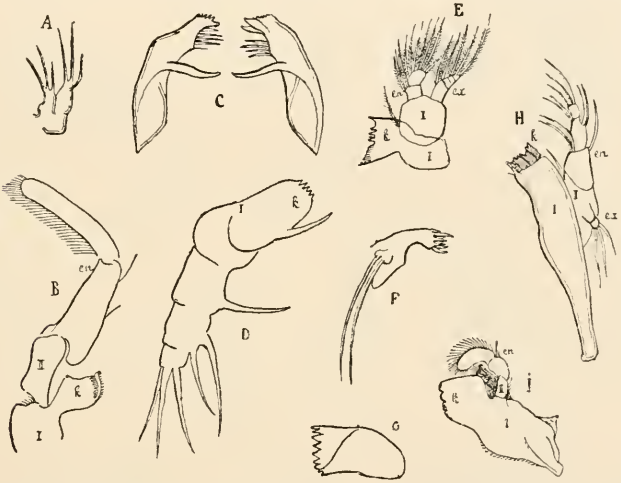

Fig. 211.—**Mandibles of various Crustaceans.** *A*, **Lucifer**, *Nauplius* (after **Brooks**). *B*, **Nebalia** ♀ (after **Claus**). *C*, **Campylaspis nodulosa**, *Cumacean* (after **Sars**). *D*, A larva of **Branchipus**, 0.8 mm. long (after **Claus**). *E*, **Notodelphys Almannii** (after **Thorell**). *F*, **Cyclops tenuicornis** (after **Claus**). *G*, **Apus lucasanus** (after **Packard**). *H*, **Xestoleberis aurantia**, *Cytherid Ostracod* (after **Dahl**). *I*, **Astacus fluviatilis** (after **Huxley**); *I*, proximal, *II*, distal joint of the protopodite; *ex*, exopodite; *en*, endopodite (feeler); *k*, masticatory part or ridge.

Leptostraca (*B*) and **Malacostraca** (*A*, *C*, *I*).—The exopodite is everywhere wanting; it is only present in the *Nauplius* stage of a few *Malacostraca*. The mandible consists of the basal masticatory or cutting joint, and a frequently 3-jointed feeler, whose first joint belongs to the protopodite, while the last two represent the joints of the endopodite. The feeler may here and there be wanting; it is entirely wanting in the *Cumacea* (*C*).

We see from the above review that among all Crustacea only the *Ostracoda* and the *Copepoda* (more especially the latter) still retain in the structure of the mandibles the original typical biramose form, since they alone retain the exopodite in the adult animal.

d. The Anterior Maxillæ (Fig. 212).

These lie, in all Crustaceans, close to the mouth, and serve chiefly for mastication, like the mandibles and the posterior maxillæ. The biramose character is much more commonly retained in them than in the mandibles, the exopodite being more frequently present.

Entomostraca.—*Phyllopoda* (*D*), the anterior maxillæ are reduced to simple unjointed masticatory ridges without feelers. In the *Ostracoda* (*B*, *C*) also the masticatory ridge is the principal part, but there is a feeler as well, and in the *Cypridæ* and *Cytheridæ* an exopodite, in the form of a fan-like plate, which is vibratile, and when the maxilla moves promotes respiration. The anterior maxillæ of the free-living *Copepoda* (*A*) have masticatory ridges, feelers, and sometimes also fan-like exopodites; in the parasitic forms, on the contrary, these parts are much reduced. The anterior maxillæ of the *Cirripedia* are simple masticatory ridges without feelers; they are wanting in the *Rhizocephala*.

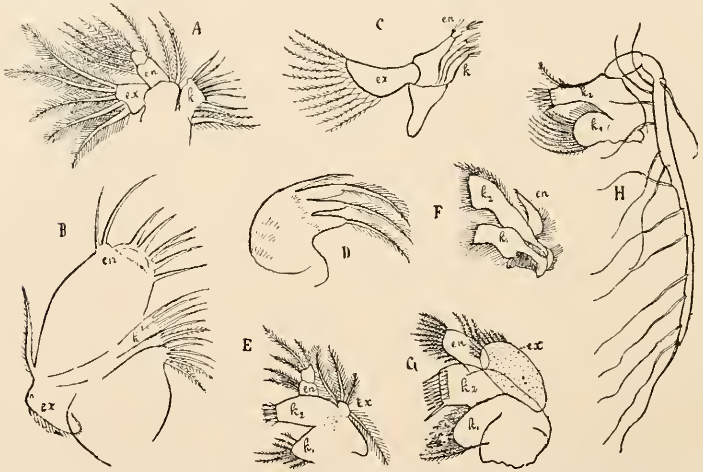

Fig. 212.—**Anterior maxillæ of various Crustaceans.** *A*, **Notodelphys agilis** (after **Brady**). *B*, **Cypridina stellifera** (after **Claus**). *C*, **Cythera viridis** (after **Zenker**). *D*, **Daphnia similis** (after **Claus**). *E*, **Euphausia pellucida**, last *Calyptopsis* stage (after **G. O. Sars**). *F*, **Astacus fluviatilis** (after **Huxley**). *G*, **Euphausia pellucida**, adult (after **G. O. Sars**). *H*, **Paranebalia longipes** (after **G. O. Sars**). *ex*, Exopodite; *en*, endopodite; *k*, masticatory ridge; k_1, inner; k_2, outer masticatory ridge.

Leptostraca.—The anterior maxillæ of *Nebalia* (*H*) are provided with two masticatory ridges (laciniæ), and carry a long, jointed, whip-like appendage, which is regarded as an endopodite. This is bent backward dorsally, at least in the female, and serves for cleaning the inside of the shell fold.

Malacostraca (*E*, *F*, *G*).—The maxillæ are flatly compressed. The exopodite is often wanting. The distal joint of the protopodite carries a masticatory ridge (lacinia interna), and so does the basal joint of the endopodite (lacinia externa). The remaining one or two joints of the endopodite form the feeler (palp).

Ontogeny and comparative anatomy enable us to trace back the anterior maxillæ of the *Malacostraca* to the typical biramose foot. In those *Malacostraca* which pass through free *Nauplius* and *Protozoœa* stages the maxillæ are distinctly recognisable as consisting of a protopodite with a masticatory ridge on the distal joint, an endopodite of two or more joints with a masticatory ridge on the basal joint, and an exopodite in the form of a fan-like plate. The exopodite is retained as a vibratile fan-like plate in most *Mysidæ* (*Euphausia*, *Thysanopus*, *Mysis*), and in a very reduced form in many *Decapoda*.

e. The Posterior Maxillæ (Fig. 213).

The posterior maxillæ have the same general typical structure as the anterior, and like the latter serve for mastication. But they

Fig. 213.—**Second or posterior maxillæ of various Crustaceans.** *A*, **Lernæa branchialis** ♂ (after **Claus**); *ms*, edge of the mouth; *md*, mandible; m_1, anterior maxilla; *cl*, chitinous ridge; m_2a, m_2b, anterior and posterior maxillipedes. *B*, **Penæidan larva** (*Acetes*?) (after **Claus**). *C*, **Eucopia australis** (after **G. O. Sars**). *D*, **Paranebalia longipes** (after **G. O. Sars**). *E*, **Astacus fluviatilis** (after **Huxley**). *F*, **Cypridina messinensis** (after **Claus**). *G*, **Cirolana spinipes** (after **Schioedte**). *H*, **Cyclops coronatus**; m_2a, inner; m_2b, outer maxillipede (endo- and exo-podite of the 2d maxilla). *I*, **Limnocythere incisa**, anterior limb (after **Dahl**). *K*, **Lysianassa umbo** (after **Goes**). *L*, **Lysiosquilla maculata** (after **Brooks**). *I*, Proximal, *II*, distal joint of the protopodite; *ki*, lacinia interna; *ke*, lacinia externa; *a*, *b*, divisions of the same.; *en*, endopodite (palp, feeler); *ex*, exopodite (fan plate). In *G*: k_1, Lacinia interna; k_2, k_3, divided lacinia externa; *k*, masticatory ridge (lacinia). In *L*: 1 and 2, joints of the endopodite.

often show more clearly than the anterior maxillæ the biramose character; *e.g.* in the *Malacostraca* the exopodite is almost everywhere retained as a vibratile plate.

Entomostraca.—In the *Phyllopoda*, the posterior maxillæ are, like the anterior, reduced to simple masticatory ridges. In the *Cladocera* they are indeed only to be found in the embryo.

The posterior maxillæ of the *Ostracoda* (*F*, *I*) show very various arrangements. They sometimes function almost exclusively as masticatory organs, sometimes they are locomotory organs as well, sometimes only the latter. In the first case the masticatory ridge is well developed, the endopodite (feeler) small and 2-jointed, the exopodite (fan plate) either rudimentary (*Cypris*) or very strongly developed (*Cypridina*). In the second case the endopodite is longer and many-jointed. In the third case the maxilla is formed like an ordinary limb and the fan plate has disappeared. The arrangement of the posterior maxillæ in the *Copepoda* is very interesting (*A*, *H*). The endopodite and exopodite are here retained as appendages, which are usually jointed. Instead, however, of their being placed on a protopodite, they are inserted direct on the body, so that we might be tempted to consider them as special limbs. They have been called anterior and posterior maxillipedes. In the parasitic *Copepoda* they serve as clinging organs and end in hooks. In the *Argulidæ* (Fig. 195, p. 291) each of the anterior maxillipedes is changed into a large adhering disc. The posterior maxillæ of the *Cirripedia* are small, much reduced, and fused together into a sort of lower lip. They are wanting in the *Rhizocephala*.

Leptostraca (*D*).—The 2d maxillæ of *Nebalia* are biramose, with protopodite, endopodite, and exopodite. The protopodite carries 3 lobate masticatory ridges. The endopodite has 2 joints. The exopodite is unjointed and narrow, and is a transition form between the jointed branch and the broad flat fan plate.

Malacostraca (*B*, *E*, *G*, *K*, *L*).—The posterior maxillæ are more easily recognised as metamorphosed biramose feet than the anterior maxillæ, in that they (except in the *Arthrostraca*) have retained besides the protopodite and the endopodite the exopodite as the so-called fan plate. The protopodite generally carries 2 masticatory ridges (laciniæ), one on the proximal, the other on the distal joint. These laciniæ are often divided.

The posterior maxillæ of the *Arthrostraca* are very much simplified, most of all in the *Amphipoda* (*K*), where the exo- and endo-podite are wanting, and both the masticatory ridges of the protopodite are simple. In the *Isopoda* the lacinia of the distal joint of the protopodite is divided; the exo- and endo-podite are wanting. In the land *Isopoda* and the parasitic forms even the protopodite, with the masticatory ridges, is more or less degenerated.

In the *Thoracostraca* the posterior maxillæ of the *Schizopoda* (*C*) show the arrangement above described as characteristic of the *Malacostraca*. Both masticatory ridges are divided (*Thysanopus*, *Euphausia*), or the proximal remains undivided (*Mysis*, *Lophogaster*, *Siriella*, *Eucopia*). In the *Cumacea* the endopodite (palp) is wanting, and the exopodite is small. In the *Stomatopoda* the exopodite is wanting, but on the other hand fan-like lobes are developed on the 2-jointed endopodite. The proximal masticatory ridge is undivided, the distal divided. In the *Decapoda* (*B*, *E*) the proximal as well as the distal masticatory ridge is divided; the endopodite (palp or feeler) is small and unjointed (in the larva only has it two or more joints), and the exopodite is well developed in the shape of a fan plate, with a crescent-shaped process directed backwards, which regulates the streaming of water in the branchial cavity.

f. The Paragnatha.

We may here in passing notice certain peculiar processes which in the *Thoracostraca* and a few *Entomostraca* (*Ostracoda* and *Copepoda*) rise independently between the mandibles and maxillæ on the ventral integument of the head, and are called **paragnatha**. They cannot be considered as separate limbs, as they are never innervated by special ganglia. They may perhaps represent the proximal masticatory ridges of the anterior maxillæ which have become independent. In *Apseudes* (*Anisopoda*) a ridge-like portion is marked off from them.

2. The Limbs of the Trunk.

The limbs of the trunk can be deduced from biramose feet. Their number varies in the *Entomostraca*, but is constant in the *Malacostraca*. In the latter we always distinguish, in correspondence with the segmentation of the trunk, 8 pairs of thoracic limbs and 6 pairs of abdominal limbs or pleopoda.

There is nothing to prevent us from assuming that the trunk appendages of the *Entomostraca* correspond with those of the *Malacostraca*, pair with pair from before backwards.

a. Entomostraca (Fig. 215).

Phyllopoda.—The *Branchiopoda* and *Cladocera* must be described separately. *Branchiopoda* (Fig. 214 ; Fig. 215, *C*) : the numerous (10 to 36) pairs of trunk limbs are formed pretty much alike. They are wanting on a varying number of posterior (abdominal) segments. All the limbs are leaf-shaped swimming feet with branchial appendages. They also serve for whirling food within reach. Their structure is essentially as follows. An unjointed or indistinctly jointed stem carries on its inner side (that turned to the median plane of the body) 6 appendages or lobes (endites) and on the outer side a flat respiratory plate and a pouch- or sac-like branchial appendage (epipodite). It is at present impossible, without straining, to deduce all these parts from the typical component parts of a biramose limb. The respiratory plate is generally held to be an exopodite. In the *Limnadiadæ* (*Limnetis*, *Estheria*, *Limnadia*) there are 10 to 27 pairs of swimming feet. The respiratory plate is divided into two. The *Apodidæ* (*Apus*) usually possess 35-50 pairs of swimming feet. The endites are jointed, and may be described as flagellate appendages ; they are very long (the 5th especially) on the 1st pair of swimming feet. The 11th pair of feet carry on

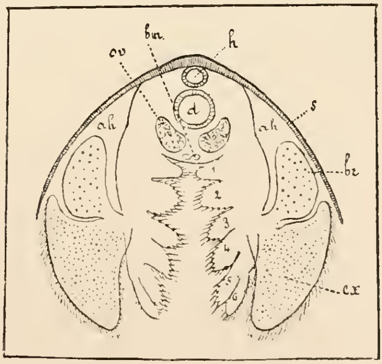

Fig. 214.—**Apus.** Transverse section in the neighbourhood of the 7th or 8th pair of feet. *h*, Heart ; *d*, intestine ; *ov*, ovaries ; *bm*, ventral chord ; *ah*, respiratory cavity between the shell (*s*) and the body ; 1-6, endites ; *br*, gills ; *ex*, respiratory plate (after **Packard**).

each side a basin-like brood capsule serving for the reception of the eggs, formed out of the shaft and its respiratory plate. Each of the limb-bearing trunk segments lying behind the 11th carries several (up to 6) pairs of swimming feet, gradually diminishing in size, an arrangement which is not yet sufficiently explained. The *Branchiopoda* (*Branchipus*) generally possess 11 pairs of swimming feet.

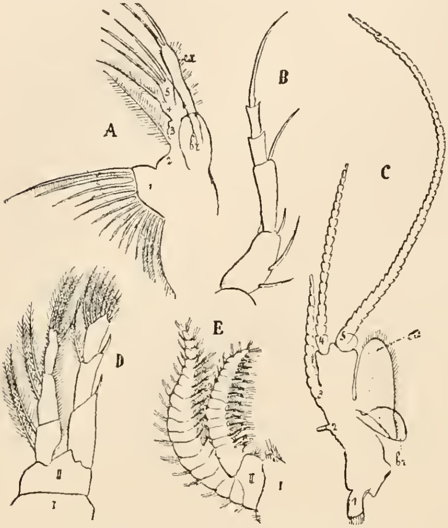

FIG. 215.—**Trunk feet of some Entomostraca.** *A*, **Daphnia similis** ♀, 2d limb (after **Claus**). *B*, **Limnocythere incisa**, last (3d) limb, *i.e.* 2d trunk limb (after **Dahl**). *C*, **Apus longicaudatus** ♂, 1st limb (after **Packard**). *D*, **Notodelphydæ, Doropygus porcicauda** ♀, swimming foot of the 4th pair (after **Brady**). *E*, **Balanus perforatus**, 2d cirrus (after **Darwin**). 1, 2, 3, 4, 5, Endites; *ex*, respiratory plate or exopodite; *br*, gill; *I* and *II*, joints of the protopodite.

The *Cladocera* (Fig. 215, *A*), in contradistinction to the *Branchiopoda*, are distinguished by the small number (4 to 6) of their trunk limbs. The special form of these trunk limbs in some genera recalls the swimming feet of the *Branchiopoda*, and they carry branchial appendages, especially in *Sida* and *Daphnia*. The most anterior trunk feet may, however, become slender and more leg-like, and finally through degeneration of the branchial appendage and the respiratory plate may become long seizing feet (*Polyphemus*, *Leptodora*).

Ostracoda.—The reduction in the number of limbs here goes even further than in the *Cladocera*. We find only 2 pairs, which (Fig. 215, *B*) are long and many-jointed and without branchial appendages and exopodites. The anterior pair serve as creeping or clinging feet, the posterior as cleaning feet. In *Cypridina* the latter are inserted dorsally on the trunk, and are here long many-jointed appendages (*cf.* Fig. 193, p. 289). Locomotion is effected chiefly by the limbs of the head.

Copepoda (Figs. 194 and 195, pp. 290 and 291 ; Fig. 215, *D*).—The 4 or 5 pairs of feet are limited to the anterior part of the trunk, which as thorax is opposed to the limbless abdomen. The most anterior pair is inserted on the 1st thoracic segment, which is fused with the head, and is generally unlike the other pairs in its form. The thoracic limbs, as rowing feet, cause the swimming movement of the *Copepoda*. They, unlike those of the *Phyllopoda*, exhibit in a fine typical manner the biramose character, as they consist of a protopodite of 2 joints, an exo- and an endo-podite. The exo- and endo-podites generally have 3 joints (in the *Argulidæ* they are long and many jointed) and function as flat oars. Adaptation to a parasitic mode of life in the *Copepoda* leads to the reduction and occasionally to the disappearance of the thoracic feet, *e.g.* in the *Chondracanthina* the 3d, 4th, and 5th pairs of thoracic feet are wanting, and in the *Lernæopodidæ* all the thoracic feet have disappeared.

Cirripedia (Fig. 215, *E*).—The trunk extremities of these Crustaceans are biramose; their exo- and endo-podites are long and many-jointed, and are described as tendril-like feet. They are alternately protruded and withdrawn through the shell- or mantle-cleft, and serve for taking in particles of food and at the same time as respiratory organs. Six pairs of tendril-like feet are found in the *Lepadidæ* and *Balanidæ*, 3 or 4 pairs in the *Abdominalia*. In the *Proteolepadidæ* and *Rhizocephala* the tendril-like feet entirely disappear.

b. Leptostraca.

Nebalia, in the morphology of its trunk limbs, represents in many respects a transition form between the *Entomostraca* and the *Thoracostraca*. We can distinguish thoracic feet and abdominal feet (pleopoda) corresponding with the division of the trunk into a thorax of 8 segments (exactly answering to the *Malacostracan* thorax) and an abdomen (pleon) of 8 segments. The 8 pairs of thoracic feet are similar to one another, as in most *Entomostraca*. They are (Fig. 216) lamellate, strongly recalling the leaf-shaped limbs of the *Phyllopoda*, between which and the thoracic feet of the *Malacostraca* they form a connecting link. Each thoracic foot of *Nebalia* consists of the 3 parts characteristic of a biramose foot, viz. a protopodite of 2 joints, an exopodite, and an endopodite. The proximal or basal joint of the protopodite carries a doubly-tipped branchial lamella (epipodite), probably corresponding with the branchial appendage of the trunk feet in the *Phyllopoda*. On the one side of the distal segment is inserted the 5-jointed endopodite as a direct prolongation of the protopodite, and on the other the unjointed exopodite in the form of a branchial lamella, probably homologous with the respiratory plate on the trunk feet in the *Phyllopoda*.

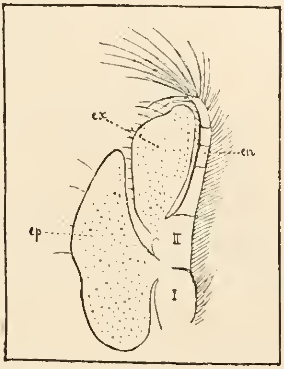

Fig. 216.—**Nebalia, leaf-shaped thoracic foot (after Claus).** *I*, *II*, Joints of the protopodite; *en*, endopodite; *ex*, exopodite; *ep*, epipodite.

In the abdomen (pleon) only the 6 anterior segments carry limbs. The 6 pairs of limbs probably correspond with the 6 pairs of pleopoda in the *Malacostraca*. The 4 anterior pairs (Fig. 225, *D*) serve for swimming; they are typical biramose feet (with proto-, exo-, and endo-podites), and show some similarity to the swimming feet of the *Copepoda*. An epipodite is wanting. The last 2 pairs of pleopoda (Fig. 225, *E*) are short and uniramose, and consist of one or two joints.

c. Malacostraca.

The trunk feet fall into thoracic feet and abdominal feet (pleopoda) in correspondence with the division of the trunk into a thorax of 8 segments and an abdomen (pleon) of 7. We find 8 pairs of thoracic feet and 6 pairs of pleopoda, the last abdominal segment being always devoid of appendages. It is better to consider the extremities of the thorax and of the abdomen separately.

The Thoracic Limbs.

As a varying number of the anterior thoracic segments may fuse with the head, a varying number of the anterior thoracic feet often enter into close relations with the mouth, as accessory organs for the taking in of food (foot-jaws, maxillipedes). The thoracic foot of *Nebalia* described above may be considered as the primitive form of the thoracic feet in the *Malacostraca*.

In a typical *Malacostracan* thoracic limb the proximal joint of the protopodite carries an epipodite, while the exopodite and the 5-jointed endopodite are attached to the distal joint. Very often both the exopodite and the epipodite disappear, and the thoracic foot is then an unbranched, 7-jointed limb. The proximal joint of the protopodite occasionally fusing with the skeleton of the thorax, the distal joint alone is recognisable.

Arthrostraca (Fig. 217).—Here, where the most anterior thoracic segment is fused with the head, the most anterior pair of thoracic feet are associated with the oral limbs as a pair of **maxillipedes**. The absence of the exopodite is the general rule for the thoracic feet of the *Arthrostraca*. The proximal joint of the protopodite often fuses with the thoracic skeleton. On the basal joint of some thoracic feet there is, in the female, a lamellate appendage, the brood plate or lamella. The brood plates cover over a cavity, the brood pouch, on the ventral side of the thorax, and into this pouch the eggs enter and there develop (Fig. 218).

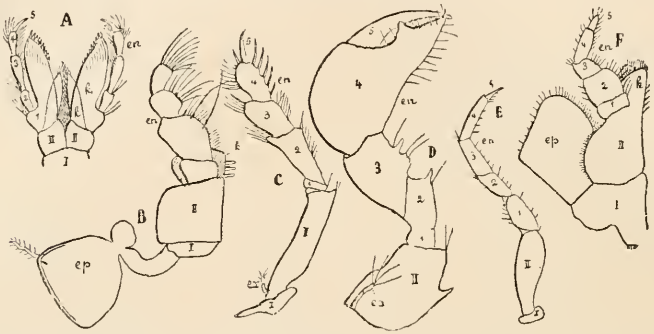

Fig. 217.—**Thoracic limbs of some Arthrostraca.** *A*, 1st pair of thoracic feet (maxillipedes) of **Amphithoë penicillata (Costa).** *B-D*, **Apseudes.** *B*, 1st right thoracic foot; *C*, 3d thoracic foot; *D*, 2d thoracic foot (after **Boas**). *E* and *F*, **Asellus.** *E*, 3d thoracic foot; *F*, 1st thoracic foot (after **Boas**). *I*, *II*, Joints of the protopodite; 1-5 joints of the endopodite; *k*, k_1, masticatory ridges; *ep*, epipodite; *ex*, exopodite; *en*, endopodite.

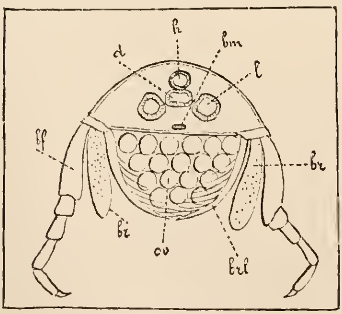

Fig. 218.—**Corophium longicorne** (*Amphipod*). Transverse section through the thorax (after **Delage.**) *d*, Intestine; *h*, heart; *bm*, ventral chord; *l*, liver; *br*, gill; *brl*, brood lamella; *ov*, eggs in the brood cavity; *bf*, thoracic feet.

The first thoracic foot (maxillipede) is characterised by the fact that the distal joint of the protopodite, and in the *Amphipoda* the proximal joint of the endopodite as well, carries a masticatory plate (lacinia).

The *Amphipoda* are distinguished by the fact that the middle and posterior thoracic feet carry on the basal joints of their protopodites pouch-like gills (epipodites) (Fig. 218), which, however, by the fusing of the basal joints with the skeleton of the trunk may be inserted directly on the latter. They are not directed outwards in the way characteristic of epipodial appendages, but they rise from the inner side of the basal joints. The gills of the *Caprellidæ* (Fig. 198, p. 295) are generally limited to the 4th and 5th pairs of thoracic feet, and these thoracic feet are then reduced to the proximal joint of the protopodite. In the *Isopoda* gills are wanting on the thoracic feet, except on the maxillipede, on which an epipodial appendage in the shape of a firm plate has been retained (Fig. 217, *F*). The *Anisopoda* deviate in many ways from other *Isopoda* (Fig. 217, *B-D*), especially the genus *Apseudes*. The anterior thoracic foot (maxillipede) (*B*) possesses a large epipodial appendage, which by its vibration causes a constant current of water in the respiratory cavity formed by the shell-fold. **On the 2d and 3d thoracic feet (*C*, *D*) of Apseudes there are rudimentary exopodites,** a fact of great importance in tracing back the thoracic feet of the *Arthrostraca* to biramose feet. The thoracic feet of the second pair are transformed into strong chelate feet in the ordinary manner, *i.e.* the ultimate (5th) joint of the endopodite is opposable to a distal process of the penultimate (the 4th).

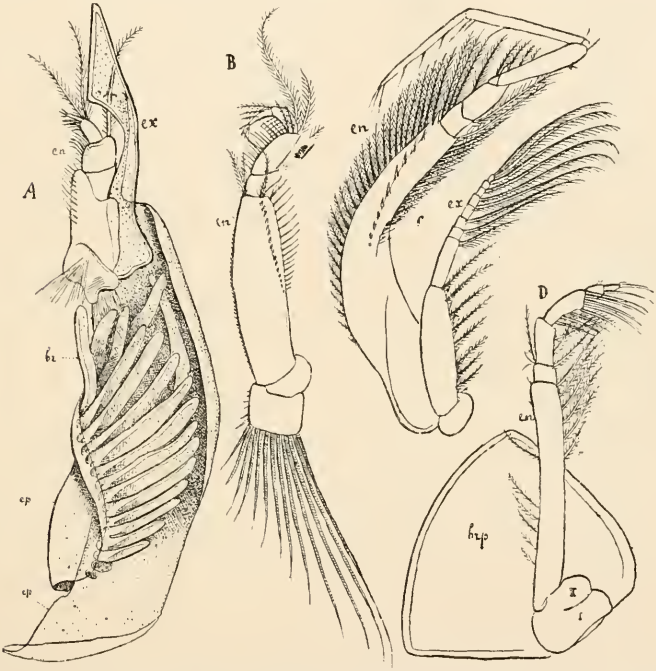

FIG. 219.—**Thoracic feet of Diastylis stygia ♀ (after G. O. Sars).** *A*, 1st, *B*, 2d, *C*, 4th, *D*, 6th thoracic feet. *ep*, Epipodial plate; *br*, gill on the same; *en*, endopodite; *ex*, exopodite, which in *A* is a hard lamella; *brp*, brood plate.

Thoracostraca.—In the *Cumacea* (Figs. 199 and 219) the most anterior thoracic foot has become a maxillipede. The remaining thoracic feet are long. Brood-lamellæ occur on the basal joints of the 2d to the 6th pairs in the female. The exopodite is wanting in the 1st (?), 2d, and 8th pairs; in the female usually also in the 6th and 7th; on the other feet it is present and serves for swimming. The endopodite has 5 joints. An epipodial appendage is developed only on the 1st thoracic foot (maxillipede), but here is very large. It has numerous branchial tubes. The distal joint of the protopodite of the maxillipede carries a masticatory ridge.

Among the *Stomatopoda* (Figs. 200 and 220) the 5 anterior pairs of thoracic feet are formed very differently from the 3 posterior pairs. The latter arise from the 3 free posterior segments of the thorax, which are not covered by the cephalo-thoracic shield. The **5 anterior pairs**, which have moved to the neighbourhood of the mouth, have no exopodite in an adult condition, though it is to be found in their larval stages (Fig. 220). They all possess a disc-shaped epipodial appendage which serves for respiration. The endopodite and the protopodite together only contain 5 joints. These 5 anterior pairs of feet are armed with prehensile hooks. Such a prehensile hook is formed by the last joint of a foot moving upon the last joint but one, like the blade of a knife upon its handle. Very powerful hooks of this kind are developed in the 2d pair of limbs for catching prey. The **last 3 pairs of thoracic feet** serve as ambulatory feet. They are biramose feet with somewhat reduced endopodites; the exopodite here forms the limb-like prolongation of the protopodite. Epipodial appendages are wanting.

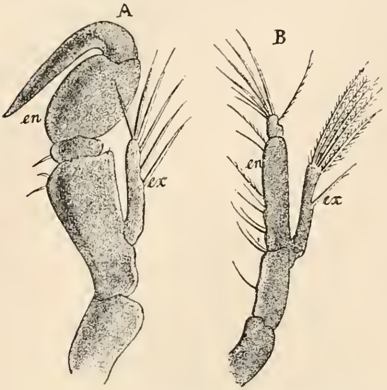

FIG. 220.—**Thoracic feet of a Squilla larva**, after **Claus.** *A*, 2d maxillipede. *B*, one of the subsequent 3 thoracic feet. *en*, Endopodite; *ex*, exopodite.

In the *Schizopoda* the thoracic feet are very interesting, connected on the one hand with those found in the *Leptostraca*, and leading on the other to those of the *Decapoda*. All the 8 pairs of thoracic feet are still more or less similarly formed, and are biramose. It is best to describe the *Euphausidæ* first, then the *Lophogastridæ*, and lastly the *Mysidæ*.

In the *Euphausidæ* (Fig. 221, *F-I*) the thoracic feet consist of the 2-jointed protopodite, a 5-jointed endopodite, and an exopodite which is composed of a one-jointed shaft and a flagellum which is frequently ringed. All the 8 pairs of thoracic limbs have epipodial appendages on the basal joints of the protopodites; these appendages are simply pouch-like on the first pair, but are more or less branched on the other pairs, and form gills. The 2 anterior pairs of thoracic feet are slightly different from the subsequent pairs, the proximal joint of the protopodite having a ridge-like process. Herein we see the beginning of the metamorphosis of these thoracic feet into maxillipedes. In *Euphausia* the endopodite is wanting in the last two pairs, in *Thysanopus* in the last pair.

In the *Lophogastridæ* (Fig. 221, *A* and *B*) the 1st thoracic foot has already become a maxillipede, and the 2d also approaches the form of one. On the 1st pair the epipodial appendage becomes a broad vibratile plate. In the female brood-lamellæ are found on the basal joints of the protopodites of the other feet. Gills arise near this basal joint, but from the integument of the thorax itself; these correspond with the epipodial gills of the *Euphausidæ*, and may be described as appendages dislocated from the proximal joint of the protopodite.

In the *Mysidæ* (Figs. 201, 221, *C-E*) both the 2 anterior pairs of thoracic limbs are maxillipedes with masticatory ridges. The first maxillipede carries a vibratile epipodial plate. Some or all the other feet may in the female carry brood-lamellæ (Fig. 222). Branchial appendages are wanting on the thoracic limbs of the *Mysidæ*.

The *Decapoda* (Figs. 223, 224, 202, 203) have the **three** anterior pairs of thoracic feet transformed into maxillipedes, which no longer serve for locomotion but only for taking in food. The exopodite is well developed in them, and flagellate; the epipodite lies in the branchial cavity in the form of a long lamella. In the *Brachiura* it is whip-like and resembles a cleaning foot. The anterior maxillipedes have

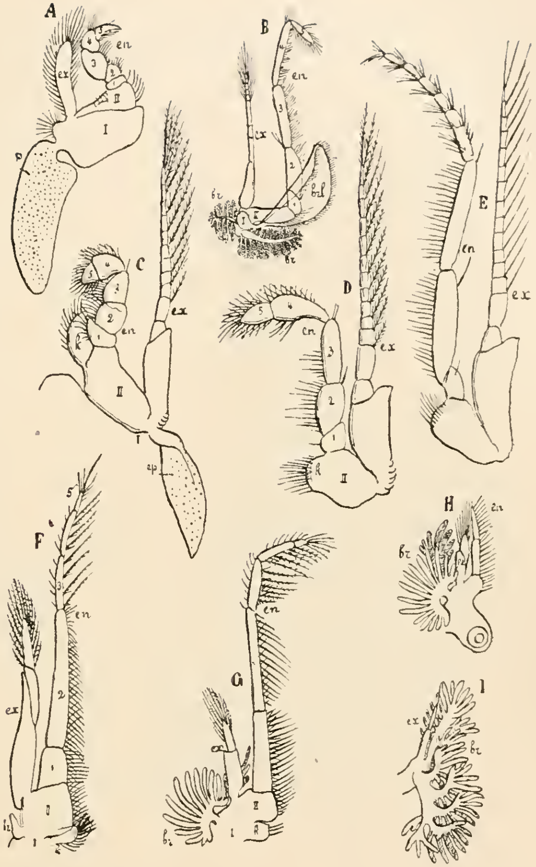

FIG. 221.—**Thoracic feet of Schizopoda** (after **G. O. Sars**). *A* and *B*, **Lophogaster typicus.** *A*, 1st thoracic foot (maxillipede); *B*, 2d thoracic foot of the ♀, with brood-lamella. *C-E*, **Mysis flexuosa.** *C*, 1st thoracic foot (maxillipede); *D*, 2d thoracic foot (maxillipede); *E*, 3d thoracic foot. *F-I*, **Thysanoessa gregaria.** *F*, 1st, *G*, 5th, *H*, 7th, *I*, 8th thoracic feet. *I*, *II*, Joints of the protopodite, 1-5, of the endopodite; *en*, endopodite; *ex*, exopodite; *br*, gills; *ep*, epipodial plate; *brl*, brood-lamella; *k*, masticatory ridge.

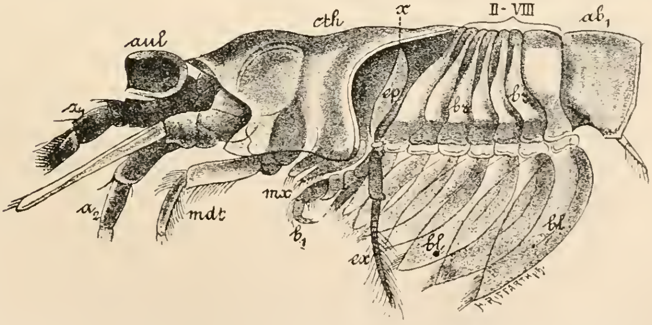

FIG. 222.—**Boreomysis scyphops** ♀ (after **G. O. Sars**). The free portion of the cephalo-thorax cut off at *x* to show the free thoracic segments *II-VIII* lying beneath with the branchial folds *br*. *aul*, Cup-shaped ophthalmic lobe without eye (without pigment or visual apparatus); a_1, a_2, anterior and posterior antennæ; *mdt*, mandibular feeler; *mx*, maxillæ; b_1, 1st thoracic foot with exopodite (*ex*) and epipodite (*ep*), the latter in the uncovered branchial cavity *bl*, brood lamellæ of the 2d-8th removed thoracic feet; ab_1, 1st abdominal segment; *cth*, cephalo-thorax.

well-developed masticatory ridges. In contradistinction to the maxillipedes, the 5 posterior pairs of thoracic feet are described as ambulatory feet. The *Decapoda* owe to them their name. They are distinguished by the want of the exopodite, so that the appendage consisting of the protopodite and endopodite is a simple limb of 7 joints. The exopodites, however, may be present in larval stages, and in a few cases may be retained as rudiments in the adult. The basal joint of the ambulatory feet carry gills, which project up into the respiratory cavity. The *Decapodan* gills, however, must be described in a special section. The anterior ambulatory feet are often chelate; the first pair are generally very powerful. In the cray-fish the 3 anterior pairs of ambulatory feet are chelate; the most anterior ambulatory foot is provided with the well-known large forceps.

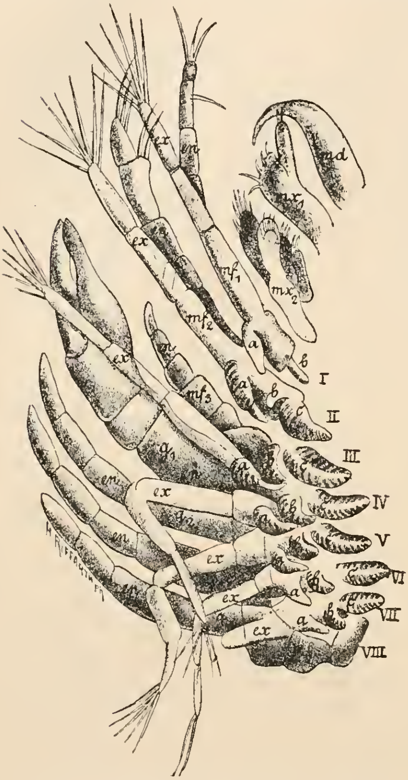

Fig. 223.—**Older larva of Calliaxis in advanced Mysis stage. Gills and extremities of the cephalothoracic region** (after **Claus**). *md*, Mandible; mx_1, anterior, mx_2, posterior maxillæ; *I-VIII*, thoracic feet, of which mf_1=1st maxillipede, mf_2=2d maxillipede, mf_3=3d maxillipede, g_1-g_5,=ambulatory feet; *ex*, exopodites; *en*, endopodites; *a*, epipodites =podobranchiæ; *b*, arthrobranchiæ; *c*, pleurobranchiæ.

The Abdominal Feet (Pleopoda) (Fig. 225).

The 6 anterior of the 7 abdominal segments typically carry limbs, while the last segment, the **telson**, is always limbless.

Arthrostraca.—In the *Amphipoda*, setting aside for the present the aberrant group of the *Caprellidæ*, we find that the pleopoda are well developed as typical biramose feet. The 3 anterior pairs of pleopoda are directed forwards, and are strong swimming feet with many-jointed exo- and endopodites. The 3 smaller posterior pairs of pleopoda (*G*), also mostly biramose, are directed backwards and pointed; they often serve for springing. The pleopoda are rarely lamellate. In the *Caprellidæ*, where the abdomen is usually rudimentary, it carries at the most 3, at the least 2, much-degenerated limbs, which are better developed in the male (as copulatory feet) than they are in the female.

Isopoda.—The pleopoda of the *Isopoda* are biramose limbs, whose endo- and exo-podites are unjointed, and generally delicate-skinned, lamellæ, which serve for respiration. The last (6th) pair of pleopoda either forms together with the last abdominal segment a rowing fin (*F*), as in the marine *Isopoda*, or is stylet-shaped, as in fresh-water and land *Isopoda*. In the parasitic *Bopyridæ* and *Cryptoniscidæ* the pleopoda are reduced or entirely wanting. In the land *Oniscidæ* the outer lamellæ of the anterior pleopoda contain air chambers. In the *Anisopoda* the pleopoda are biramose swimming feet, not serving for respiration.

Thoracostraca.—In the *Stomatopoda* we find on the strong abdomen 6 pairs of well-developed typical biramose pleopoda. The 5 anterior pairs are swimming feet, each of whose outer lamellæ carries a branched gill. The 6th pair of pleopoda form with the telson (7th abdominal segment) a strong caudal fin.

In the *Cumacea* the 6th pair of pleopoda (*A*, p_6) consists of long bifurcated processes. The pleopoda of the 5 anterior abdominal segments are wanting in the female; in the male they are swimming feet (*H*), and either present in their full numbers or in 2 to 3 pairs.

In the *Schizopoda* the 6th pair of pleopoda (*C*) forms with the telson a caudal fin. Where there is an auditory organ it lies on the inner lamella of this pleopod. The 5 anterior pairs of pleopoda are well-developed biramose swimming feet, in the male at least. The 2 anterior pairs serve as copulatory organs in the *Euphausidæ*. In the male of *Siriella* the pleopoda carry gills (*B*).

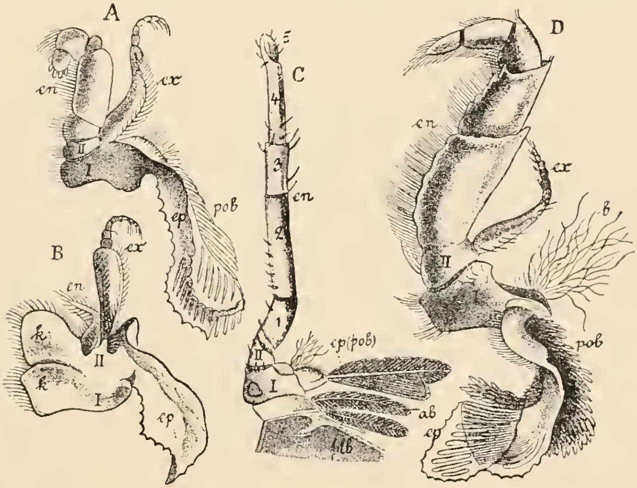

Fig. 224.—**Thoracic feet of Astacus fluviatilis (after Huxley).** *A*, 2d thoracic foot (2d maxillipede). *B*, 1st thoracic foot (1st maxillipede). *C*, Part of transverse section through the thorax, showing an ambulatory foot and gills. *D*, 3d thoracic foot (3d maxillipede). *I*, *II*, Joints of the protopodite; 1-5, of the endopodite *en*; *ex*, exopodite; *pob*, podobranchiæ; *ab*, arthrobranchiæ; *plb*, pleurobranchiæ; *k*, masticatory ridge.

Decapoda (*I-N*).—The development of the pleopoda stands in direct relation to the development of the abdomen itself. In the long-tailed *Decapoda* (*Macrura*) 6 pairs of biramose pleopoda are generally found. The 6th pair with the telson forms a strong caudal fin. The 5 anterior pairs play no very important part in locomotion. In the *Brachyura* the pleopoda, in correspondence with the great reduction of the abdomen, are reduced. A caudal fin is usually wanting. In the male only the 2 anterior pairs of pleopoda are found, in the female 4 pairs. The caudal fin is generally reduced in the *Anomura*, and the pleopoda are truncated and only developed on one side. The 2 anterior pairs of pleopoda very generally serve in the *Decapodan* male as copulatory organs. In the female the pleopoda often carry the eggs after their discharge and fertilisation.

C. The Respiratory Organs—Gills.

Respiration always takes place in Crustaceans by means of the outer integument. In small Crustaceans, in which the cuticle lying over the hypodermis is thin and delicate, the whole body surface breathes. This is especially the case in *Ostracoda*, *Copepoda*, many *Cladocera*, and many *Cirripedia*, which have no specific respiratory organs.

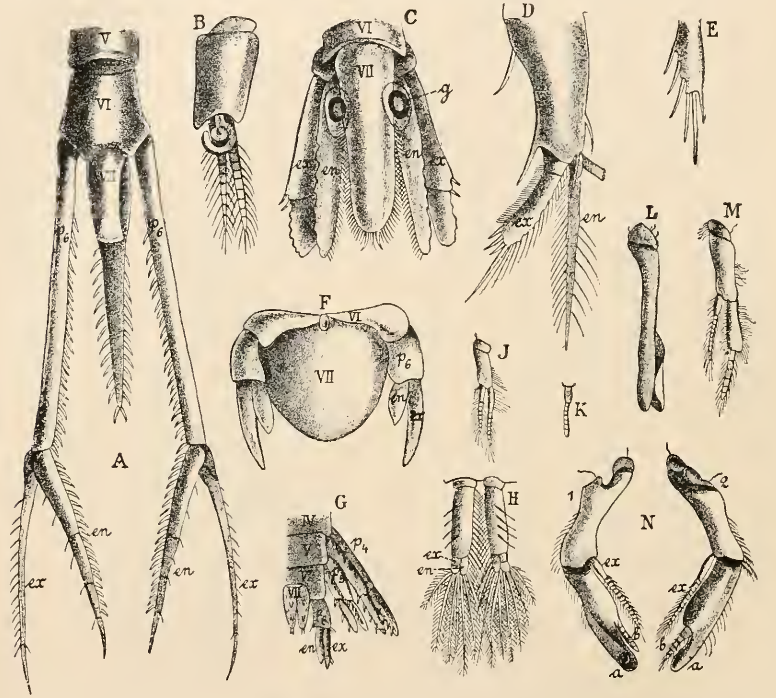

Fig. 225.—**Pleopoda (abdominal feet) of Leptostraca and Malacostraca.** *A*, End of the abdomen of **Diastylis stygia (after G. O. Sars)**; *V*, *VI*, *VII*, abdominal segments; *VII*, telson; p_6, pleopoda of the 6th segment; *en*, endopodite; *ex*, exopodite. *B*, 2d pleopod with gills, exo- and endo-podite of **Siriella Thompsonii (after G. O. Sars).** *C*, End of the abdomen (caudal fin) of **Siriella gracilis** (after **G. O. Sars**); *VI*, 6th abdominal segment; *VII*, 7th abdominal segment (telson); *en*, *ex*, endo- and exo-podites of the 6th pleopoda, which together with the telson form the caudal fin; *g*, auditory organ. *D*, An anterior pleopod of **Nebalia** (after **Claus**); *ex*, exopodite; *en*, endopodite. *E*, **Nebalia**, 6th pleopod of the ♀ (after **Claus**). *F*, **Anilocra** (*Isopod*), caudal fin; *VI*, 6th abdominal segment; *VII*, telson; p_6, 6th pleopod with exopodite (*ex*) and endopodite (*en*) (after **Delage**). *G*, **Lysianassa producta** (*Amphipod*); end of the abdomen with the 4th, 5th, and 6th pleopoda, p_4, p_5, p_6; *IV*, *V*, *VI*, *VII*, abdominal segments; *en*, endo-, *ex*, exo-podite (after **Goes**). *H*, **Diastylis stygia**, 1st pair of pleopoda; *ex*, exo-, *en*, endo-podite (after **G. O. Sars**). *I-N*, **Astacus fluviatilis.** *I*, 3d pleopod of male; *K*, 1st pleopod of female; *L*, 1st pleopod of male; *M*, 3d pleopod of the female; *N*, 2d pleopod of the male. 1, Anterior surface; 2, posterior surface; *ex*, exopodite; *a*, the rolled-up plate of the endopodite; *b*, jointed end of the endopodite (after **Huxley**).

In the great majority of Crustaceans, however, the respiration is particularly active at definite parts of the body, even if in addition the whole integument or a large portion of the same is capable of respiration in a lesser degree.

The respiratory functions in the Crustacea, as elsewhere, are promoted and facilitated by various adaptations. Among these we must note (1) the increase of the respiratory surface, the outer integument, (2) the flowing of the blood to and from the respiratory parts, (3) adaptations which serve to bring about a continual change of the aerated water which bathes the respiratory parts, and (4) adaptations designed for the protection of the necessarily delicate-skinned respiratory organs.

The principal increase of the respiratory surface is due to the integumental fold which rises so generally from the head and appears in very different forms as mantle, dorsal carapace, bivalve shell, or cephalo-thoracic shield. Wherever this fold remains soft-skinned it always helps in the respiration. It is often only the inner wall of the fold which remains soft-skinned, and we frequently meet with adaptations which serve for the purpose of setting in motion the water found in the cavity between the fold and the body (respiratory cavity). There are in *Malacostraca* (*Zoœa larvæ*, *Tanaidæ*, *Mysidæ*, *Stomatopoda*) epipodial appendages of the maxillæ or of the anterior thoracic feet, which, during the movements of the limbs which carry them, vibrate and cause a stream of water in the respiratory cavity in which they lie. In a similar way in the *Ostracoda* the movement of the fan-like plates, the so-called branchial appendages, which may occur on the 4th, 5th, and 6th pairs of limbs, bring about a constant stream of water over the body surface. In the higher *Malacostraca*, especially in the

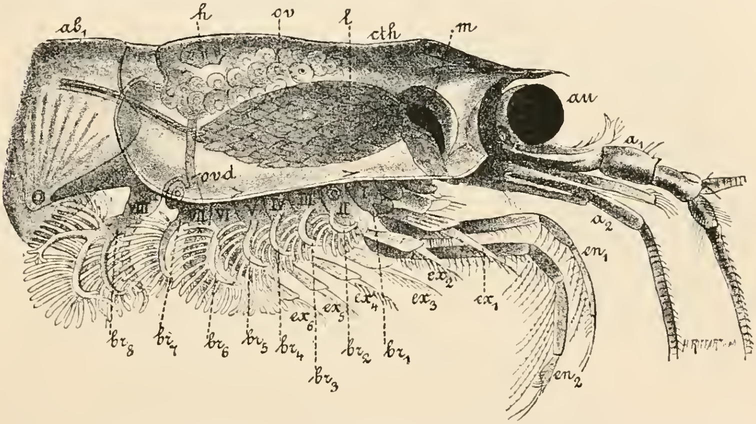

FIG. 226.—**Euphausia pellucida** ♀ (after **G. O. Sars**), cephalo-thorax (*cth*) and first abdominal segment (ab_1) from the side. *h*, Heart; *ovd*, oviduct; *ov*, ovary; *l*, liver; *m*, stomach; *au*, eye; a_1, anterior, a_2, posterior antenna; ex_1-ex_6, exopodites of the 6 anterior thoracic limbs; en_1, en_2, endopodites of the 2 anterior thoracic limbs; the 4 following are not drawn; endo- and exo-podites of the 7th and 8th thoracic limbs rudimentary; br_1-br_8, gills on the protopodites (*I-VIII*) of the thoracic limbs; br_1, first gill, a small epipodial appendage.

Decapoda, the integumental fold, which becomes very hard and thick, loses its respiratory significance, and as branchiostegite becomes a protective cover to the delicate gills which lie laterally in the respiratory cavity under it.

In the *Balanidæ* a pair of fold-like projections of the mantle stand out into the mantle cavity. These folds may again form numerous lateral folds, so that the mantle surface is very much increased. These formations have been assumed to be gills.

In some *Cyprididæ* (*Ostracoda*) the body carries on each side near the dorsal middle line, under the shell, a row of small branchial lamellæ.

The function of respiration in the large majority of Crustaceans is performed by the limbs or their appendages. This is comprehensible, since the change of the water caused by the movement of the limbs is of the greatest use in promoting respiration.

In many *Lepadidæ* among the *Cirripedia* the tendril-like feet have cylindrical or lancet-shaped appendages which with doubtful accuracy have been indicated as gills. They are found on the first pair or pairs, and occasionally on all of the tendril-like feet, and are usually inserted on them near the base.

The leaf-shaped swimming feet of the *Phyllopoda* are very well suited for respiration. The appendages which are called gills and respiratory plates in this order have already been described. The gills of the *Phyllopoda* are epipodial appendages, perhaps corresponding with the gills of the *Thoracostraca*.

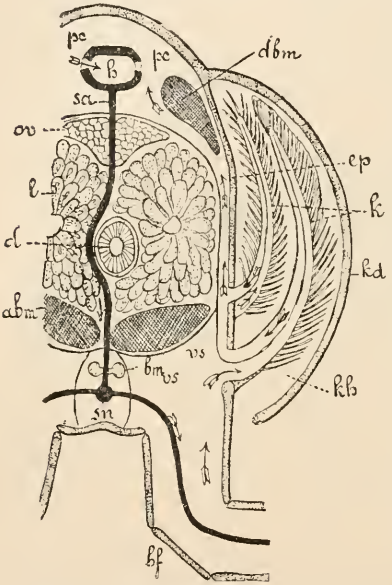

Fig. 227.—**Transverse section through the cephalo-thorax of the Cray-fish near the heart, diagrammatic:** *kd*, Branchiostegite; *k*, gills; *kh*, respiratory or branchial cavity; *ep*, lateral wall of the cephalo-thorax; *pc*, pericardium; *h*, heart; *sa*, sternal artery; *l*, hepatopancreas; *d*, intestine; *abm*, ventral longitudinal muscles running to the abdomen; *dbm*, dorsal longitudinal muscles running to the abdomen; *bm*, ventral chord; *sn*, subneural vessel; *bf*, ambulatory foot; *vs*, ventral sinus; *ov*, ovary. The arrows indicate the direction in which the blood flows (after **Huxley** and **Plateau**).

In the *Leptostraca* (*Nebalia*), besides the delicate shell-fold, the lamellate thoracic feet function in a special manner as respiratory organs. Their two branchial plates (epipodite and exopodite) correspond with the branchial and respiratory plates of the *Phyllopoda*. The branchial plate (epipodite) of the proximal joint of the protopodite is morphologically equivalent to a *Decapodan* gill.

In the *Isopoda* the delicate-skinned lamellæ of the pleopoda serve for respiration, either both the lamellæ of a foot or only the inner, the outer one being hard-skinned and serving as a covering plate to protect the inner one.

The gills of the *Stomatopoda* (*Squilla*) are found as branched appendages on the outer lamellæ of the abdominal swimming feet (pleopoda). The arrangement of the gills in *Siriella* (*Mysidæ*) is similar; they here also occur in the males as appendages of the pleopoda, but on their inner branches.

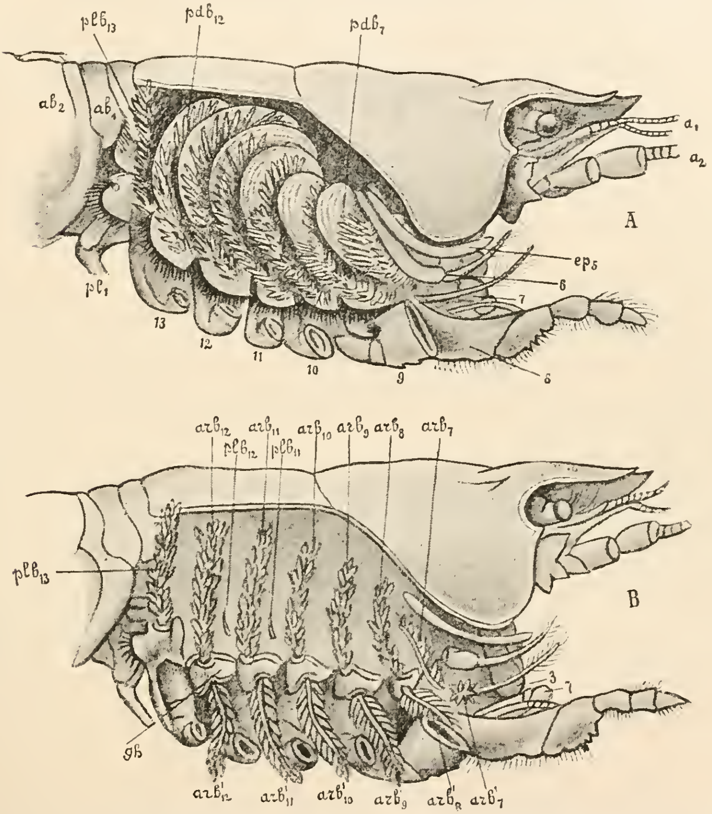

Fig. 228.—*A* and *B*, **Gills of Astacus fluviatilis.** In *A* the branchiostegite is removed. The gills are seen in their natural position. In *B* the podobranchiæ are cut off, and the outer arthrobranchiæ turned back downwards. Twice the natural size. a_1, a_2, 1st and 2d antennæ; 3, mandible; ep_5, epipodite of the 2d maxilla; 6, 1st maxillipede; 7, 2d maxillipede; 8, 3d maxillipede; 9, forceps (cut-off); 10-13, the 4 succeeding ambulatory feet; pl_1, 1st pleopod; ab_1, ab_2 1st and 2d abdominal segments; *pdb*, podobranchiæ; *arb*, inner, arb^1, outer arthrobranchiæ; *plb*, pleurobranchiæ; the numbers attached show the appendages to which the gills belong, in order from before backward, beginning with the anterior antenna as No. 1; *gh*, articular membrane between the body and basal joint of the protopodite (after **Huxley**).

The gills of the *Amphipoda*, *Schizopoda* (except the *Mysidæ*), and

Decapoda are always originally epipodial appendages on the basal joints of the protopodites of the thoracic feet. They may be considered as homologous formations, and perhaps correspond with the gills of the *Phyllopoda* and the basal branchial plates (epipodites) of *Nebalia.*

The pouch-shaped Amphipodan gills have already been considered.

Schizopoda.—The branchial tufts of the *Euphausidæ* (Fig. 226), whose branches are feathered, project freely from the basal joints of the protopodites of the thoracic limbs into the surrounding water without being covered by the lateral lamellæ of the cephalo-thoracic shield. The branching of the gills becomes increasingly complicated from the anterior to the posterior thoracic limbs. On the most anterior thoracic limb the gill is a simple appendage.

In *Lophogaster* we find 2 to 7 such gills. These consist of 3 feathered branches, the upper one of which lies in a branchial cavity covered by the lateral lamella of the cephalo-thoracic shield. The gills are said not to rise direct from the basal joint of the protopodite, but close to it from the body. None the less they should be considered as dislocated epipodial appendages.

The gills of the *Decapoda* (Figs. 227, 228) deserve more detailed description. Over the sides of the thorax to the right and left there is always an arched extension of the cephalo-thoracic shield, which, as branchiostegite (Fig. 227, *kd*), covers a respiratory cavity (*kh*) in which the gills (*k*) lie. The branchiostegite extends ventrally to the points of insertion of the thoracic limbs, where the respiratory cavity on each side communicates by means of a longitudinal slit with the surrounding medium. We distinguish in the first place, according to their manner of insertion, three sorts of gills—podobranchiæ, arthrobranchiæ, and pleurobranchiæ. The **podobranchiæ** arise from the basal joints of the thoracic limbs, the **arthrobranchiæ** from the articular membranes between the basal joints and the body, and the **pleurobranchiæ** from the body itself, but directly above the basal joints of the thoracic limbs to which they belong. All gills are to be considered phylo-genetically as epipodial appendages of the basal joints of the protopodites, the arthro- and pleurobranchiæ having moved from their original places. Again, we distinguish two sorts of gills, according to their special form, viz. trichobranchiæ and phyllobranchiæ. In the **trichobranchiæ** numerous branchial filaments stand round a common stem or a common axis, like the bristles of a bottle brush. In the **phyllobranchiæ** the branchial filaments are small lamellæ arranged in two rows on the stem, like the

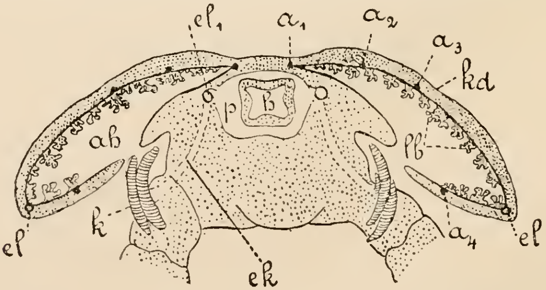

Fig. 229.—**Birgus latro. Diagrammatic transverse section in the region of the heart (after Semper).** *kd*, Branchial or lung cover; *h*, heart; *k*, gills; *ah*, respiratory cavity; *p*, pericardium; *ek*, branchial blood-canals leading to the heart; a_1, a_2, a_3, a_4, lung or shell vessels leading from the heart; *lb*, respiratory tufts; *el*, pulmonary vessels leading to the heart; el_1, the same near their entrance into the pericardium.

barbs on the shaft of a quill. Phyllobranchiæ and trichobranchiæ, between which there are many transitory forms, are not found together in the same species. Trichobranchiæ are found in the *Macrura* (with the exception of the *Sergestidæ*, *Carididæ*, and the genera *Gebia* and *Callianassa*); phyllobranchiæ are found in all *Anomura* and *Brachyura*, and in those *Macrura* which do not possess trichobranchiæ.

Podobranchiæ, arthrobranchiæ, and pleurobranchiæ may occur together, even on the same thoracic segment. They undergo many modifications and degenerations. The arrangement of the branchial apparatus in the various *Decapodan* genera and species may be given in branchial formulæ. We shall here give the branchial formulæ of *Astacus fluviatilis* and of *Cancer pagurus*.

Branchial Formula of Astacus fluviatilis (Cray-fish), after Huxley.

Thoracic segments and limbs.	Podobranchiæ.	Arthrobranchiæ.		Pleurobranchiæ.	Total.
		Anterior.	Posterior.		
VI. 1st maxillipede	0 (ep.)	0	0	0	= 0 (ep.)
VII. 2d ,,	1	1	0	0	= 2
VIII. 3d ,,	1	1	1	0	= 3
IX. 1st ambulatory foot	1	1	1	0	= 3
X. 2d ,, ,,	1	1	1	0	= 3
XI. 3d ,, ,,	1	1	1	Rudim.	= 3 + Rudim.
XII. 4th ,, ,,	1	1	1	Rudim.	= 3 + Rudim.
XIII. 5th ,, ,,	0	0	0	1	= 1
	6 + ep. +	6 +	5 +	1 + 2 Ru.	= 18 + ep. + 2 R.

Branchial Formula of Cancer pagurus (after Huxley).

Thoracic segments and limbs.		Podobranchiæ.	Arthrobranchiæ.		Pleurobranchiæ.	Total.
			Anterior.	Posterior.		
VI. 1st	maxillipede.	0 (ep.)	0	0	0	= 0 (ep.)
VII. 2d		1	1	0	0	= 2
VIII. 3d		1	1	1	0	= 3
IX. 1st	ambulatory foot.	0	1	1	0	= 2
X. 2d		0	0	0	1	= 1
XI. 3d		0	0	0	1	= 1
XII. 4th		0	0	0	0	= 0
XIII. 5th		0	0	0	0	= 0
		2 + ep.	+ 3	+ 2	+ 2	= 9 + ep.

While in other *Decapoda* the water enters the respiratory cavity through the lower longitudinal slit, in the *Brachyura* the water passes in and out only through certain small apertures, which are variously placed. Many *Brachyura* and *Anomura* may live for a longer or shorter time or almost exclusive on land, and show various adaptations which make it possible for them to retain water in the respiratory cavity, or to draw back into that cavity water which leaves it, or to breathe air direct. It would lead us too far to describe all these adaptations in detail. We shall only consider the respiratory organs of *Birgus latro* (*Anomura*), which lives in holes in the earth (Fig. 229). The respiratory cavity of this animal falls into two parts, an upper partly closed, and a lower more open, division, the lower edge of the branchiostegite being bent inwards and somewhat upwards. The reduced gills lie in the lower division. The upper division holds air and functions as a lung. The integument of the outer cover (branchiostegite) of this upper division carries a great number of branched tufts, projecting into the air-filled cavity, and containing complicated arrangements of vascular spaces. For the special relation of the vascular system to the respiratory organs in *Birgus*, see the section on the circulatory system.

The manner in which in the Crustacea the blood which has become poor in oxygen is conducted out of the body to the respiratory organs, and the blood rich in oxygen conducted out of the respiratory organs into the body, will be described in the section on the blood-vascular system.

II. The Integument.

The chitinous secretion of the hypodermis (body epithelium) which we met with in the *Annulata* is even more strongly developed in the *Arthropoda*. It covers the whole surface of the body and its appendages as a cuticle, serving not only for protection, but also as **outer skeleton** (exo-skeleton) for the attachment of the muscles. This chitinous envelope is very differently constituted in the different divisions of the Crustacea, sometimes even in different parts of the same animal. In most *Decapoda* and *Stomatopoda*, many *Amphipoda* and *Isopoda*, and on the shell-fold of *Ostracoda* and *Cirripedia*, however, the usually thick chitinous cuticle becomes very hard and firm by deposits of lime salts (carbonate and phosphate of lime); in certain *Brachyura*, *Cirripedia*, and *Ostracoda* it is even as hard as stone. The cuticle is, however, always comparatively thin, delicate, and flexible between the joints and on the respiratory surfaces.

The constitution of the exoskeleton presents obstacles to the growth of the body. These are overcome by moulting or ecdysis. Under the old exoskeleton a new one is developed, which is at first soft and extensible; but after the first has been thrown off it soon hardens. The metamorphoses of the Crustaceans take place by means of several repeated moults. In this process not only the outer chitinous integument of the body, but the cuticular lining of the alimentary canal also is removed and renewed.

The cuticle, of whose further structure we cannot here speak more in detail, is penetrated by fine perpendicular pores.

Dermal glands, which take part in excretion, a fact which may be proved by feeding with carmine, are very common, especially in soft-skinned Crustaceans.

It is hardly possible as yet to give a detailed comparative account of the structure and distribution of the various forms of glands. But we may give a few cases which for one reason or another are specially interesting.

The segmentally arranged **ventral** and **leg glands** of *Branchipus* consist of small groups of dermal gland cells, found on the segments of the middle body. In every segment a pair of ventral glands are found on the outer sides of the double ganglion of the ventral chord, and a pair of leg glands in the basal lobes of the leg. The segmental repetition, the character as dermal glands, the position (in the region of the legs), and their rod-like secretion entirely justify the opinion that these glands are homologous with the spinning and setiparous glands of the *Annelida* and the coxal glands of other *Arthropoda*.

In the basal joints of the 8 pairs of thoracic limbs of *Nebalia* hypodermal glands have been observed; it is probable that these perform excretory functions. Their position recalls the leg glands of *Branchipus*.

We may here further mention—the dermal glands which occur in the basal joints of certain limbs of the *Phronimidæ*; and the beautifully constructed dermal glands in the limbs of the *Corophiidæ*; the unicellular dermal glands scattered in various parts of the body of *Orchestia*; the scattered dermal glands of the *Anisopoda* (*Tanais*, *Apseudes*); the hook glands of *Caprellidæ*; and the so-called cement glands of female *Decapoda*, which lie on the ventral side of the abdomen, and whose hardening secretion serves for the attachment of the eggs.

In *Tanais* and the *Corophiidæ* the secretion of the above-mentioned glands hardens in water, and probably helps, by cementing together foreign particles, to form the tubes inhabited by these animals.

Special interest is claimed by the uni- and multi-cellular dermal glands lying scattered under the chitinous cuticle of the *Corycæidæ* (*Copepoda*), because in them the connection of the gland cells with nerve fibres can be easily observed. A unicellular dermal gland with cuticular duct, which opens through a pore of the chitinous integument of the body, is in the *Corycæidæ* generally coupled with a terminal ganglion cell lying under a sensory seta. The nerve which runs to this pair of cells divides into 2 threads, one of which is connected with the gland cell and the other with the ganglion cell.

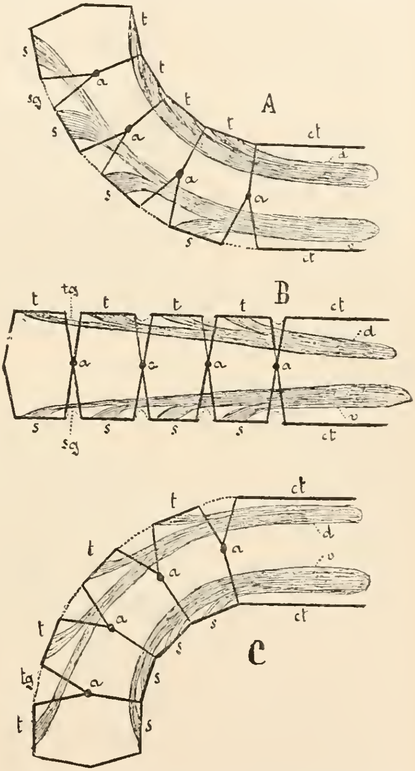

Fig. 230.—**Diagrams to demonstrate the mechanism of the motion of the segmented body in the Arthropoda.** One larger segment (*ct*) and 4 smaller. The exoskeleton is denoted by black lines, the interarticular membranes by dotted lines. The hinges between consecutive segments are marked *a*. *t*, Tergal (dorsal) skeleton; *s*, sternal (ventral) skeleton; *d*, dorsal longitudinal muscles = extensors (and flexors in an upward direction); *v*, ventral longitudinal muscles = flexors. In *B*, the row of segments is stretched; in *A*, by the contraction of the muscle *d*, bent upwards; in *C* downwards. *tg*, Tergal; *sg*, sternal interarticular membranes.

III. The Musculature.

A continuous dermo-muscular tube, such as is characteristic of the worms in general, and specially of the *Annulata*, is wanting in the Crustaceans, and indeed in the Arthropoda generally. The development of the cuticular integumental covering into a much firmer exoskeleton makes a greater localisation of the musculature possible.

We may assume, that in the homonomous segmented ancestors of the Crustacea, whose conjectural organisation we have already in many points diagrammatically sketched, 4 strongly-developed longitudinal muscles ran through the body. Two of these muscles ran dorsally and two ventrally on each side of the middle line. They were segmented in correspondence with the segmentation of the body, and in such a manner that the single muscle segments or myomeres lay intersegmentally, *i.e.* with one end attached to the integument of one segment, and the other to the integument of the next following or next preceding segment.

We have no difficulty in assuming that the dorsal and ventral pair of longitudinal muscle strands answer to the 4 similarly placed masses of longitudinal muscles which occur in the *Polychæta*. We can find nothing, certainly, corresponding with the circular musculature of the *Annelida*. Traces of the latter may perhaps, however, be seen in the muscles which run at right angles to the longitudinal muscles, and which are attached on the one hand to the integument of the body, and on the other to the basal portion of the appendages which they move.

Setting aside at first the muscles belonging to the inner organs, we can arrange the whole musculature of the body in three principal groups, viz. (1) the musculature of the body, (2) the musculature of the limbs, and (3) the musculature common to both.

The formation and segmentation of the body and limbs in different divisions varies so much in details that a comparative review of the musculature cannot be attempted. We may, however, explain the principle according to which the muscles are arranged, and perform their functions not only in all Crustaceans, but universally in all Arthropoda. We have to bear in mind—(1) that the passive locomotory organ, the skeleton, is in the Arthropoda an exoskeleton, which is in each segment of the body and in each joint of its extremities a **chitinous tube**; (2) that the muscles lie on the inner side of the skeleton, and are attached to the same from within; (3) that the muscles are stretched intersegmentally, *i.e.* between the consecutive segments; (4) that the chitinous integument between two segments is thin and flexible, forming the interarticular membrane; (5) that the tubular exoskeleton of two adjacent segments or joints is hinged together in each case at two transversely opposite points.

The arrangement and working of the musculature is illustrated by Fig. 230, which shows us 5 segments, one larger (*ct*) and 4 smaller, in vertical projection. The firm hard portions of the exoskeleton are marked by strong outlines, the delicate and flexible interarticular membranes (*tg*, *sg*) by dotted lines. The hinges between 2 consecutive skeletal segments are marked *a*. Such a hinge is found on each side; in the projection the corresponding right and left hinges are seen as one. A dorsal muscle (*d*) is attached to the larger segment (*ct*), and runs through the smaller segments, being inserted in the dorsal or **tergal** skeleton (*t*) of each by means of a bundle of fibres. A ventral muscle (*v*) does the same on the ventral or sternal side (*s*).

The skeletal segments may be compared to a double-armed lever whose fulcrum lies in the hinges. If the dorsal muscle contracts, it draws the dorsal arm of the lever (the tergal portion of the skeleton) in the direction of the pull towards the larger segment; the tergal interarticular membranes become folded, the ventral stretched, and the 4 segments bend upwards (Fig. 230, *A*). If the ventral muscle contracts, while at the same time the dorsal slackens, the row of segments will be bent downwards (Fig. 230, *C*).

It is evident that the same effect would be attained if the dorsal and ventral muscles, instead of collectively running from the smaller segments to the larger segment, only ran from one segment to the next following, as we assumed to be the case in the racial form, and as is really the case in the thorax and abdomen of many Crustaceans (*Branchipus*, many *Isopoda*, *Amphipoda*, etc.) The row of segments would then likewise bend dorsally on the contraction of the dorsal myomeres, and ventrally on the contraction of the ventral.

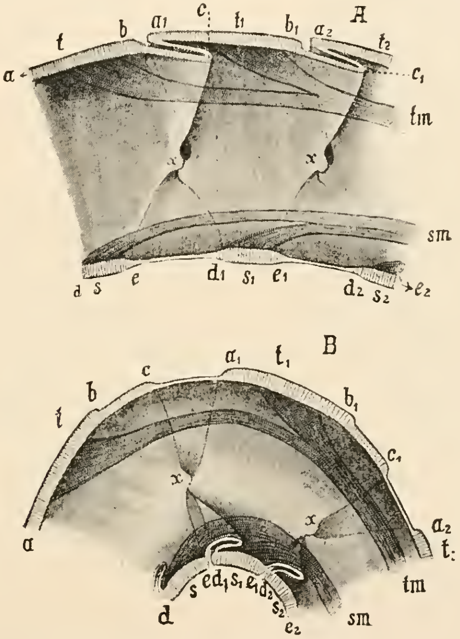

FIG. 231.—Two abdominal segments of the Cray-fish, diagrammatic. t, t_1, t_2, Tergal; s, s_1, s_2, sternal exoskeleton; x, hinges; b-c, b_1-c_1, articular facets, which when the row of segments is straightened take the position shown in B; a_1-b_1, a_2-b_2, c-a_1, c_1-a_2, e-d_1, e_1-d_2, interarticular membranes; *tm*, tergal; *sm*, sternal longitudinal muscle. *A*, Row of segments nearly straightened; *B*, Row of segments bent ventrally by the contraction of the sternal longitudinal muscle, stretching the intertergal membranes.

In reality only the ventral bending takes place in the Crustacea; the comparatively weakly developed dorsal longitudinal muscles serve only for straightening the body, as we see from the movements of the abdomen of the Cray-fish (Figs. 231 and 232). In its normal position the abdomen is somewhat stretched, and lies more or less as a straight posterior prolongation of the cephalo-thorax. Each dorsal (tergal) skeletal segment (Fig. 231, *A*, t, t_1, t_2) has its most anterior somewhat thinner portion (b-c, b_1-c_1) pushed some distance under the posterior edge of the preceding segment. The interarticular membrane (c-a_1, c_1-a_2) being bent backwards and outwards. The ventral hard skeleton consists of relatively narrow transverse segmental stripes (d-c, d_1-c_1, d_2-c_2), connected by large intersegmental membranes (c-d_1, c_1-d_2), which in a state of rest are somewhat stretched. The pair of dorsal muscles (*tm*) are attached on the one hand anteriorly to the lateral walls of the cephalo-thorax (corresponding with the large segment of our diagram, Fig. 230), and inserted, on the other hand, by just as many pairs of bundles as there are abdominal segments, to the inner surfaces of the terga, a pair of muscles being inserted in each.

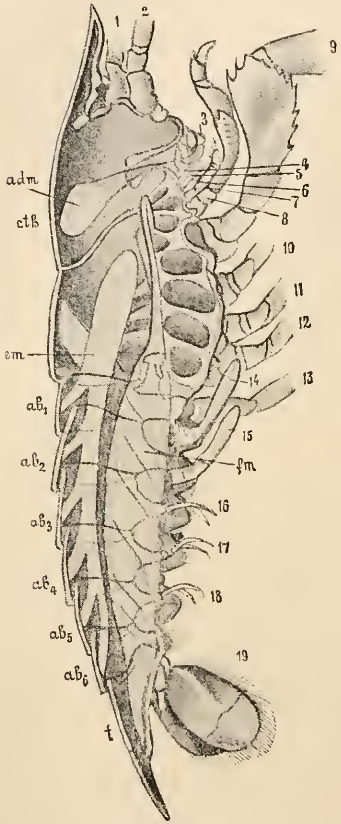

FIG. 232.—**Astacus fluviatilis. Longitudinal section to represent the most important muscles and their relation to the exoskeleton (after Huxley).** *cm*, Extensor; *fm*, flexor of the abdomen; *adm*, adductor of the mandibles; *cth*, cephalothorax; ab_1-ab_6, abdominal segments; *t*, telson; 1-19, limbs, 1-13, of the cephalothorax, 14-19, of the abdomen.

The pair of ventral or sternal muscles (*sm*) are attached anteriorly to the ventral side of the cephalo-thorax to a row of processes of the exoskeleton directed inwards, and partly bound together by transverse ridges, which roof over the thoracic portion of the ventral chord and the sub-neural vessel. Posteriorly the sternal longitudinal muscles are successively inserted on the inner sides of the sternal skeleton of the abdominal segments. The fibres of this muscle are twisted like the strands of a rope.

If the pair of sternal or flexor muscles contracts, the abdominal row of segments corresponding with our diagram bends ventrally (Fig. 231, *B*) till, as is the case in swimming, the telson touches the ventral side of the cephalo-thorax. While in this position the intersternal membranes of the abdomen are folded, the whole tergal integument is stretched, and the tergal articular facets and interarticular membranes are drawn out from under the terga which cover them, and come freely to the surface. If now the sternal muscle slackens, and the pair of tergal or extensor muscles (Fig. 231, *A*; Fig. 232) contracts, the abdomen is straightened, the terga pass under one another like the tiles of a roof, and the intersternal membranes are stretched. A dorsal bending of the body is impossible, first because the intersternal membranes do not allow of further stretching, and secondly, because the terga can only be pushed one beneath the other as far as the posterior limit of their articular facets. This is best exemplified by the illustration (Fig. 231, *A*).

The mechanism for the movement of the appendages is in principle the same as that of the body. It is, however, evident that if the hinges of the joints of an appendage were arranged at equal distances along two parallel straight lines the row of joints of the extremity could only bend in one plane, as is indeed the case in the row of body segments. But the two hinges of the consecutive joints are in reality so placed as to make free movement possible. The exoskeleton of the body segments is related to the exoskeleton of the basal joints of the appendages which it carries just as a large joint of a limb is to a smaller. The muscles which on the one hand are inserted in the exoskeleton of the first joints of the extremities, by preference attach themselves on the other to the tergum of the corresponding segment.

The mechanism of the forceps (chelæ) of the Cray-fish (Fig. 233) is as follows. The forceps is formed by the two terminal joints of the chelate foot. The last joint but one is produced into a pointed process (*zf*). The last joint (*eg*) articulates with it in the ordinary way by means of two opposite hinges.

Round the hinges the two joints are connected by means of a thin and flexible interarticular membrane. Two muscles serve in the way shown in the illustration for moving the terminal joint. By the contraction of the smaller the movable joint describes an arc away from the fixed process (Fig. 233, *B*), opening the forceps. If the much stronger muscle which lies on the other side of the hinge contracts the chela closes (*A*).

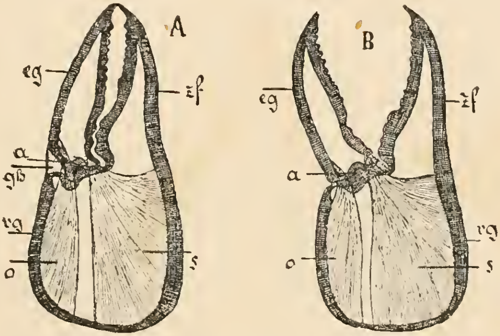

FIG. 233.—**Forceps of the large chelate foot of the Cray-fish**, diagrammatic. *A*, closed. *B*, Open. *eg*, Terminal joint; *vg*, last joint but one with the pincer process *zf*; *a*, hinge on which the terminal joint moves; *gh*, interarticular membrane; *o*, opening muscle (abductor); *s*, closing muscle (adductor).

The muscles of Crustaceans are often attached to the exoskeleton by means of sinewy and even chitinous terminal pieces. In the latter case we can speak of an endoskeleton. Both arrangements serve for the increase of the surface of attachment of the muscles.

In those *Entomostraca* in which the strongly-developed shell-fold surrounds the whole body as a bivalve shell (*Ostracoda*, *Estheridæ*), a strong **shell-muscle** connecting the two valves transversely serves for closing the shell. We find such a shell-muscle among the *Malacostraca*, also in the *Leptostraca* (*Nebalia*).

As in all Arthropoda, the body musculature is transversely striated.

IV. The Enteric Canal.

The intestine of the Crustacea has a simple straight course through the body. The **mouth** lies on the ventral side of the head, bordered and protected by an **upper** and an **under lip** (paragnatha); it is surrounded by appendages which serve for the taking in of food (mandibles, maxillæ, and maxillipedes). The **anus** is found in the terminal segment of the body. We must distinguish, according to their ontogenetic origin and structure, 3 sections in the intestine: the fore-gut, the hind-gut, and the connecting mid-gut. The fore- and hind-guts, proceeding respectively from the ectodermal stomodæum and proctodæum of the larva or embryo, are lined internally by a chitinous cuticle (intima). This cuticle, secreted by the hypodermis, passes at the mouth and anus into the chitinous exoskeleton. Only the epithelium of the **mid-gut**, which proceeds from the mesenteron, is of endodermal origin. The mid-gut in almost all Crustaceans is distinguished by the possession of diverticula which play the part of a **hepato-pancreas.**

As in other divisions of the animal kingdom, so also in many Crustaceans, pronounced parasitism has brought about a degeneration of the enteric canal. In the parasitic *Cirripedia* we find various stages of degeneration leading to the condition of the *Rhizocephala*, in which an enteric canal is wanting not only in the adult animals, but also in the free-swimming larvæ. In the parasitic *Isopoda* the hind-gut with the anus, and sometimes a large part of the mid-gut as well, may entirely disappear.

A. The Fore-gut.

There is a characteristic difference between the condition of the fore-gut in *Entomostraca* and *Malacostraca*. In the former it is a simple alimentary tube (œsophagus), which, passing between the œsophageal commissures, runs dorsally, to pass later into the mid-gut which runs backwards. In the *Malacostraca*, on the contrary, it falls into at least two divisions, that which follows the buccal cavity, the ascending narrower **œsophagus**, and the broader **masticatory** or **fore-stomach** which lies in the head, and which leads to the mid-gut. Special salivary glands entering the œsophagus seem generally to be wanting in the Crustacea (such glands have only been observed in Crayfish), but glands emerging on the upper lip, in the buccal cavity, and on the maxillæ, are common; these are usually called salivary glands. They probably belong to the category of the leg- and the other dermal glands.

For the present we set aside the special modifications which the fore-gut may undergo; its structure is essentially the following. Its wall consists of a layer of hypodermis cells, which rest upon an outer, often chitinous, basal membrane, and secrete, like the hypodermis of the integument, internally, a chitinous cuticle (intima). The fore-gut is embraced by circular muscular hoops, serving to narrow its lumen; groups of muscles, mostly paired, attached on one side to the intestinal wall, on the other to a portion of the neighbouring integument, effect its expansion and other movements. The hypodermis of the œsophagus is often difficult to discover.

Entomostraca.—The end of the œsophagus often projects in the form of a cone or funnel into the first part of the mid-gut, somewhat as does the uterus of a mammal into the vagina. This projection, which in *Branchipus* is bi-lobed, and set with small cuticular papillæ, perhaps corresponds with the masticatory stomach of the *Malacostraca.*

The intima of the œsophagus is generally longitudinally folded, which permits of its enlargement.

In the *Ostracoda* the œsophagus may be enlarged before passing into the mid-gut into a so-called crop.

In the *Leptodora* (*Daphnidæ*) two divisions have been distinguished in the fore-gut, an ascending pharynx and a strikingly wide œsophagus running backwards. This latter may perhaps belong to the mid-gut.

Malacostraca.—The possession of a **masticatory** or **fore-stomach** is characteristic of the Crustacea belonging to this second principal division. It is found in the *Leptostraca*, though in a somewhat simpler form than in the other *Malacostraca.* The masticatory stomach is a spacious sac of varying form. It is chiefly distinguished by the fact that its wall projects into its cavity in the form of definitely arranged folds, ridges, valves, plates, lamellæ, and other prominences, on which the chitinous intima is specially strongly developed, so as together to form a very complicated framework. The special form of the masticatory stomach, with its projections, pouches, etc., and its chitinous framework, is extremely important in classification. A more detailed account, however, would take far too much space. The masticatory stomach generally falls into two divisions, an anterior **cardiac division**, into which the œsophagus enters, and a posterior **pyloric division**, which opens into the mid-gut. In the anterior division the food which has already been torn in pieces by the oral appendages is still further cut and ground up by the masticatory framework, and the digestion takes place chiefly in the posterior division, into which the secretions of the glands of the mid-gut enter.[1] The special formation of the wall with its chitinous framework, in this second division, both hinders too rapid passage of the food to the mid-gut, and prevents its return into the masticatory stomach.

The parts of the masticatory framework are moved by suitably arranged muscles, which are attached to the neighbouring integument.

In many parasitic *Isopoda*, which suck in food in a fluid condition, the masticatory stomach is much simplified.

The intestine of the *Entoniscidæ* will be described at the end of this section (p. 341).

In the *Decapoda*, on the anterior wall of the cardiac division of the masticatory stomach, are found two concretions, principally consisting of carbonate and phosphate of lime; these are the so-called **crab's eyes** or **gastroliths.** In

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[1] See section on the mid-gut of the *Decapoda* (p. 340).

the Cray-fish they are developed in summer and are largest just before the skin is cast. During this process they reach the cavity of the masticatory stomach, are there ground up, dissolved, and re-absorbed. It is highly probable that they yield the calcareous material for the hardening of the new after the casting of the old skeleton.

The whole intima of the fore-gut, together with the complicated chitinous framework of the masticatory stomach, is removed when the integument is shed; it is vomited from the mouth.

B. The Mid-gut.

This represents the endodermal portion of the enteric canal, and its epithelium shows clearly its endodermal origin even in the adult, being differently constituted from the ectodermal epithelium of the fore- and hind-guts. The mid-gut again differs from the two other divisions of the intestine in having no chitinous intima answering to the outer chitinous cuticle of the body. It is nearly always distinctly marked off from the fore- and hind-guts by constrictions or valve-like arrangements. Besides this its anterior end, and occasionally its posterior end also, is marked by the entrance of glandular diverticula which represent invaginations of its wall. These, among which the hepatopancreas of the higher *Malacostraca* shows the greatest development, we shall describe in the section on the **diverticula of the mid-gut.** The form and extension of the mid-gut are very varied, while in the *Entomostraca* and many *Malacostraca* it represents by far the largest portion of the enteric tube, running from the head to near the posterior end of the body; it has in other *Mala-*

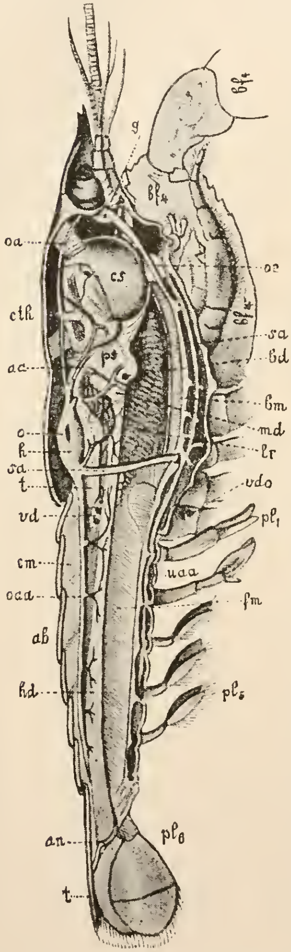

Fig. 234.—**Astacus fluviatilis, median section of the body, seen from the right side.** The thoracic feet and antennæ of the left side are incompletely drawn (after **Huxley**). *oa*, Ophthalmic artery (aorta cephalica); *aa*, antennal artery; *cth*, cephalo-thorax; *o*, lateral ostium of the heart; *h*, heart; *sa*, sternal artery; *t*, testes; *vd*, vas deferens; *em*, extensor muscles of the abdomen; *oaa*, upper abdominal artery (arteria abdominalis); *ab*, abdomen; *hd*, hind-gut; *an*, anus; *t*, telson; *g*, brain (supra-œsophageal ganglion); *bf*$_4$, 4th thoracic foot (chelate foot); *oe*, œsophagus; *cs*, cardiac portion of the stomach; *ps*, pyloric portion of the stomach; *bd*, right aperture of the hepatopancreas into the stomach; *bm*, ventral chord; *md*, mid-gut; *lr*, liver (hepatopancreas); *vdo*, male genital aperture; *pl*$_1$, *pl*$_5$, *pl*$_6$, 1st, 5th, and 6th pleopoda; *uaa*, lower abdominal artery; *fm*, flexor muscles of the abdomen.

costraca (at least in the *Decapoda*, *Isopoda*, and probably also in the *Anisopoda*) almost entirely disappeared as a special division of the enteric tube. It is here used up in the formation of its strongly developed glandular diverticula, the hepatopancreatic tubes. In these cases the hind-gut which proceeds from the ectodermal proctodæum represents by far the largest portion of the enteric tube, running through the body from the masticatory stomach to its hindermost end.

The fact that in the *Isopoda* and the *Decapoda* the whole enteric tube with the exception of the point of entrance of the hepatopancreas, proceeds from the embryonic or larval stomodæum and proctodæum is ontogenetically established; in the other *Malacostraca* ontogenetic investigations as to the limit between mid- and hind-guts have yet to be made. Up to the present time conclusions as to the extent of the hind-gut have been based exclusively upon that of the chitinous intima.

The walls of the mid-gut and of its diverticula show the same general structure. The distinct epithelium is placed on a basal membrane and sometimes shows on the surface turned towards the lumen of the intestine a (non-chitinous) cuticular limiting membrane. On the outer side of the basal membrane the mid-gut and its diverticula are encircled by hoop-like, regularly repeated, circular muscles, which are seldom transversely striated. Longitudinal muscles are more rare, and where they occur are not numerous. They lie on the inner side of the circular muscles. In life we can observe, not only in the mid-gut but also in its diverticula, rhythmical waves of contraction, which are often very strong; these also bring about, especially in the smaller *Entomostraca* without hearts, a sort of circulation of hæmolymph in the lacunar system of the body.

The Mid-gut of the Entomostraca.

This generally falls into an anterior widened division (stomach, chyle stomach, stomach-intestine) and a posterior narrower division which we might designate the small intestine. The diverticula of the mid-gut, present usually in a single pair, open into the former division.

The details of the arrangement of the **mid-gut diverticula** of the *Entomostraca* are very varied. The two diverticula of the *Branchiopoda* are themselves subdivided. They vary greatly in size. In *Apus* they have lateral branches beset with numerous glandular lobes. In the *Cladocera* (Fig. 192, p. 289) two short horn-like diverticula are generally found, which are directed forwards. In the *Ostracoda* the two diverticula are so long that they often project on both sides into the shell fold. Diverticula of the mid-gut are wanting in a good many *Copepoda*; in others they are present singly or in pairs, simple, or else complicated by the formation of accessory cœca. The arrangement of the two diverticula of the disc-shaped flattened *Branchiura* (*Argulus*) (Fig. 195, p. 291) recalls that in many *Branchiopoda*. Each of the two diverticula divides first into an anterior and a posterior branch, each of which again branches, and the branches penetrate as far as the lateral edges of the cephalo-thorax. In the generally longitudinally folded stomach of the non-parasitic *Cirripedes* diverticula also not unfrequently enter; *Balanus* has 8 diverticula, which may be branched (*B. perforatus*).

The Mid-gut Diverticula of the Malacostraca.

Among these we shall first distinguish those which enter at the anterior end of the mid-gut from those which enter at the posterior end. The former are universal. They correspond with the mid-gut diverticula of the *Entomostraca*, and are generally called **livers**. Taking into account their physiological activity, however, the name of **hepatopancreas** is more suitable.

In the *Leptostraca* we find 4 pairs of hepatic tubes, 3 pairs of which, one upper, one lateral, and one lower, are very long and run along the mid-gut, reaching far into the abdomen. The short 4th pair stretches to the front of the head. The tubes join on each side to form a short wide sinus, and these sinuses, uniting at the two sides, enter by a common aperture the posterior end of the masticatory stomach ventrally.

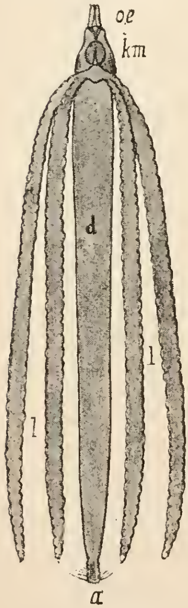

Fig. 235.—**Enteric canal of Asellus aquaticus (after G. O. Sars).** *oe*, Œsophagus; *km*, masticatory stomach; *d*, mid-gut; *a*, anal-gut (rectum); *l*, hepatic tubes (hepatopancreas).

In the *Arthrostraca* also there are 1 to 3 pairs of diverticula entering the beginning of the mid-gut which is occasionally widened so as partly to surround the masticatory stomach. Among these there are often 2 (in the normal *Amphipoda* 4) tubes running backwards along the intestine, which, according to their function and the structure of their epithelium, specially deserve the name of a hepatopancreas.

The arrangement of the glands of the mid-gut in the *Schizopoda*, the *Cumacea*, and the **larvæ** of the *Decapoda* is similar to that in the *Leptostraca* and *Arthrostraca*. They are distinguished by 3 pairs of long hepatic tubes entering the most anterior portion of the mid-gut. In the *Stomatopoda*, distributed along the whole length of the mid-gut, there are 10 pairs of branched tufts of hepatic tubes. The adult *Decapoda* are distinguished by the possession of a paired hepatopancreas, which to the right and left enters the posterior and lower end of the masticatory stomach. By means of much branching the liver assumes the character of a very voluminous tubular gland filling a large part of the cephalo-thorax, and falling on each side into 3 lobes—an anterior, a lateral, and a posterior. If we examine only the extreme forms of the cells which unite to form the epithelium of the *Malacostracan* liver, we can distinguish two sorts of cells: first, **ferment cells**, whose varied secretions (which may be liquid or solid, coloured or colourless) digest fibrine; second, **hepatic cells**, whose fatty secretion contain a colouring matter related to the gall pigment of vertebrates. In consequence of these observations we cannot describe the glands of the mid-gut simply as a liver, but rather as a hepatopancreas. We cannot, also, carry out a sharp distinction of the cells into ferment cells and hepatic cells; many transition forms occur.

The glandular cæca which enter the posterior end of the mid-gut are found in the *Amphipoda*, *i.e.* in the *Caprellidæ* and the *Crevettina*. They occur as one pair, except in *Melita*, which has only one such glandular tube. Physiologically they must (in the *Crevettina*) be considered as urinary glands. Morphologically they cannot be compared with the Malpighian vessels of the *Tracheata*, since they do not belong to the hind-gut, but to the mid-gut.

In the posterior portion of the mid-gut of *Nebalia* there is at the inner side of the dorsal enteric wall a longitudinal channel, which, at the end of the mid-gut, is continued into a cæcum, reaching into the anal segment posteriorly, and ending in two lateral projections.

C. The Hind-Gut.

The hind-gut in Crustaceans is as a rule short and limited to the last segment or segments of the body. Its epithelium is lined with a frequently very strong chitinous intima. Its wall is almost always provided with well-developed hoop-like circular muscles. Special muscles or groups of muscles (dilators) are stretched between the hind-gut and the neighbouring integument (and widen the former by their contraction). In those *Isopoda*, *Anisopoda*, and *Decapoda* in which the hind-gut is very long, taking the place of the small intestine of other Crustacea, we find these dilators only at the posterior differentiated division of the hind-gut, called the rectum.

Among the *Amphipoda*, *Orchestia* has a hind-gut which is strikingly long for this group, reaching as far forward as into the 7th thoracic segment.

The **anus** lies in the terminal segment—**dorsally** in the *Entomostraca*, **ventrally** in the *Malacostraca*.

Special glands or diverticula entering the hind-gut are wanting in the Crustacea.

In the *Lynceidæ* among the *Cladocera*, however, a glandular contractile cæcum is found ventrally in the hind-gut, which in *Pleuroxus* is prolonged into a long vermiform appendage wound round the gut.

In the *Stomatopoda* it is said that 2 glandular saccules enter the anal gut. As other excretory organs are wanting in the adult animals these are supposed to have excretory functions.

In the meantime it is not certainly proved that these glands of the *Lynceidæ* and *Stomatopoda* really belong to the hind-gut and not rather to the terminal division of the mid-gut.

The widening of the hind-gut on the contraction of the dilators draws in water through the anus, and subsequent contraction of the lumen of the gut expells it again with fæcal particles. It has been stated without sufficient foundation that these sucking movements, at least in certain *Entomostraca* (*Phyllopoda*), imply a respiratory function in the hind-gut.

The chitinous intima of the hind-gut is ejected through the anus when the integument is shed.

The peculiar modification which the enteric canal undergoes in the **females of many parasitic Isopoda** can here only briefly be described, taking as an example *Portunion mænadis* (*Entoniscidæ*). The narrow œsophagus leads into a large sac composed of two lateral sacs. The inner wall of the sac projects into its lumen in the shape of numerous long processes covered with chitinous intima. In this division of the gut, which has been called the **cephalogaster**, the absorption of the food takes place. The cephalogaster is continued posteriorly into a second division, the typhlosolis, whose wall, much thickened dorsally, projects into the lumen in such a way that the latter in a transverse section is crescent-shaped, the concave side being directed upwards. A strong cuticle lines the typhlosolis and carries closely-placed long and stiff hairs which, projecting from the opposite walls, mingle in such a way as to form a fine sieve apparatus, only admitting of the passage of fluids. The typhlosolis, which is fastened to the body wall by a pair of strong muscles, is followed by a third extremely muscular division, which is called Rathke's organ, and carries on energetic rhythmic contractions. A small tubular blindly closed terminal division, which is the only representative of the mid-gut, receives the ducts of two large contractile hepatic tubes. A hind-gut and anus are wanting. The whole intestine stretches only to the 3d thoracic segment. *Portunion mænadis* sucks the blood of its host (*Carcinus*). The peculiar structure of the enteric canal, in which Rathke's organ and the cephalogaster alternately contract and expand, seems adapted to this sucking process.

The enteric canal of the minute male of *Portunion* which lives in the body of the female does not show the peculiar transformation which it undergoes in the female. It is straight, and possesses two hepatic tubes, a hind-gut, and an anus.

V. The Nervous System.

The nervous system of the Crustacea is constructed on the same type as that of the *Annulata*, and must be derived from the latter. The result of research in comparative anatomy and ontogeny justify us in giving the following diagrammatic representation of its general structure and original constitution. This scheme stands in direct relation to the generalised plan of the segmentation of the body of the Crustacean sketched above (p. 300). In the most anterior segment of the body (head segment) the **brain** (supra-œsophageal ganglion), consisting of two symmetrical lateral halves, lies in front of and over the œsophagus, giving off nerves to the unpaired eye, the anterior antennæ and the frontal sensory organs (see below). Each of the other segments of the body possesses two ganglia (a double ganglion) lying very near each other in the ventral middle line. The two ganglia of each segment (the two symmetrical halves of each double ganglion) are connected together by means of a transverse commissure, and with the corresponding ganglia of the preceding and subsequent segments by longitudinal commissures. The two most anterior longitudinal commissures which connect the double ganglion of the second segment with the brain embrace the œsophagus. These are the **œsophageal commissures.** The whole central nervous system thus consists, as in the *Annulata*, of the **brain** and **the segmented ventral chord (ventral ganglionic chain)**, whose segmentation corresponds with the segmentation of the body. From each double ganglion of the ventral chord nerves proceed to the body musculature of the segment to which it belongs, and to the musculature of the limbs with which that segment is provided. There are therefore one double ganglion for the 2d pair of antennæ (in the 2d segment), a similar one for the 2 mandibles (in the 3d segment), 2 pairs of ganglia for the anterior and posterior pair of maxillæ (in the 4th and 5th segments), and so on, a pair of ganglia in each segment for the limbs which belong to it.

It must, however, be specially noted that the assumption of a special ganglion for the posterior antennæ is not yet securely established. Such a ganglion would have to be compared with the infra-œsophageal ganglion, and the segment corresponding with it to the first trunk segment of the *Annulata*. In most Crustaceans, however, the nerves for the posterior antennæ do not arise from a distinct ganglion but from the œsophageal commissures; their places of origin in the higher Crustacea have indeed moved as far forward as the brain. There are, however, many important reasons, to be brought forward later, in favour of the assumption of an originally distinct pair of ganglia and a special segment for the posterior antennæ.

All the more important and striking deviations from the typical Crustacean nervous system can be classed under the following heads.

1. Approximation **of the two ganglia of a double ganglion** by the shortening of the transverse commissure which unites them, and finally the fusing of these two ganglia into one; its composition out of two lateral ganglia can, however, often be seen externally, and always internally, on examination of its finer structure.

2. Approximation **and contact of the longitudinal commissures** connecting the consecutive ganglia.

3. Approximation **and contact of the consecutive ganglia** by the shortening of the longitudinal commissures. This may lead to the fusing of the consecutive ganglia into one ganglionic mass, in which the original composition out of several ganglia can sometimes be clearly recognised; at other times, however, this is very indistinct, or even quite unrecognisable.

4. **Longitudinal displacement and shifting of the ganglia,** generally from behind forward. Ganglia may be displaced from one segment into another.

5. **Shifting of the points at which nerves leave the ventral chord.** These displacements, however, apparently never affect the real origin of the nerves in the centres of the nervous system.

6. **Entire disappearance of ganglia.** This is perhaps only to be proved with certainty of the most posterior ganglia of the body.

All these changes go hand in hand with transformations of the whole organism, especially with modifications in the segmentation of the body and in the development of the extremities. In the young stages of many Crustaceans it often happens that certain ganglia are still separate which in adult animals are fused. We see from this how important the knowledge of ontogeny is for a right comprehension of the morphology of the nervous system.

The concentration of the nervous system (the fusing of originally distinct ganglia to form larger ganglionic masses) can be observed in most of the natural divisions of the Crustacea.

For the sake of clearness we shall in each group of the Crustacea place the most conspicuously segmented nervous system in the foreground, while the description of the deviating, concentrated, or simplified nervous systems will be distinguished by the use of small print.

Entomostraca.

The nervous system of the *Phyllopoda* (Fig. 236, *D*), especially that of the *Branchiopoda* (*Branchipus*, *Artemia*), best corresponds with the scheme of the Crustacean nervous system given above. The transverse commissures between the ganglia of the ventral chord are tolerably long, and so the whole ventral chord has the character of a **ladder nervous system.** The two ganglia of a double ganglion are connected together by **two** transverse commissures. We must note as specially important that the pairs of ganglia for the oral appendages, *i.e.* for the mandibles and maxillæ, have remained distinct. Behind these 3 pairs of ganglia come (in *Branchipus*) the 11 pairs of ganglia of the limb-carrying segments, then the 2 pairs of ganglia in the genital segments. Behind these, ganglia only occur as rudiments in the two following segments.

The nerves for the posterior antennæ arise out of the œsophageal commissures, which are provided with a layer of ganglionic cells; this layer can the better be considered the ganglion of the 2d antennæ, since in front of the mandibular ganglion, and behind the œsophagus, the œsophageal commissures are connected by a double tranverse commissure, corresponding with the double transverse commissures of the other ganglia of the ventral chord.

The nerves for the unpaired frontal eye, for the paired stalked eyes, and for the anterior antennæ spring from the brain.

In correspondence with the greatly reduced segmentation of the whole body in the *Cladocera* (*Phyllopod*) its central nervous system is also much less pronounced. The ladder-like ventral chord consists of 7 pairs of ganglia, the foremost of which (infra-œsophageal ganglion) innervates the mandibles and maxillæ, and the other 6 the 6 pairs of limbs. In front of the infra-œsophageal ganglion we find here a transverse commissure connecting the œsophageal commissures. The nerve for the 2d antennæ arises from the infra-œsophageal ganglion. In *Leptodora* the 6 ventral ganglia in the adult animals are fused into one ventral ganglionic mass, while in the young animals they are still tolerably distinct.

The nervous system of the *Ostracoda* deserves further investigation. The ventral chord of *Cythere* which follows the brain and œsophageal commissures is said to consist of an infra-œsophageal ganglion and 4 subsequent ventral ganglia. The infra-œsophageal ganglion is said to show its composition out of two ganglia and to innervate the jaws, while the 3 subsequent ganglia give off nerves to the limbs, and the last ganglion nerves to the most posterior divisions of the body and the genital apparatus.

In contrast with the above, the ventral chord of *Halocypris* appears much concentrated. It consists of an infra-œsophageal ganglion with nerves to the jaws and maxillipedes, and a small ventral ganglion. Out of the latter arise 2 pairs of nerves, which probably innervate the musculature of the limbs and the abdomen.

In the various divisions of the *Copepoda* the central nervous system shows several degrees of centralisation, from a more or less decentralised condition to the almost complete fusion of brain and ventral chord to form one ganglionic mass, pierced through by the œsophagus. The segmentation is most complete in the free-swimming *Copepoda*, from which all the others are to be derived. In the *Calanidæ*, for example, we have (apart from the brain) a ventral chord consisting of 7 ganglionic swellings which stretches more or less far into the abdomen.

In other free-living *Copepoda* the number of ganglia is reduced, and the abdominal ganglia become small or disappear. But in the *Corycæidæ* (Fig. 236, *H*) we already have only one single ganglionic mass surrounding the œsophagus, from which nerves radiate to the sensory organs, extremities, the musculature of the body, etc. The nervous system in various delicate parasitic *Copepoda* shows a similarly concentrated, though partly also reduced, condition.

The nervous system of the Carp-lice (*Argulidæ*, Fig. 236, *G*), which are closely connected with the true *Copepoda*, is relatively highly developed. The concentrated ventral chord consists of 6 ganglia with much-shortened longitudinal and transverse commissures. The 4 posterior ganglia supply the 4 pairs of limbs, the 2 anterior the jaws, maxillipedes, and clinging feet. At the points at which the œsophageal commissures join the brain there are 2 ganglionic swellings, from which nerves go to the 2d antennæ.

Among the *Cirripedes* the nervous system of the *Lepadidæ* is the most richly segmented. They possess a brain, long œsophageal commissures, and 5 or 6 ventral ganglia. The nervous system of the so-called *Cypris-like larvæ*, that is, of those which develop into hermaphrodite individuals, is similar.

The so-called **complementary males** of the *Lepadidæ*, on the contrary, and their *Cypris-like larvæ*, only possess a cerebral ganglion (supra-œsophageal ganglion) and a thoracic ganglion, which alone represents the whole ventral chord. In the *Balanidæ* the ventral ganglia are fused into one large ventral ganglionic mass. Degeneration goes very far in the whole nervous system of the *Rhizocephala* (*Sacculina*, *Peltogaster*), which are so much degenerated by parasitism; we here find it in the form of one single ganglion, from which various nerves radiate (*cf.* Fig. 248, p. 373). This ganglion is said not to correspond with the larval supra-œsophageal ganglion, but to arise anew in the development of the adult animal.

Malacostraca.

I. **Leptostraca.**—The interesting genus *Nebalia*, which of all living *Malacostraca* stands nearest to their racial form, possesses an extraordinarily richly segmented nervous system. If this pronounced segmentation recalls, on the one hand, the nervous system of the *Phyllopoda* (*Branchiopoda*), it shows on the other (especially in the structure of the brain) a decidedly Malacostracan character. The ganglia for the posterior antennæ are moved far forward on the œsophageal commissures, and form, as in all *Malacostraca*, the most posterior division of the brain. The transverse commissure, which corresponds with them, however,

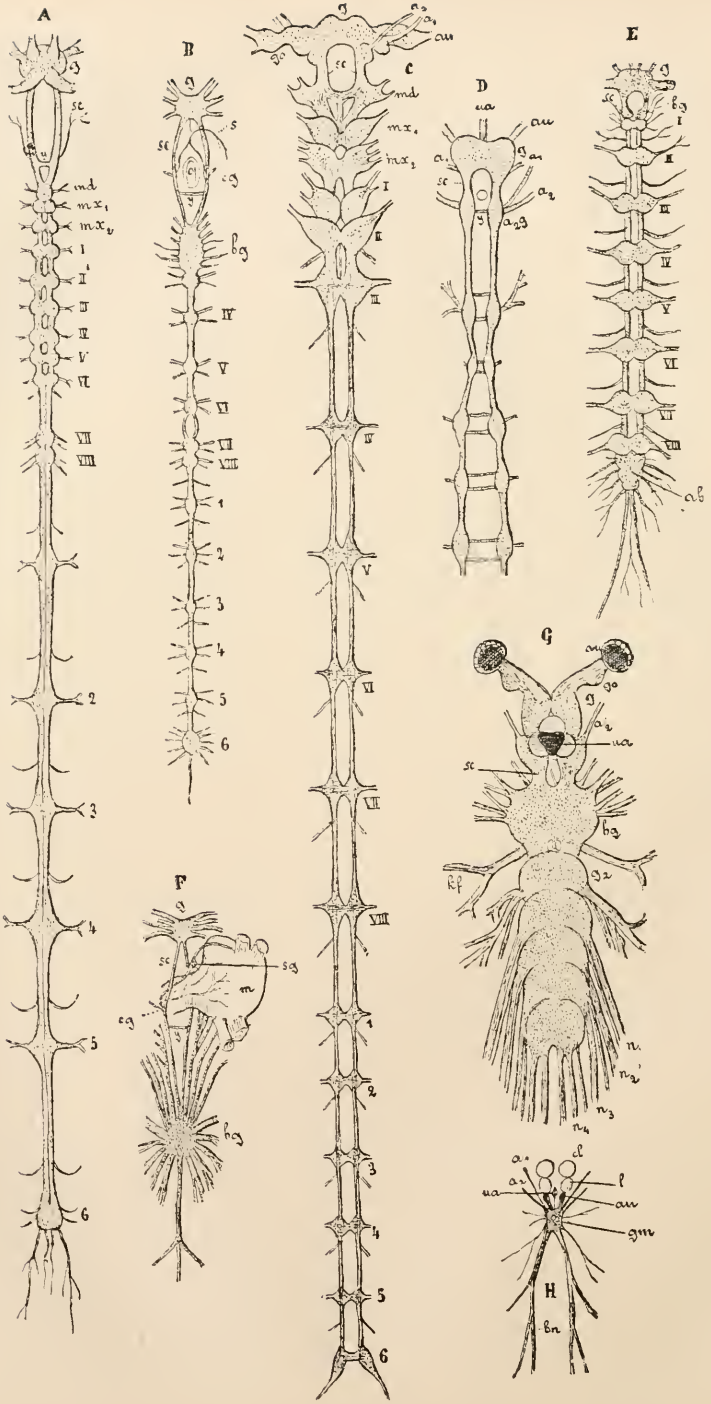
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Fig. 236.

FIG. 236.—Central nervous systems of various Crustaceans. *A*, Of **Euphausia pellucida** (after **G. O. Sars**). *B*, Of **Astacus fluviatilis** (after **Vogt** and **Yung**). *C*, Of **Apseudes Latreillii** (combined from several figures by **Claus**). *D*, Of **Limnadia** (after **Klunzinger**), anterior portion. *E*, Of **Asellus aquaticus** (after **G. O. Sars**). *F*, Of **Maja squinado** (after **Milne Edwards**). *G*, Of **Argulus Corregoni** (after **Claus**). *H*, Of **Sapphirina Edwardsii** (after **Haeckel**). *gg*, Brain; *au*, nerves of the paired eyes; *ua*, unpaired eye with its nerve; *go*, ganglion opticum; a_1, nerve of the 1st antenna; a_2, of the 2d antenna; *sc*, œsophageal commissures; *y*, post-œsophageal tranverse commissure of the same (commissure of the antennal ganglia of 2d antenna?); a_2g, ganglion of the 2d antenna (in *D*); *md*, mandibular ganglion; mx_1, mx_2, ganglia of the 1st and 2d pairs of maxillæ; *I-VIII*. thoracic ganglia; *bg*, sub-œsophageal ganglion, consisting of several fused ganglia; 1-6, abdominal ganglia; *s*, sympathetic nervous system; *sg*, ganglion of the same; *cg*, commissural ganglion; *m*, stomach (in *F*); *ab*, fused abdominal ganglia (in *E*). In *G*, g_2 signifies 2d ventral ganglion; n_1-n_4, nerves for the 4 pairs of limbs; *kf*, nerve for the clinging foot. In *H*, *gm* signifies the ganglionic mass (brain fused with ventral chord) broken through by the œsophagus; *cl*, corneal lens; *l*, lens; *bn*, posterior strong nerves, the lateral pairs of which go to the limbs.

has remained separate behind the œsophagus and in front of the mandibular ganglia. **The ganglia of all the pairs of limbs, even those of the oral limbs, have remained separate on the ventral chord,** which has 17 ganglionic swellings. We thus find, counting from before backward: (1) a mandibular ganglion, (2) and (3) 2 maxillary ganglia; (4) to (11) 8 thoracic ganglia, and (12) to (17) 6 abdominal ganglia. It is a significant fact that in the larva the 6 abdominal ganglia are followed by a small 7th swelling, belonging to the limbless 7th abdominal segment; this, however, entirely disappears at a later stage. This fact is rightly interpreted to mean that there must originally have been more than 6 pairs of pleopoda.

In contradistinction to the ladder-like nervous system of the *Phyllopoda*, the ganglia in *Nebalia* are fused in the middle line to form a double ganglion, and the longitudinal commissures are moved nearer each other. The latter are very much shortened in the thoracic region in correspondence with the abbreviation of the thoracic segments.

II. **Arthrostraca**, *Anisopoda*.—The richly segmented nervous system of *Apseudes* (Fig. 236, *C*) is closely connected with that of *Nebalia*. The brain and œsophageal commissures are followed by an infra-œsophageal section, in which we can clearly distinguish the separate ganglia for the mandibles, the two pairs of maxillæ, and the pair of maxillipedes. It is important to note that the maxillipedal ganglion, which corresponds with the first thoracic ganglion of *Nebalia*, is here more closely connected with the preceding ganglia, in keeping with the commencing transformation of the first pair of thoracic feet into a pair of maxillipedes. The 4 infra-œsophageal ganglia are followed by 7 double ganglia for the thorax and 6 for the abdomen, the last and largest of which is probably composed of two or more fused together. The ganglion for the posterior antennæ is moved towards the brain, but the transverse commissure corresponding with it is clearly visible behind the œsophagus, in front of the mandibular commissure. The ganglia of the ventral chord are clearly double, and connected by two separate longitudinal commissures.

In *Tanais* fusings and displacements seem already to have taken place in the ventral chord. The ventral chord here has, it is said, only 12 ganglia.

Isopoda.—Among the true *Isopoda* several genera (such as *Sphæroma*, *Idothea*, *Glyptonotus*) are, in the rich segmentation of their nervous systems, closely connected with *Apseudes*. In *Sphæroma* we even find a 7th abdominal ganglion. The double nature of the central nervous system is everywhere more or less distinctly marked. The transverse commissure corresponding with the ganglia of the 2d pair of antennæ seems to be more or less completely fused with the mandibular commissure.

In many *Isopoda* there is fusion in the ventral chord and displacement and reduction of the pairs of ganglia. The mandibular, maxillary, and maxillipedal ganglia in the first place fuse to form an infra-œsophageal ganglionic mass. Then a reduction in the number of the ganglia takes place chiefly in those of the abdomen. In some *Isopoda* 5 abdominal ganglia occur, in others (*Porcellio*, *Oniscus*, *Asellus*, Fig. 236, *E*) we find as the remains of the abdominal ventral chord only one ganglionic swelling attached to the last thoracic ganglion, and in others even this is wanting. The number of the separate thoracic ganglia is less frequently reduced.

In those *Entoniscidæ* (*Portunion mænadis*) which are specially strongly modified through parasitism we find, besides the brain (which is everywhere retained), 2 thoracic ganglia and one abdominal ganglion at some distance from them, under the heart; while in the not less strongly modified parasitic *Bopyridæ* 7 thoracic ganglia are said to occur.

Amphipoda.—Here in all cases we have a fusing of the anterior ganglia of the ventral chord, so that the nervous system no longer shows at any point that segmentation which we meet with in many *Isopoda*. In the nervous system of the *Gammaridæ* we can still distinguish, apart from the brain, an infra-œsophageal ganglion consisting of several fused ganglia, and further 7 thoracic ganglia in the 7 free thoracic segments, and 4 abdominal ganglia in the 4 anterior abdominal segments.

In *Phronima* the centralisation goes still further. There are only 5 thoracic ganglia behind the infra-œsophageal ganglionic mass, which consists of 6 fused ganglia. The last of the 4 abdominal ganglia is formed by the fusion of 3 ganglia which are still separate in the embryo. Not only the points of divergence of the nerves for the 2d antennæ, but also those of the nerves of all the oral appendages are shifted forward on to the œsphageal commissures. The nervous system of many *Hyperidæ* is similar to that of *Phronima*. In others, however, concentration goes still further, as not only the last 2 thoracic but also the last 2 abdominal ganglia may fuse together. In the most extreme cases we thus find only an infra-œsophageal ganglionic mass, 4 thoracic and 3 abdominal pairs of ganglia. In the *Caprellidæ* the reduced abdomen retains no ganglia. Besides the brain and the sub-œsophageal ganglion which supplies the mandibles, maxillæ, and maxillipedes, we find 7 thoracic ganglia, the 7th of which lies behind the 6th in the last thoracic segment but one. Three small ganglia belonging to the abdomen follow close behind the 7th thoracic ganglion. In young animals 4 more pairs of abdominal ganglia begin to form, and then fuse with the 3 small ganglia of the adult animal above mentioned.

III. **Thoracostraca.**—In many *Schizopoda* (*Euphausia*, Fig. 236, *A*, *Boreomysis*) all the ganglia for the oral and thoracic limbs, 11 in number, seem to have remained separate.

In others the number is evidently reduced by the fusing of originally separate ganglia. In *Gnathophausia* we find besides the infra-œsophageal ganglion (which most probably consists of the fused mandibular and maxillary ganglia) 8, in *Eucopia* however only 6, thoracic ganglia. The most anterior thoracic ganglion has in this latter case probably united with the infra-œsophageal ganglion, and the last thoracic ganglion with the last but one. This is made probable by the fact that in the last thoracic segment no ganglion occurs. In *Mysis* (*relicta*) the thoracic ganglia are even said to be fused into a longitudinal strand. The œsophageal commissures are in many *Schizopoda* (*Euphausia*, *Boreomysis*) connected directly behind the œsophagus and in front of the most anterior ventral ganglion by a transverse commissure, which perhaps corresponds with the commissure of the ganglia of the posterior antennæ often mentioned above.

All the *Schizopoda* seem to possess 6 abdominal ganglia. The nerves which supply the body musculature of the abdomen diverge from the longitudinal commissures half-way between 2 consecutive ganglia. This arrangement seems to be characteristic of all *Thoracostraca*.

In the *Cumacea* (*Diastylis*) the ventral chord consists of 16 pairs of ganglia; the three most anterior of these, which have moved near each other, supply the oral limbs; 7 thoracic, and 6 abdominal pairs of ganglia follow.

The nervous system of the *Stomatopoda* in its segmentation shows very clearly a close relation to the metamerism of the body. In the cephalo-thoracic portion of the ventral chord only the 3 ganglia of the 3 most posterior thoracic segments have remained separate, *i.e.* of those segments which, uncovered by the cephalo-thoracic shield, carry the biramose ambulatory feet. All the other preceding ganglia are united into a large infra-œsophageal ganglion. The œsophageal commissures are very long, and show behind the œsophagus the transverse commissures often mentioned above. The 3 posterior thoracic ganglia are followed by the 6 abdominal ganglia which are characteristic of the *Thoracostraca*.

Decapoda.—We here find many grades of concentration, from the still tolerably richly segmented nervous system of the *Macrura* to the nervous system of the *Brachyura*, in which all the ganglia of the ventral chord have fused into one single thoracic ganglionic mass. Taking as a type of the *Macrura* the *Cray-fish*, *Astacus fluviatilis* (Fig. 236, *B*), the highly developed brain gives off the nerves for the eyes, the anterior antennæ, and from its posterior part for the posterior antennæ. The œsophageal commissures are of considerable length and connected behind the œsophagus by a transverse commissure. In the course of each œsophageal commissure lies a small ganglion, the so-called commissural ganglion. From these 2 commissural ganglia various nerves diverge, among which the visceral nerves and the nerves of the mandibles are to be specially noted. The latter indeed have their roots in the infra-œsophageal ganglion, but are united with the œsophageal commissures as far as the commissural ganglia. The œsophageal commissures enter an infra-œsophageal ganglionic mass which consists of 6 united ganglia, *i.e.* of the mandibles, 2 maxillæ, and 3 maxillipedes. The last swelling of this infra-œsophageal ganglionic mass (the 3d maxillipedal) is pretty clearly marked off. The 5 distinctly separate large thoracic ganglia for the 5 posterior thoracic segments and their extremities (the ambulatory feet) follow, and of these the 4th and 5th ganglia are very near each other. In the abdomen we find 6 ganglia, the last is the largest, and, as in all *Malacostraca*, may well represent 2 or even more originally separate ganglia. In the *Cray-fish*, as in nearly all *Thoracostraca*, the 2 ganglia of the originally double ganglion and the longitudinal commissures between the consecutive ganglia of the ventral chord are so closely connected in the middle line that their double nature is not outwardly perceptible. The longitudinal commissures separate from each other only between the penultimate and antepenultimate thoracic ganglia (6th and 7th), so as to let the sternal artery pass between them.

In a few *Macrura* the 2 most posterior thoracic ganglia are fused, or there is a close approximation of all the cephalo-thoracic ganglia (*Carididæ*, *Palinurus*). Here, however, the 6 abdominal ganglia remain separate, while in the *Paguridæ* only 1 abdominal ganglion is present, in correspondence with the great reduction of the abdomen. We finally come to the *Brachyura* (Fig. 236, *F*), in which, in correspondence with the great reduction of the abdomen and the concentration of the cephalo-thorax, the whole ventral chord is fused together into a great thoracic knot, from which numerous nerves radiate out to all sides.

Sympathetic Nervous System.

This seems to occur in all *Malacostraca*, at least it has been observed with considerable uniformity in representatives of the three principal divisions, the *Leptostraca*, *Arthrostraca*, and *Thoracostraca*. In the Cray-fish a nerve with double roots arises on each side out of the commissural ganglion, proceeds forwards to the upper lip and mounts upwards at the sides of the œsophagus. The two nerves unite on the upper side of the stomach to form a median nerve which swells into a ganglion. From this ganglion a branching nerve runs backwards and spreads out in the wall of the stomach and gives off branches to the liver and also probably to the heart. The sympathetic nervous system is further connected by an unpaired nerve with the posterior portion of the brain.

So highly developed a sympathetic nervous system seems wanting in the *Entomostraca*. But it is noteworthy that in the *Phyllopoda* (*Branchipus*) a nerve arises on each side out of the œsophageal commissures which runs to the upper lip. The 2 nerves unite to form a labial ring, which is connected with a median ganglion and gives off nerves to the upper lip, the muscles of the œsophagus, etc.

Structure of the Brain.—The brain of the Crustacea rises in the *Malacostraca* to a very high degree of complication. This complication, which reaches its highest point in the *Decapoda*, is seen in the complicated arrangement of the ganglionic cells and of the courses of the fibres, and shows itself externally by the formation of lobes. It is probable that the brain of the ancestors of the Crustaceans contained the centres for the unpaired frontal eye, for the anterior antennæ and perhaps also for the frontal sensory organs, together with the fibrous connections between these centres themselves, between these centres and the œsophageal commissures, and lastly the anterior transverse connections of the œsophageal commissures. A higher complication is caused in most of the Crustacea now living (all *Malacostraca* and many *Entomostraca*), first by the occurrence of the paired eyes, and second by the fact that the originally infra-œsophageal ganglia of the posterior antennæ unite with the brain from behind. We can in these cases distinguish three principal regions in the brain. **First**, an anterior region (fore-brain), with the centres for the unpaired eye (where this persists) and for the paired eyes. The optic nerves of the latter, whose fibres in the brain of the higher Crustacea form a chiasma, enter on each side a frequently very large optic ganglion, which is the largest accessory lobe of the fore-brain. Besides this the fore-brain has, especially in the higher *Malacostraca*, other lobate formations. **Second**, a mid-brain which adjoins the fore-brain, and contains the centres for the nerves of the anterior antennæ. **Third**, the hindermost region of the brain (hind-brain), which is formed by the ganglia for the posterior antennæ, whose transverse commissure is to be found behind the œsophagus, where it has, as already described, often remained as a separate transverse commissure between the œsophageal commissures.

Neurochord strands or **giant nerve tubes**, like those with which we became acquainted in the *Annulata*, occur in the ventral chord of the *Thoracostraca*. An intermediate nerve also, of varying extent, has here and there been observed in the ventral chord.

VI. The Sensory Organs.

A. Eyes.

These are, as a rule, well developed in the Crustacea, and often show a high degree of complexity, especially in the *Malacostraca*, occasionally also in certain *Entomostraca*. Visual organs are either wanting or very much reduced in the adult condition of most of the parasitic and attached Crustacea (*Cirripedia*), also in many deep-sea forms and in others which live in dark places. Setting on one side a few divergent forms of Crustacean eyes, we can distinguish 2 kinds, which may occur simultaneously in the same animal: the **unpaired frontal eye** (accessory eye) and the paired lateral eyes (principal eyes). Both belong to the head. The unpaired eye lies above the brain, the paired at its sides.

The **unpaired eye** occurs in the young larval forms of all Crustaceans (**Nauplius eye**): it is always retained in the adult *Entomostraca*, sometimes well developed, sometimes in a reduced condition. In the *Malacostraca* it degenerates in the course of development. From the universal distribution of the unpaired eye in the *Entomostraca* and young *Malacostraca* we may conclude that it was present in the ancestors of the Crustaceans.

Paired eyes are found in all *Malacostraca* and many *Entomostraca*. They are either movable stalked eyes or fixed sessile eyes. The first may be imagined to arise out of unstalked eyes by the raising of that part of the head immediately surrounding the eye, by its articulation, and further growth into a stalk. Formerly the stalked eyes were often erroneously considered to represent a pair of extremities. In the development of the Crustaceans the paired eyes always appear much later than the unpaired eye, and we have reason for assuming that the unpaired eye is phylogenetically older than the paired. The following is a short review of the occurrence and distribution of the paired or principal eyes.

Entomostraca.—**Phyllopoda**: in the *Estheridæ* and *Apusidæ* the paired eyes have moved towards each other in the middle line. The *Branchiopoda* have movable **stalked eyes.** The two principal eyes of the *Cladocera* have fused in the middle line to form a trembling frontal eye, which, however, is wanting in *Monospilus*. **Ostracoda**: the *Cipridinidæ* possess besides the unpaired eye paired movable lateral eyes. In the *Cypridæ* and *Cytheridæ* also paired eyes occur, which may fuse together to form one unpaired eye. Whether these correspond with the paired eyes of other Crustaceans is not known. **Copepoda**: the *Carp-lice*, which are nearly related to the *Copepoda*, possess besides the unpaired eye 2 large lateral eyes. In the true *Copepoda* the latter are generally wanting, but paired eyes do occur, *e.g.* in *Pontellidæ*, and these perhaps correspond with the lateral eyes of other Crustacea. The paired eyes of the *Corycaeidæ* on the contrary do not easily admit of such a comparison. It is, however, not improbable that the racial forms of the *Copepoda* possessed paired compound eyes, which have been again lost. **Cirripedia**: in the adult animals the paired eyes are wanting throughout, but on the other hand the *Cypris-like larvæ* of the attached forms are provided with large lateral eyes.

Malacostraca.—Lateral eyes occur everywhere. They are stalked in the *Leptostraca* and all *Thoracostraca* except the *Cumacea*. In the last case the sessile eyes are generally fused in the middle line; they may, however, be altogether wanting. In the *Arthrostraca*, which have also been called the **Edriophthalmata** (in contradistinction to the other *Malacostraca*, which are known as the **Podophthalmata**), the eyes are sessile. The facts that movable stalked eyes occur in the *Phyllopoda* (*Branchipus*), and that the eyes of *Leptostraca* (*Nebalia*), which in every way stand nearest the racial form of the *Malacostraca*, are similarly stalked, make it appear probable (other facts also being taken into consideration) that the paired eyes of the *Arthrostraca* were once stalked.

Among the *Amphipoda* the *Phronimidæ* show peculiarities. They possess two pairs of compound eyes, one frontal pair and one in the region of the cheek. The two eyes of the same side, however, must have proceeded by division from the single eye of the *Amphipoda* which in the *Hyperidæ* is very large superficially.

Structure of the Eyes.—The unpaired eye was formerly described as an x-shaped eye-spot, with or without a refractive body. On account of its general distribution in the *Entomostraca*, it is also called the Entomostracan eye. Its structure will be best illustrated by means of an example.

The frontal eye of *Calanella mediterranea* (Fig. 237), a free-living *Copepod*, consists of 3 single eyes united together, 1 unpaired median and ventral, and 2 lateral and dorsal. Each single eye is composed of a pigment cup and a strongly refractive transparent "lens" laid in and on it. The term "lens" is, however, not applicable. It is composed of several cells, each of which is connected, whether at its outer or inner side is not yet quite certain, with a fibre of the optic nerve, and must therefore be considered as a retinal cell.

The great similarity in structure between such a single eye and the eyes of *Platodes* should not be overlooked. The three-fold structure of the unpaired Crustacean eye seems to be characteristic. Occasionally, *e.g.* in *Branchipus*, 3 separate nerves leave the brain to run to the 3 single eyes.

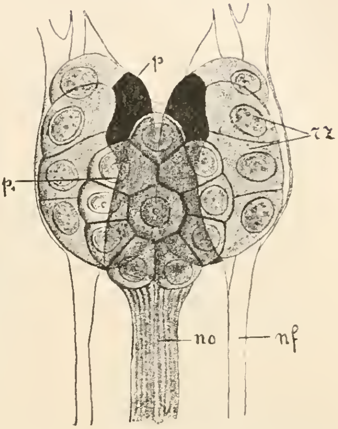

Fig. 237.—Eye of **Calanella mediterranea** ♀ juv, from below (after **Grenacher**). *p*, Pigment plates of the paired ; p_1, of the unpaired portion ; *rz*, retinal cells ; *no*, optic nerve ; *nf*, nervi frontalis.

The structure of the paired lateral eyes of the Crustacea (stalked and unstalked) is much more complicated. We have here the **compound eye** so characteristic of the *Arthropoda*. Even though, in single divisions of the Crustacea, it presents important modifications and complications in its structure, we nevertheless evidently have to do (with a few exceptions to be mentioned later) with **homologous** visual organs. Let us take for description the paired eye of *Branchipus*, which presents in a tolerably simple manner the typical structure of the compound eye. The movable stalk of the hemispherical eye of *Branchipus* (Fig. 238, *B*) contains the **optic nerve**; this swells in the stalk into a ganglion, the **ganglion opticum**, which must be reckoned as belonging to the brain. The optic ganglion is followed at the distal end near the base of the eye by a second ganglion, the **retinal ganglion**. Nerve fibres radiate towards the eye from the nerve cells of this retinal ganglion. The eye itself is separated from the cavity of the eye stalk by a thin basal membrane. The nerve fibres which radiate from the retinal ganglion penetrate this membrane to enter the retinal cells immediately on the other side of it. The eye represents the half of a hollow sphere with thick walls, whose outer spherical surface corresponds with the outer surface of the eye, and whose inner (concave) surface corresponds with the basal membrane. It consists of numerous closely packed single eyes arranged radially. In each **single eye or ommatidium** (Fig. 238, *E*) we distinguish three chief constituents :—

1. The **Retinula**, *i.e.* that portion of the whole retina of the compound eye which belongs to each of the single eyes. This is the proximal portion coming next to the basal membrane.

2. The **crystal cone**, and

3. The **hypodermal elements** with the superjacent chitinous cuticle, the **cornea** of the Arthropodan eye.

A. The **Retinula** consists of 5 long cells regularly grouped round a central axis: into the proximal ends of each of these cells a fibre from the optic nerve enters. The central axis is a tubular rod called the **rhabdom.** The 5 cells of the retinula contain pigment in the immediate neighbourhood of the rhabdom, and this pigment occurs in such large quantities in the thicker nucleated portions of the cells, that in each retinula a distal pigment layer is formed. Above this layer, terminal unpigmented portions project. These 5 ends together embrace the proximal ends of

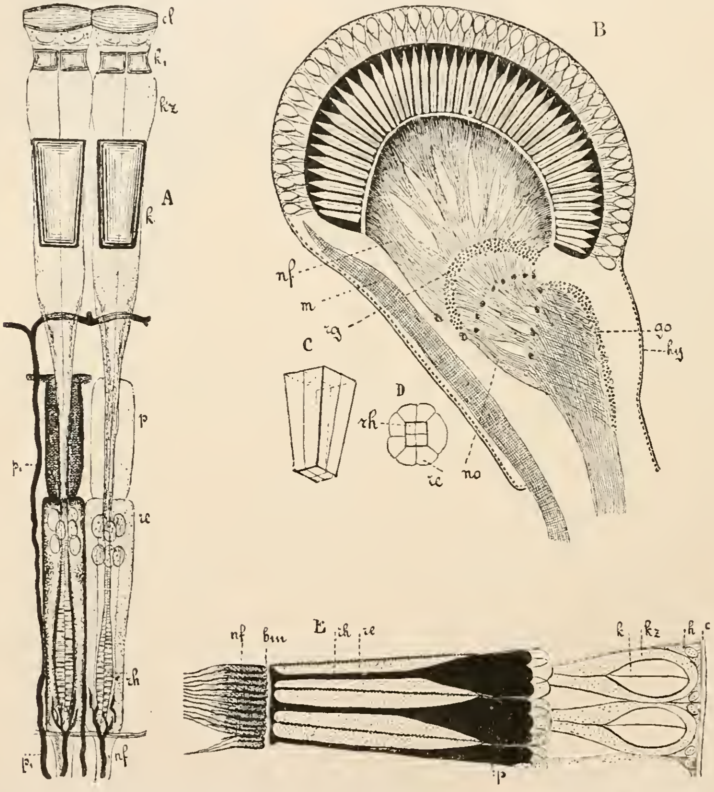

FIG. 238.—**Compound Crustacean eye.** *A*, **2 single eyes (ommatidia)** of **Palæmon Squilla.** The pigment is removed from the ommatidium on the right hand. *C*, **Isolated crystal body of an ommatidium,** consisting of 4 pieces. *D*, **Transverse section through a retinula,** about the middle of its length; *re*, retinal cells; *rh*, rhabdom consisting of 4 pieces. *B*, **Section through the stalked eye of Branchipus.** *E*, 2 ommatidia of the same animal, on a larger scale (figs. *A*, *C*, *D*, after **Grenacher,** *B* and *E*, after **Claus**); *c*, cornea (cuticle); *cl*, corneal lens; *hy*, hypodermis cells; *k*, crystal cone; k_1, outer crystal body; *kz*, crystal cells; *p*, pigment; p_1, in fig. *A*, pigment strands running between the retinulæ from the layer of nerve fibres; *re*, retinula; *rh*, rhabdom; *nf*, nerve fibres; *bm*, basal membrane; *m*, muscle; *rg*, retinal ganglion; *go*, ganglion opticum; *no*, nervus opticus.

B. the **refractive crystal cells.** These are 4 in number and together form a cone, which contains in its distal portion a solid crystal body secreted by the crystal cells. The layer of the crystal cells of the compound eye is covered by

C. The transparent smooth **chitinous integument** (**cornea**) with subjacent **hypodermis cells**, a continuation of the general body integument.

The principal distinctions to be pointed out between the stalked eye of the higher Crustacea and that of *Branchipus* are in the cornea and the optic ganglion. In the former the cornea (chitinous cuticle) is somewhat thickened over each single eye, forming for each a **corneal facet** or **corneal lens**, which is convex either on its inner or outer side or on both sides (Fig. 238, *A*, *cl*). The cornea then appears, when viewed from the surface, to be divided into regular polygonal areas, each of which corresponds with a corneal lens of a single eye.

Again, whereas the ganglion opticum is simple in *Branchipus*, in the stalked eyes of the *Malacostraca* it falls into 3 ganglia also placed in the eye stalk.

There are many important variations in detail in the structure of the Crustacean compound eye; these chiefly concern the number of cells in a retinula, the number of crystal cells in a single eye, the number of single eyes in the whole eye, and the specific arrangement of the elements. The *Decapoda* and *Isopoda* possess 7 retinular cells, the Branchiopoda and *Amphipoda* 5, the *Schizopoda* 4. The single eyes of the *Cladocera* have 5 crystal cells, the *Decapoda* and the *Branchiopoda* 4, the *Isopoda*, *Amphipoda*, and *Schizopoda* 2. In the *Isopoda* only a few single eyes are found which are not closely packed (4 in *Asellus*, 20 in *Porcellio*). The isolated corneal lenses (not flattened into polygonal facets) are here biconvex.

Each of the paired eyes of the *Corycacidæ* consists of one single eye, which in *Corycaeus* is strikingly large and long. It is in many respects markedly different from the ommatidia of the compound eyes of other Crustacea.

In the *Euphausidæ* among the *Schizopoda* there are, besides the two compound stalked eyes, other "accessory" eyes. These are found on the basal joints of the second and penultimate pairs of thoracic feet, and further, one in the ventral middle line of the abdomen between the pleopoda of each of the 4 anterior segments. Whether these organs belong to the category of visual organs is very doubtful; we only know for certain that they are luminous.

B. Other Sensory Organs.

Among the other sensory organs of the Crustacea the most widespread are the tactile, and what are generally supposed to be olfactory, organs. In many *Entomostraca* we find, in addition, the so-called **frontal sensory organs** of unknown physiological significance. **Auditory Organs** occur in all the *Decapoda*, and have also been observed in isolated cases in other divisions. Other structures which have been described as sensory organs with unknown functions must be passed over in silence, because of their sporadic occurrence and also because too little is known about them.

1. **Specific Organs of Touch.**—The points of the limbs, especially of such as serve for locomotion or for holding food, possess a finer sense of touch than the other parts of the surface of the body.

Special Tactile Setæ are the principal organs of touch. These are found chiefly on the antennæ, but also on other extremities, and occasionally also on the body itself. These setæ are distinguished from other setæ, spines, etc., whose function is almost entirely mechanical, by the fact that one or more ganglion cells lie at their bases connected by nerve fibres with the general nervous system (Fig. 239, *D*).

2. **Olfactory Organs** are found in the shape of pale delicate knobs, filaments, tubes, or points (Fig. 239, *A*, *B*), which are often grouped in bundles or transverse rows, and occur on the anterior antennæ.

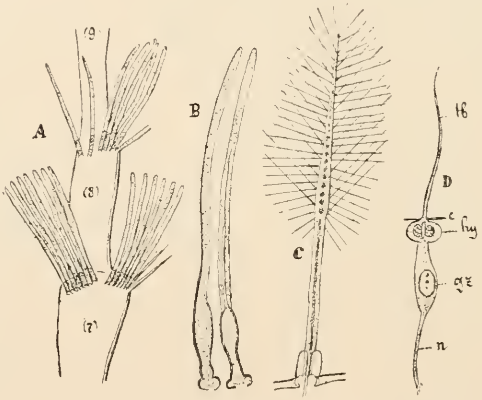

FIG. 239.—*A*, 7, 8, 9, joints of a 13-jointed flagellum of the anterior **Antenna of Nebalia (male) with the olfactory tubes.** *B*, Two **Olfactory tubes**, more strongly magnified. *C*, **Feathered sensory seta (auditory hair)** from the antepenultimate pair of thoracic limbs of **Apseudes**, with cuticular basal capsule. *D*, **Tactile hair** (*tb*) of **Branchipus.** *c*, Body cuticle; *hy*, hypodermis cells of the seta; *gz*, ganglionic cell; *n*, nerve fibre (after **Claus**).

Less frequently similar structures are also found on the second antennæ. They always occur in greater numbers in the male than in the female. The chitinous cuticle of these olfactory processes is thickest at their bases; towards their free end it is thin and delicate. At the base of each olfactory process a nerve fibre enters without forming a ganglionic cell, and continues into the interior of the process, running through it and filling it to its free end. The nerve fibres originate in ganglionic cells which, lying in the same or preceding joint of the antenna, belong to the antennal nerve.

Whether the so-called **Calceoli** of the *Amphipoda* are olfactory organs, or whether, perhaps, they represent a kind of auditory organ, must remain undecided.

3. **Frontal Sensory Organs.**—The characteristic position of these organs which occur in one pair is the frontal region very near the brain. They are projecting filaments, cones, rods, or other cuticular

appendages, into which 2 nerves, the frontal nerves, enter, generally forming ganglionic cells. In *Branchipus*, in place of the cuticular process, there is only an inconsiderable thickening of the cuticle with large hypodermis cells surrounded by ganglionic cells lying under it. Frontal sensory organs have been observed not only in the *Entomostraca* and *Entomostracan* larva, but also in the *Malacostracan* larva (*i e.* when it is a *Nauplius*), and from this we are justified in concluding that they were original structures present in the *Crustacean* racial form.

4. **Auditory Organs of the Decapoda.**—These lie on the basal joint of the anterior antennæ (antennulæ). In all *Decapoda* they occur as pit-shaped depressions of the chitinous integument, which generally remain open, but in a few cases (*Hippolyte*) may close and form a vesicle. In the open auditory vesicles the aperture is often covered by a compact row of setæ projecting from one of the edges, less frequently by a thin projecting fold. The auditory pits contain sand particles taken in from outside, which probably function as otoliths, like the concretions of fluorcalcium in the closed auditory vesicles. At the base of the auditory pits, or on the inner wall of the auditory vesicles, feathered hairs arise; these are (1) otolith hairs, which carry the otoliths, and (2) free hairs, projecting into the cavity of the auditory pit. The distinctly marked, swollen base of the auditory hair is extremely delicate and thin-walled, and permits a considerable oscillation of the hair in response to the waves of sound. The auditory nerve, which branches from the antennal nerve and has its root in the brain, first sends off fibres to single ganglionic cells. Filaments from these ganglion cells enter the auditory hairs at their bases and are attached near their points to rod-shaped bodies.

It is usually said of the **two closed auditory vesicles of the** *Mysidæ* (*Schizopoda*), that they lie in the tail. More correctly, they lie in the inner lamella (endopodite) of the last pair of pleopoda, which, together with the telson, form the caudal fin. Their structure does not deviate essentially from that of the Decapodan auditory organs. They are innervated from the last abdominal ganglion.

Oxycephalus (*Amphipoda*) possesses two auditory vesicles lying above the brain and containing otoliths.

There is some justification for classing the sensory organs of the *Decapoda*, *Schizopoda*, and *Amphipoda* above described as auditory organs; but we must not fail to mention that more recent experimental investigations greatly support the view that they also serve for regulating the position of the body, and for maintaining its equilibrium.

Feathered setæ, which in structure show great agreement with the auditory hairs of the *Decapoda*, occur on the antennæ and also in other parts of the body in many *Malacostraca*, and have often been considered as auditory organs. This is, however, still an undecided point. It is, however, probable that the auditory organs of the *Decapoda* have developed phylogenetically by the localisation of feathered sensory hairs and by the pit-like depression of those parts of the integument which carried them. The utilisation of foreign particles of sand as otoliths also supports this view.

VII. The Blood-Vascular System and the Body Cavity.

In the Crustacea (and in the Arthropoda generally) we find **no closed blood-vascular system. Those portions of the circulatory system which are provided with special walls, stand in open communication with blood lacunæ.** These lacunæ have no special walls, but are only spaces between the various organs of the body, and represent the body cavity.

Scheme of the Circulatory System.—According to what is now known of the Crustacea we may imagine the circulatory system in the racial form of these animals to be essentially as follows: **A contractile, tubular, dorsal vessel (heart)** runs longitudinally through the body in the middle line above the intestine. The direction of the flow of blood in this dorsal vessel is from behind forward, as in the dorsal vessel of the *Annulata.* In each body segment the dorsal vessel possesses a pair of lateral slit-like apertures, the so-called **ostia**, through which its interior is in open communication with the blood sinus surrounding it; this is the **pericardial sinus**, a part of the body cavity. The blood fluid (hæmolymph) enters the dorsal vessel through an aperture at its posterior end as well as through the lateral ostia from the pericardial sinus, and flows out at its anterior end. It then runs backward through the lacunar system more or less constantly in contact with the integument of the body and limbs where respiration takes place, and finally re-enters the pericardial sinus.

Entomostraca.—The scheme just sketched corresponds more exactly with the circulatory system of the *Branchiopoda* (*Phyllopoda*) than with that of any other known Crustacean. The contractile dorsal vessel (heart) of *Branchipus* (Fig. 191, p. 288) runs through the whole trunk and possesses a pair of ostia in all segments except the last, in which there is one terminal ostium. Anteriorly the heart is continued into an **Aorta** without ostia which enters the head and opens into the lacunar system of the body. In this latter system a ventral principal stream from before backward can be distinguished incompletely separated from the pericardial sinus by a septum stretched transversely over the enteric wall. The respiration takes place in the whole surface of the delicate integument of the body and limbs, but is apparently specially active in the branchial sacs. From the ventral principal stream an accessory stream runs into each limb down one side to the point, there to bend round and to run back up the other side to rejoin the principal stream.

The heart of the other *Entomostraca* (Figs. 192 and 193, p. 289) (where such an organ occurs) is always much shortened, sac or pouch-shaped and only supplied with one pair of ostia. Anteriorly, in front of the anterior terminal ostium, the heart is sometimes (in many *Copepoda*, *Branchiura*, and *Cladocera*) continued into a longer or shorter aorta. A posterior ostium is added to the heart of the *Copepoda.* The ostia through which the blood flows into the heart are generally provided with valves to prevent its return into the pericardial cavity on the contraction of the heart.

The heart is always placed above the intestine in the most anterior trunk region.

With regard to the **presence of the heart** in the *Entomostraca*, all *Cladocera* possess hearts. Among the *Ostracoda* it is only found in the *Halocypridæ* and *Cypridinidæ*, among the *Copepoda* only in the *Calanidæ*, *Pontellida*, and *Branchiura*. In the latter it lies far back in front of the so-called caudal fin and is continued anteriorly in a long aorta as far as the brain. In the *Cirripedia* a separate blood-vascular system is altogether wanting.

It would be a mistake to assume that those *Entomostraca* which appear to be **simple** forms because of the want of a heart and generally of a separate blood-vascular system, are therefore also **original** forms. As in the worms, so also in Crustaceans, the want of this system of organs must certainly be considered as a derived condition. The causes why a reduction of the heart goes as far as complete disappearance are indeed only known to a very small extent. Small size of body may here and there have some influence, occasionally the rhythmical movements of other inner organs (*e.g.* the stomach of many *Copepoda*) seem to suffice to set in circulation the blood or cœlomic fluid in the lacunar system; a heart is thus rendered superfluous.

We have one remarkable exception to all that has been said above as to the circulatory system in the Crustacea. One genus of parasitic *Copepoda* (*Lernanthropus*) possesses a richly branched blood-vascular system widely spread in the body and its appendages, and completely closed from the body cavity. A heart is wanting. The yellowish red blood is propelled along the principal vessels by the movements of the enteric canal, and flows forwards in two ventral longitudinal trunks and backwards through an unpaired dorsal vessel.

Malacostraca, Leptostraca.—A knowledge of the circulation in the *Leptostraca* (*Nebalia*, Fig. 196, p. 293) is of great importance; it recalls in many respects that of the *Branchiopoda*, and in others points to that of the *Malacostraca*. The long tubular heart stretches from the most posterior head region through the whole thorax into the 4th abdominal segment, and possesses 7 pairs of ostia. The 3 most anterior of these lie laterally in the heart in the posterior part of the cephalic region, the 3 following dorsally in the 2d, 4th, and 5th thoracic segments, and the 7th and largest in the 6th thoracic segment. In the last 2 thoracic segments, and in the abdomen the heart has no ostia. These pairs of (venous) ostia through which the blood enters the heart from the pericardial sinus, are, as in all Crustaceans, provided with valves. The heart is continued into an anterior and a posterior aorta, through which the blood flows out into the body. Valves hinder its return from the two aorta into the heart. Besides the aorta, branched arteries occur in both pairs of antennæ and in the abdomen. The principal portions of the lacunar blood-vascular system are the pericardial sinus and a sinus lying under the intestine.

The **respiration** is in all cases specially active at the thin inner surface of the shell (which is kept clean by long maxillar feelers), and in the lamellate exo- and epipodites of the thoracic feet. In these parts a brisk circulation takes place. The blood which flows through the shell comes from the anterior aorta and re-enters the heart by the dorsally placed ostia.

Arthrostraca.—First of all we must here point out an important difference in the position of the heart in the two principal divisions of the *Arthrostraca*, the *Isopoda* and *Amphipoda*. In the *Isopoda* by far the largest portion of the heart, which is provided with 1 to 2 pairs of ostia, lies in the **abdomen**; in the *Amphipoda*, however, the tubular elongated heart which is almost everywhere provided with 3 pairs of ostia lies in the **thorax**. This difference may be explained by supposing that the *Isopoda* have retained only the abdominal portion, and the *Amphipoda* only the thoracic portion of the primitive Malacostracan heart which ran through nearly the whole length of the body, and was provided with many pairs of ostia. The localisation of the respiration has probably played the chief part in bringing about this differentiation, since in the *Isopoda* respiration takes place in the rami, and principally in the endopodites of the abdominal feet (pleopoda), but in the *Amphipoda* chiefly in the pouch-like branchial appendages of the thoracic feet.

In the *Anisopoda* the heart lies as in the *Amphipoda* in the thorax.

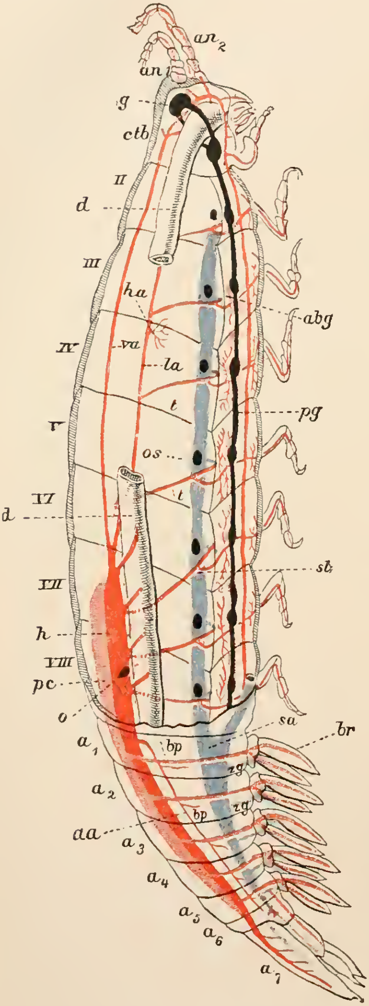

FIG. 240.—**Diagram of the circulatory system of the Isopoda**, seen from the side. The right thoracic and cephalic walls removed. A part of the intestine (*d*) cut away (after **Delage**). Arterial system red, venous system blue, nervous system black. an_1, Anterior; an_2, posterior antennæ; *ctb*, cephalo-thorax; *II-VIII*, 7 free thoracic segments; a_1-a_7, 7 abdominal segments; *br*, gills (pleopoda); *g*, brain; *d*, intestine; *h*, heart; *o*, ostium of the heart; *pc*, pericardium; *va*, anterior aorta; *la*, lateral arteries; *t*, thoracic arteries; *ha*, hepatic artery; *sl*, lateral sinuses of the thoracic region; *sa*, abdominal sinus; *abg*, points of insertion of the thoracic feet; *pg*, subneural vessel (the dotted line should stop at the red line); *bp*, branchio-pericardial vessels; *zg*, vessels leading to the gills; *aa*, abdominal aorta; *os*, ostia (?) of the lateral sinuses.

The following is a rather more detailed description of the circulation of the *Arthrostraca*.

Isopoda (Figs. 240 and 241). The heart, which lies for the greater part in the abdomen, and is provided with 1 to 2 pairs of lateral ostia, is closed blindly behind. Out of it 11 arteries arise, viz. (*a*) a medio-dorsal thoracic aorta running to the head and the eyes, and supplying the cerebral ganglia, and the 2 pairs of antennæ, (*b*) one pair of lateral arteries for the anterior thoracic segments, and the posterior cephalic region together with the extremities of these regions, (*c*) 3 pairs of thoracic arteries for the 3 posterior thoracic segments and their extremities, (*d*) 1 pair of abdominal aortæ for the abdomen and its limbs, which function as gills. The thoracic aorta forms anteriorly in front of the brain a ring which embraces the œsophagus, from which a **subneural artery** runs longitudinally under the ventral chord the whole length of the body. This also gives off branches to the limbs. Besides the blood lacunæ which lie between the viscera, there is generally in the thorax a large, paired, ventral blood sinus, which in the abdomen becomes unpaired. 5 pairs of vessels conduct the venous blood out of the abdominal sinus into the pleopoda which function as gills. 5 pairs of efferent vessels (veins) conduct the blood which has become arterial in the gills into the pericardial sinus; it passes thence through the ostia into the heart, and by the contraction of this latter it is again dispersed through the arteries.

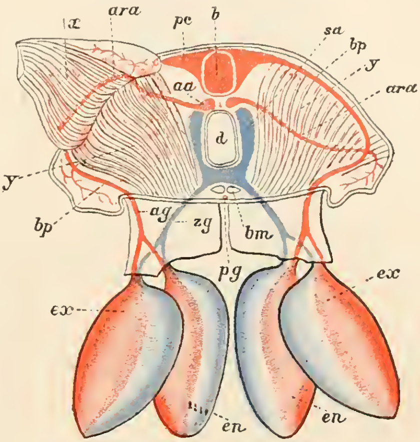

Fig. 241.—**Conilera cylindracea** (after **Delage**). Transverse section of the abdomen. Most of the letters have the same meaning as in Fig. 240. *b*, Heart; *x* and *y*, muscle layers (muscle lamellæ) for moving the gills (pleopoda), flexor and extensor; *x*, is laid back; *ara*, the abdominal arteries which supply them; *ex*, outer; *en*, inner branchial lamella of the pleopoda (exo- and endopodites); *ag*, efferent; *zg*, afferent branchial vessel; *bm*, ventral chord; *pg*, subneural vessel; *sa*, abdominal sinus.

Amphipoda (Fig. 242). The *Amphipoda* present a striking contrast to the *Isopoda* in that in the latter the vascular system, in the former the lacunar system, is the most pronounced. The long tubular heart which generally lies in the 5 or 6 anterior free thoracic segments, usually possesses 3 pairs of ostia, less frequently one (*Corophium*) or 2 (*Platyscelidæ*). It is continued into an anterior and a posterior medio-dorsal aorta, which pour the blood either direct or through further arterial branches into a large ventral sinus which lies between the integument and the intestine and runs through the whole length of the body. Special afferent blood streams (vessels?) conduct the mixed blood into the extremities of the thorax and abdomen, thus also into the branchial pouches of the thoracic limbs. Special efferent streams collect the blood in these extremities (thus also the blood which has become arterial in the gills) and conduct it back through 7 vascular loops in the thorax and through 6 in the abdomen into the pericardium, which stretches back beyond the heart to the end of the abdomen. In *Corophium* the abdominal portion of the pericardium and the abdominal vascular loops are wanting. The blood-vascular system of the *Caprellidæ* agrees in the main with that of other *Amphipoda*, allowance being made for the reduction of the abdomen.

It follows, from the above description, that in the *Amphipoda* the arterial blood cannot in any way be sharply distinguished from the venous blood.

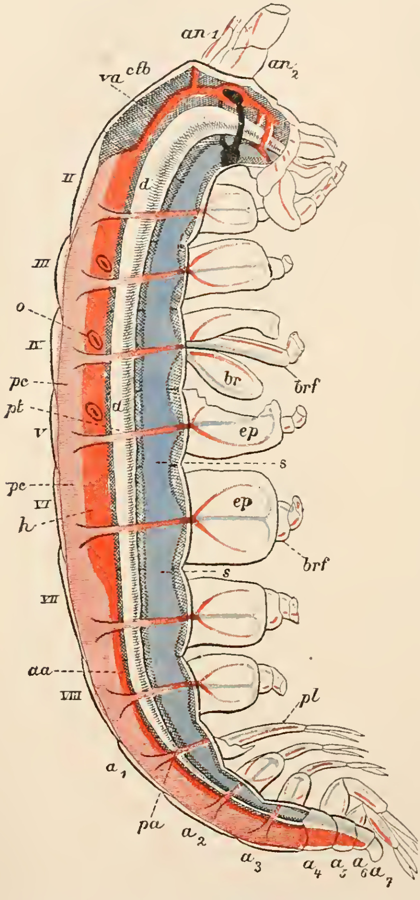

FIG. 242.—**Diagram of the circulatory system of the Amphipoda**, from the side (after **Delage**). Most of the lettering as in Fig. 240. *pt*, Pericardial vessels rising from the epimeres (*ep*), extremities (*brf*), and gills (*br*) of the thorax; *pa*, pericardial vessels of the abdomen; *s*, ventral sinus; *ep*, epimeres. The epimeres of the thoracic segments *IV* and *V* partly cut off; *pl*, pleopoda.

Anisopoda.—This division of the Arthrostraca, though in many points approaching more nearly the organisation of the *Isopoda* than that of the *Amphipoda*, shows in its blood-vascular system greater similarity to the latter. Two abdominal aortæ, however, arise from the posterior end of the thoracic heart, and the pericardial sinus is continued into the abdomen. The heart of *Apseudes* possesses two ostia on the left side and only one on the right; in youth the 2 pairs of ostia are present. As to the significance of this fact see below (p. 367).

In all *Arthrostraca* the paired ostia, as well as the points of origin of the aorta are provided with valves.

Thoracostraca.—The circulatory system here is linked on to that of the *Isopoda*. Starting with the *Stomatopoda*, the circulatory system of the older larvæ of *Squilla*, known as *Alima* and *Erichthus*, which can hardly be distinguished from that of the adult, have been the most carefully investigated. The heart (Fig. 243) extends as a many-chambered dorsal vessel from the maxillar region (behind the stomach) through the thorax and the abdomen to the end of the 5th abdominal segment. Two divisions can be distinguished in it, a short, wide anterior, and a long posterior division. **Probably the anterior division alone cor-**

FIG. 243.—**Circulatory system of an older Squilla larva** before it has passed into the *Squilla* form (after **Claus**). *h*, Heart, continued posteriorly into the many-chambered dorsal vessel which is richly provided with pairs of ostia (*o*); *ac*, cephalic aorta; *ao*, optic artery; aa_1, aa_2, arteries of the two pairs of antennæ; *am*, marginal artery of the dorsal shell; *ast*, arteria sternalis; *al*, hepatic artery; *as*, shell artery; a_1, 1st lateral artery of the dorsal vessel; aab_1 to aab_6, lateral arteries of the abdomen; *dr*, glandular saccules on the hind-gut; *l*, hepatic lobes in the telson; p_6, 6th pleopod (uropod); *kb*, branchial leaves (epipodial appendages of the oral feet).

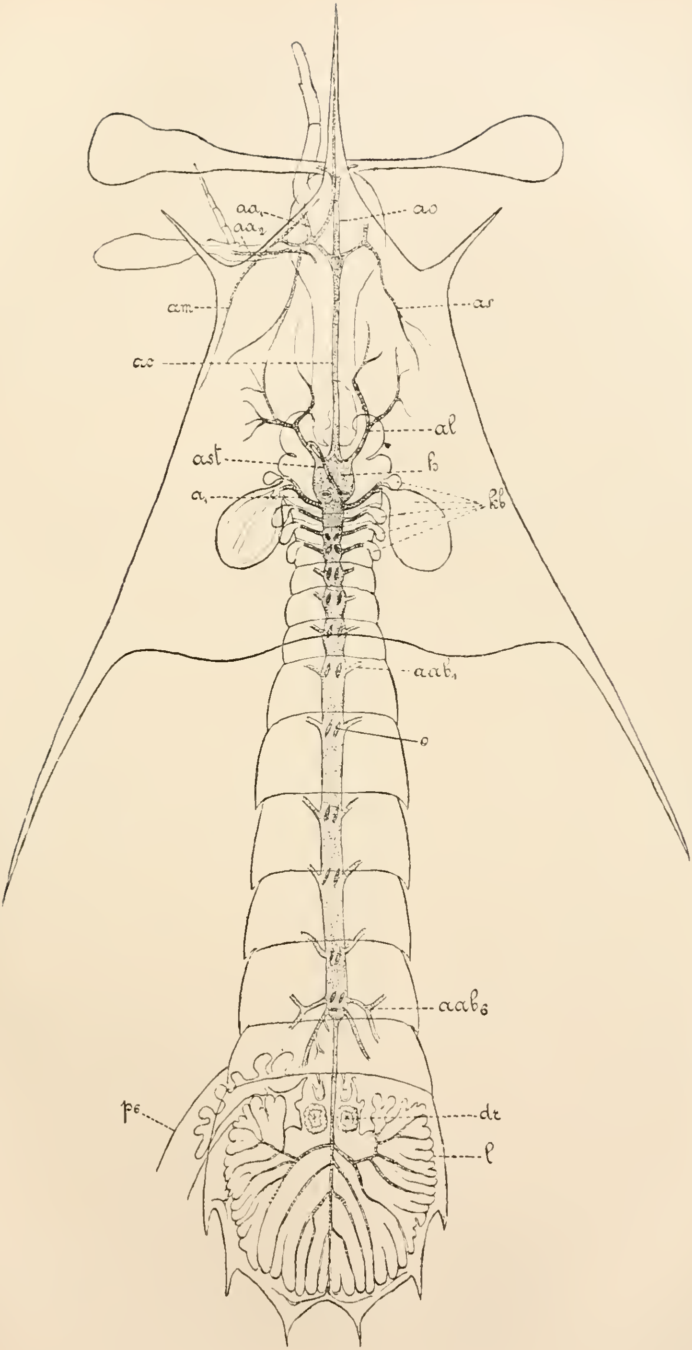

FIG. 243.

responds with the heart of the Decapoda. It reaches to the posterior limit of the first maxillipedal segment, possesses a large pair of ostia, and gives off the following vessels: (*a*) an anterior unpaired cephalic aorta (*ac*), (*b*) and (*c*) an anterior weaker and a posterior stronger pair of arteries. The second division, the many-chambered dorsal vessel, possesses 12 pairs of ostia, and gives off 13 pairs of arteries and an unpaired posterior aorta. To complete the whole picture of the circulatory system and to show its relation to that of the *Isopoda*, we must add that a median **subneural vessel** runs under the ventral chord through the whole body, that the whole **venous system is lacunar**, and that there are two principal venous sinuses, one ventral, and the other dorsal. The arterial system, on the other hand, is composed of richly-branched vessels having walls of their own and breaking up into capillaries.

As to the more detailed arrangements, the **cephalic aorta** supplies the eyes, the two pairs of antennæ, the brain, and the anterior lateral regions of the shell. The **most anterior pair of arteries** supplies the mandibles and maxillæ, and the central part of the shell. The **large 2d pair of arteries** probably supplies the maxillæ and maxillipedes; one artery passes between the longitudinal commissures of the ganglia of the 1st and 2d maxillipedal segments to connect itself with the subneural vessel (compare the **sternal artery** of the *Schizopoda* and *Decapoda*). The **subneural vessel** gives off primarily vascular loops to the ganglia of the ventral chord, but it also gives off branches to the limbs. The **13 pairs of arteries** of the many-chambered dorsal vessel supply the thorax and abdomen with their extremities in such a way that the pair of arteries belonging to a pair of ostia spread out, not in the segment in which the ostia occur, but in that immediately in front of it. The whole heart seems to have been shifted back one segment, so that the pair of ostia lying in the first abdominal segment (there are 7 pairs of ostia in the abdomen) originally belonged to the most posterior thoracic segment. The **posterior aorta** richly supplies the telson with lateral branches. In the **venous system** paired lateral blood sinuses conduct the blood out of the extremities and other organs into the large ventral sinus. The blood streams thence [into the pericardial sinus and through the ostia back into the heart. It is only in the abdomen, whose limbs carry the gills, that the blood which has become arterial appears to flow direct back into the pericardial sinus, avoiding the ventral sinus.

A comparison with younger *Squilla* larvæ of the so-called *Erichthoid* stage makes it highly probable that 2 pairs of anterior ostia of the dorsal vessel there present **disappear** in the course of development. While, as a rule, in the many-chambered dorsal vessel a pair of ostia lies over each outgoing pair of arteries, there are no ostia to correspond with the two most anterior pair.

Among the *Thoracostraca* a chambered dorsal vessel provided with many pairs of ostia and reaching into the abdomen is only found in the *Stomatopoda*. This more primitive condition has here been retained, evidently in connection with the localisation of the respiration in the branchial tufts of the abdominal limbs.

The blood-vascular systems of all the other *Thoracostraca*, at least of the *Schizopoda* and *Decapoda*, closely resemble one another, and must be contrasted with that of the *Stomatopoda*. [The blood-vascular system of the *Cumacea* is not yet thoroughly investigated; it probably agrees to a great extent with that of the *Schizopoda* and *Decapoda*.]

The **heart** of the *Schizopoda*, *Decapoda*, and *Cumacea* appears, as contrasted with that of the *Stomatopoda*, extraordinarily shortened and provided with very few ostia (2 to 3 pairs). It always lies in the thorax and never stretches into the abdomen. This shortening was evidently caused by the localisation of the respiration in the thoracic region (gills of the thoracic feet, cephalothoracic shield as respiratory organ), and by the more or less extensive fusing of the thoracic segments.

Among the *Schizopoda* the heart is still elongated in *Siriella*, where it runs through nearly the whole thorax into the last thoracic segment. It is progressively shortened in *Mysis* and *Mysodopsis*. In *Euphausia* it has the concentrated form of the Decapodan heart, and has, like the latter, 3 pairs of ostia, one dorsal, one lateral, and one ventral, while in the other *Schizopoda* and in the *Zoea-larvæ* of the *Decapoda*, there are but 2 pairs of ostia.

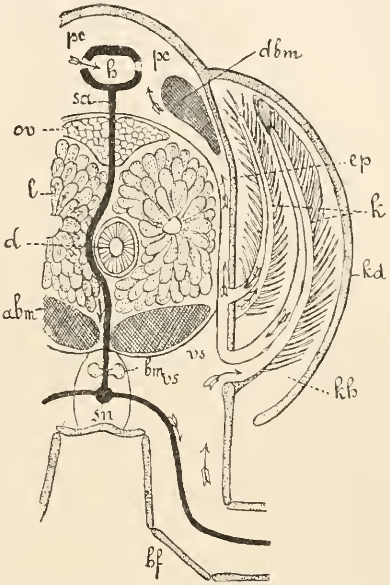

FIG. 244.—**Transverse section through the cephalothorax of the Cray-fish in the region of the heart, diagrammatic.** *kd*, branchiostegite; *k*, gills; *kh*, respiratory or branchial cavity; *ep*, lateral wall of the cephalothorax; *pc*, pericardium; *h*, heart; *sa*, sternal artery; *l*, hepatopancreas; *d*, intestine; *abm*, ventral longitudinal muscles to the abdomen; *dbm*, dorsal longitudinal muscles to the abdomen; *bm*, ventral chord; *sn*, sub-neural vessel; *bf*, ambulatory foot; *vs*, ventral sinus; *ov*, ovarium. The arrows give the direction of the flow of blood (after **Huxley** and **Plateau**).

The Circulatory system of Astacus (Fig. 234, p. 338, and Fig. 244) may be taken as an example. The following vessels rise out of the heart: (*a*) anteriorly the **unpaired cephalic aorta**, which supplies with its rich branchings the brain and the eyes. (*b*) **Two anterior lateral arteries** (also called antennal arteries). These give off branches to the stomach, the antennal glands, the anterior and posterior antennæ, and the cephalothoracic shield. (*c*) **The two hepatic arteries.** These arise at the anterior and lower edge of the heart and branch in the liver. (*d*) **The sternal artery.** This arises from the lower and posterior end of the heart, which is produced in the shape of a bulb, descends on the right or left side of the intestine, passes between the longitudinal commissures of the penultimate and ante-penultimate thoracic ganglia, to enter the sub-neural vessel below the ventral chord. This must be considered as a modified lateral artery of the heart (see *Stomatopoda*). (*e*) **The posterior aorta** arises out of the posterior end of the heart, and runs over the intestine backwards through the abdomen, giving off in each segment a pair of lateral arteries which supply the intestine, integument, and musculature of the abdomen. **The sub-neural vessel** which receives its blood from the sternal artery, is already known to us in the *Isopoda* and *Stomatopoda*, here, however, and in all *Decapoda* it plays a much larger part, since lateral branches from it supply all the limbs from the maxillæ to the last pleopoda. It also serves for nourishing the ventral chord, this being its almost exclusive function in the *Stomatopoda*, the limbs there being more often supplied by branches of the lateral arteries of the heart. All the arteries branch richly and pass into **arterial** capillaries, which **open into the venous lacunar system of the body.** Even though the flow of blood in this lacunar system is, as in all Crustaceans, regular and constant, and though venous blood canals often come into existence, we do not find among the *Decapoda* any veins with walls of their own. The system of venous cavities, taken as a whole, represents the body cavity. We can only give a few details as to the course of the venous blood. It nearly all flows together into a large ventral blood sinus in the cephalothorax, from the lateral parts of which canals conduct it into the gills, while other canals convey the blood which has become arterial in the gills away from them to the pericardial sinus. **The respiratory organs are therefore here placed in that part of the circulatory system which conveys the blood out of the body back to the heart, and this is the case in all Arthropoda.** The arterial blood coming from the gills leaves the pericardium, and, mixed with the blood which flows back out of the cephalothoracic shield, enters the heart through its ostia. The ostia as well as the points of origin of the arteries of the heart are provided with valves. The valves of the former prevent the return of the blood into the pericardium, those of the latter its return out of the arteries into the heart. When the heart contracts (systole) the blood contained in it is driven into the arteries, and when it again expands (diastole) it sucks in blood out of the pericardium through the ostia.

In the *Mysidæ* (with the exception of *Euphausia*) there are 2 or 3 unpaired hepatic arteries, springing from the ventral wall of the heart. The abdominal portion of the sub-neural vessel is wanting. In the male of *Siriella*, which carries gills on its pleopoda, the latter receive their blood from branches of the lateral arteries of the posterior aorta. In the *Schizopoda*, *Cumacea*, and *larvæ* of *Decapoda* in which the gills are not yet developed, the blood circulation in the cephalothoracic shield with its fold is very brisk, and there is no doubt that in those forms which have no special gills the respiration principally takes place in it. In *Siriella* and *Mysis* and perhaps also in other *Schizopoda* it is most probable that the integument forming the inner wall of the respiratory cavity has also a respiratory function (comp. Fig. 222, p. 321). The channels which convey the blood out of the thoracic feet back to the heart cause ridge-like projections in this integument which may be called branchial ridges. The constant vibrations in the respiratory cavity of the epipodial appendages of the first thoracic foot create a constant exchange of water in it.

We have already described (p. 329) the respiratory organ of the air-breathing *Birgus latro*. We will here briefly describe the circulation of the blood in connection with it. The respiratory organs are branched tufts which arise on the inner surface of the branchiostegite. The shell circulation which is found in all *Thoracostraca* and which also plays a great part in the respiration of many water-breathing forms, here brings about air-breathing. In the branchiostegite (here better "lung cover") and its tuft-like appendages there is a rich meshwork of blood sinuses, spread out between the vessels which conduct the blood in and out. The blood passes through a large vessel out of the venous blood sinus of the head into the lung cover. This vessel divides into 4 branches, 3 of which run to the upper and 1 to the lower portion of the lung cover, and break up into the meshwork of blood sinuses above mentioned. From this the blood which has become arterial is collected by vessels which unite into a great trunk, running first along the edge of the lung cover backwards, then upwards, and finally forwards, to unite before entering the pericardium with the vessel coming from the small gills.

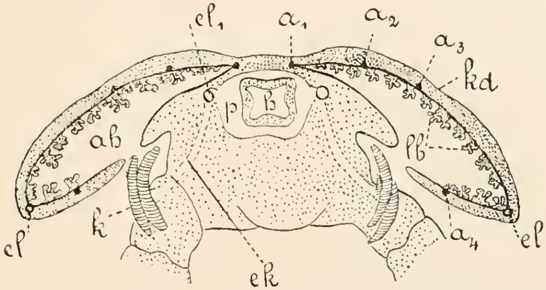

Fig. 245.—**Birgus latro. Diagrammatic transverse section in the region of the heart** (after **Semper**). *kd*, Gill or lung cover; *h*, heart; *k*, gills; *ah*, respiratory cavity; *p*, pericardium; *ek*, branchial blood channels leading to the heart; a_1, a_2, a_3, a_4, lung or shell vessels leading from the heart; *lb*, pulmonary tufts; *el*, pulmonary blood channels leading to the heart; el_1, the same near their entrance into the pericardium.

The blood of the Crustacea is usually colourless; it is occasionally, however, slightly yellow, green, or red. In the latter case, *e.g.* in the *Branchiopoda*, the colouring material of the blood is **hæmoglobin.** The colourless blood corpuscles are almost always able to change their form in an amæboid manner.

Judging from the varying position and form of the Crustacean heart, we come to the conclusion that the original Crustacean heart was, as in *Branchipus*, a long, many-chambered dorsal vessel provided with many segmental pairs of ostia. All other forms of heart have been developed from this by reduction of the anterior or the posterior portion, and by the disappearance of numerous pairs of ostia. These reductions have had for their principal causes the localisation of the respiration, the various differentiations of the different portions of the body, and the fusing of segments. The already mentioned ontogenetic fact that pairs of ostia may disappear in the course of development (*Apseudes*, *Stomatopoda*), agrees with this view. In many *Isopoda* the ostia lie alternately to the right and left in the heart; this arrangement perhaps comes into existence by the disappearance of alternate ostia in the heart at first provided with paired ostia.

The fact that in many Crustacea, *e.g.* the *Branchiopoda*, which go through a long series of metamorphoses from the *Nauplius* larva, the pairs of ostia are formed with the heart in order from before backward, cannot be brought up as an objection to the above. For this method of development corresponds in general with the manner of ontogenetic differentiation of the Arthropodan and Annelid body which takes place in that order. The whole question is closely connected with the view to be treated of later as to the phylogenetic significance of the Crustacean larval forms.

VIII. The Excretory Organs (Antennal Glands, Shell Glands).

Although comprehensive comparative investigations as to the methods of excretion are still wanting, we at least know that this function is performed in very various ways and by very various organs. We shall here take into consideration only two of these organs, the **shell** and the **antennal glands**. Certain intestinal appendages and dermal glands which also seem to serve for excretion, are mentioned in the sections on the intestine and the integument. It must not, however, be thought that this exhausts the number of parts of the body which have some share in excretion.

Confining ourselves to the antennal and shell glands, we note :—

(1) **Number and Position.** Each of these glands occurs as a single pair. The former emerge at the basal joint of the posterior antennæ. The gland itself lies either entirely in this basal joint or more or less in the adjoining cavity of the head. The shell gland lies in the shell fold or in the cephalothoracic carapace in a region which originally corresponds with the 2d maxillar segment. Its aperture lies on or near the posterior maxillæ.

(2) **Occurrence.**—The antennal gland is widely distributed in the Crustacea. It seems wanting only in the *Isopoda*. While in the *Malacostraca* it is, as a rule, best developed in the adult, in the *Entomostraca* it only appears in the larval stages, and it but rarely persists in the adult even as a rudiment. In the *Decapoda* the antennal gland has been called the green gland. The shell gland is widely distributed among adult *Entomostraca*. Among the *Malacostraca* it has been observed in *Nebalia*, and further, in the *Isopoda*, *Anisopoda*, *Cumacea*, and in the larvæ of some forms (*Sergestes*, *Euphausia*) in whose adult condition it is wanting. In *Nebalia* it is found in a reduced condition.

(3) **Structure and Development.**—The structure of the antennal gland (Fig. 246) is everywhere essentially the same. We distinguish in it (1) a terminal saccule, (2) a coiled urinary canal which emerges through (3) a urinary bladder on the basal segment of the posterior antennæ. The constitution of the epithelial wall is different in the terminal sac and in the urinary canal. The wall of the latter is often shown in transverse section to consist of one single cell, its lumen thus

being intracellular. In the higher Crustacea, however, the cells appear in greater number and more closely crowded, the lumen being intercellular. The urinary canal is very long in the *Malacostraca*, and lies in complicated coils. At its distal end (near the opening) it widens into the urinary bladder. The terminal sac, as well as the urinary canal, may be further complicated in the higher Crustaceans by the formation of lateral invaginations.

The **shell gland** has essentially the same structure as the antennal gland.

That we have to do in the antennal and shell glands with excretory organs is shown by the fact that when the animals are fed with carmine, carmine particles are after a time met with in the glandular sacs, at least in those of the antennal glands.

According to observations made on the *Cladocera*, the shell glands are said to be of mesodermal origin. The antennal glands (of the *Cray-fish*), on the contrary, are said to come from a dermal depression, and so belong to the dermal glands. These statements, however, require further confirmation.

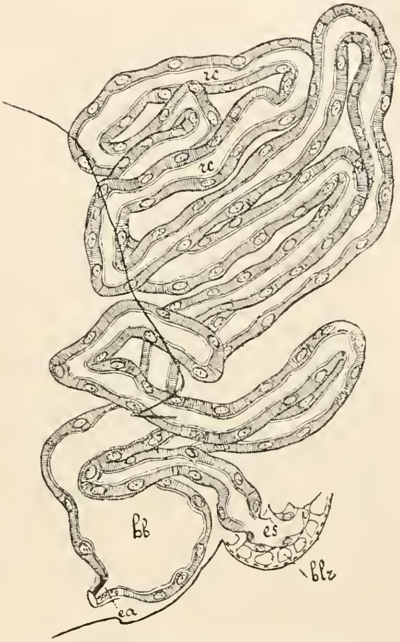

Fig. 246.—**Left Antennal Gland of Mysis** (after **Grobben**). *rc*, Urinary canal; *hb*, urinary bladder; *es*, terminal sac; *ber*, blood lacunæ; *ea*, urinary passage (efferent duct).

Morphological Importance.—Leaving out of consideration the different origins mentioned above attributed to these glands it appears probable, from their essential agreement in structure, that the shell and antennal glands are segmental homologous formations. From their wide distribution in the *Entomostraca* and *Malacostraca* or their larvæ, we may further conclude that these glands are, phylogenetically, very ancient organs, derived from the racial forms of the Crustacea. The view that they are homologous with the nephridia of the *Annulata* may be supported by many facts in their coarser and finer structure. This view would gain greatly in probability if it could be shown that both are developed out of the mesoderm. This homology has not, however, yet been established.

This is, perhaps, the place to mention the **cement glands** of the *Cirripedia*, which emerge on the last joint but one of the small adhering antennæ (anterior antennæ). The hardening secretion of these glands serves to attach the animal to the surface on which it rests.

Besides these, certain glandular tubes of the *Cirripedia*, which emerge on the outer maxillæ and were formerly taken for olfactory organs, have recently been pointed out as formations equivalent to the nephridia of the *Annulata* (segmental organs). They are said to be in open communication with the body cavity.

IX. The Connective Tissue.

The connective tissue found throughout the Crustacean body can here receive only brief attention. Plates, membranes, etc. of connective tissue lie close under the hypodermis and envelop the enteric canal and the sexual organs, and, as neurilemma, the nervous system. Connective tissue strands, fibres, mesenteries, in various places bind the inner organs together and attach them to the integument The lacunar blood-vascular system, the body cavity, is lined to a great extent, though certainly not continuously, with connective tissue.

A special form of connective tissue, widely found in Crustaceans, is the **fat body**, which varies greatly in details. This often envelops the intestine and the heart. In the connective tissue cells of the fat body are found fat-drops, fat-globules, and also often protein granules. The fat body evidently plays a part sometimes larger, sometimes smaller, in metabolism. It is generally variously developed at different ages and times of the year, and also in the two sexes. In the larval forms it is often strongly developed before the moult, which accompanies a metamorphosis, and forms a reserve of nourishment for the process of transformation. In a few Crustaceans, which take no food at the time of sexual ripeness or of the hatching process, it is strongly developed before this time and much reduced after it.

Connective tissue cells may often become star-like, branched, and occasionally contractile **pigment cells.** Pigment also occasionally occurs in hypodermal and intestinal cells.

X. The Sexual Organs.

The sexes are separate in the Crustacea, except in a few cases which will be duly mentioned.

The male and female sexual organs are constructed on one type and have a similar position in the body. They are, as a rule, paired. More than one pair never occurs. We can distinguish corresponding divisions in male and female organs; viz. first, **the germ-preparing organs** (**ovaries** in the female, **testes** in the male); second, **the ducts** of the genital glands (**oviducts,** in the female, **vasa deferentia** in the male); third, **terminal divisions** of these ducts, sharply distinguished anatomically and ontogenetically from the preceding (**vulva, vagina, receptaculum seminis** in the female, muscular **ductus ejaculatorius** in the male); and fourth, outer **copulatory organs.**

The ovaries and testes cannot in their earliest stage be distinguished. They can early be recognised as distinct cell groups in the mesoderm, their rudiments can sometimes be traced back to one or two segmentation cells.

The oviducts and vasa deferentia arise out of the mesoderm apart perhaps from the rudiments of the germ glands.

The terminal sections of the ducts arise by invaginations of the outer integument.

The outer copulatory apparatus consists either of transformed limbs or appendages of limbs, or of processes, folds, prominences, etc. of the integument.

There is no doubt that the sexual organs in all Crustacea were originally paired. Some of them may, however, become unpaired, either (as in most *Copepoda* and *Thoracostraca*) by the two germ glands becoming connected by an unpaired uniting portion, or by the two ducts uniting over a greater or smaller extent to form a common unpaired oviduct or vas deferens, or by the ducts emerging through a common aperture. We can, however, always recognise the double nature of the sexual apparatus in some one (generally the larger) portion of it.

The ovaries and testes are either simple or branched or coiled tubes or sacs which occupy in the body a dorsal position on each side of the intestine, often between the heart and the intestine. They lie in the trunk sometimes more to the front sometimes more to the back, and sometimes along nearly its whole length. Where there are connecting portions between the germ glands of the two sides they lie dorsally above the intestine.

The genital apertures are found on the ventral side except in the *Cladocera* and some *Copepoda*, where they lie dorsally.

In the *Entomostraca*, setting aside the *Cirripedia*, the apertures lie, as a rule, immediately behind the limb-bearing anterior division of the trunk, at the limit between this and the limbless terminal division called the abdomen. The single or double segment in which they emerge is called the genital segment. There is thus in the *Entomostraca* no definite constant segment of the body in which the genital apertures lie.

In the *Malacostraca*, on the contrary, apparently including the *Leptostraca*, the position of the genital apertures is definite and constant. The male genital apertures everywhere lie in the most posterior (*i.e.* the 8th) thoracic segment, usually (*Thoracostraca*) in the basal joint of the 8th pair of thoracic limbs. The female apertures are in the third from the last (the 6th thoracic segment, if we reckon in those fused with the head), and mostly in the basal joint of the protopodite. There are no exceptions to this rule.

The **Spermatozoa** of the Crustacea are often distinguished by their remarkable size and shape. In the *Decapoda* they are provided with radially arranged processes, and are, as also in other divisions of the Crustacea, immobile.

Numerous spermatozoa are often enclosed in a common envelope (spermatophore) formed by the secretions of the glandular portion of the male ducts. The **eggs** of many Crustacea possess besides a yolk membrane other accessory envelopes secreted by the female ducts. On adaptations for the care of the brood, see p. 379.

Should the view prove correct, that the oviducts and vasa deferentia and also the antennal and shell glands correspond with the Annulatan nephridia, then, considering the different position of the male and female genital apertures, several pairs (4 at the least) of the segmental nephridia of the *Annulata* have been retained in the Crustacea.

Entomostraca.—In the *Branchiopoda*, the germ glands are paired ; in *Branchipus* (Fig. 191, p. 288) they are tubular and lie in the abdomen ; in *Apus* they are richly branched and lie in the limb-bearing division of the trunk. In *Branchipus* the oviducts are widened out at their ends and enter a uterus in which the eggs remain for a time receiving a shell yielded by special uterine glands. The uterus lies in a pouch formed by a concrescence of genital prominences, the modified limbs of the two genital segments (12th and 13th trunk segments).

The vasa deferentia are also widened out at their ends (sperm vesicles) and enter a muscular ductus ejaculatorius, which, when the penis is evaginated, is drawn out with it inside it. The penis is an ectodermal outgrowth of the second genital prominence.

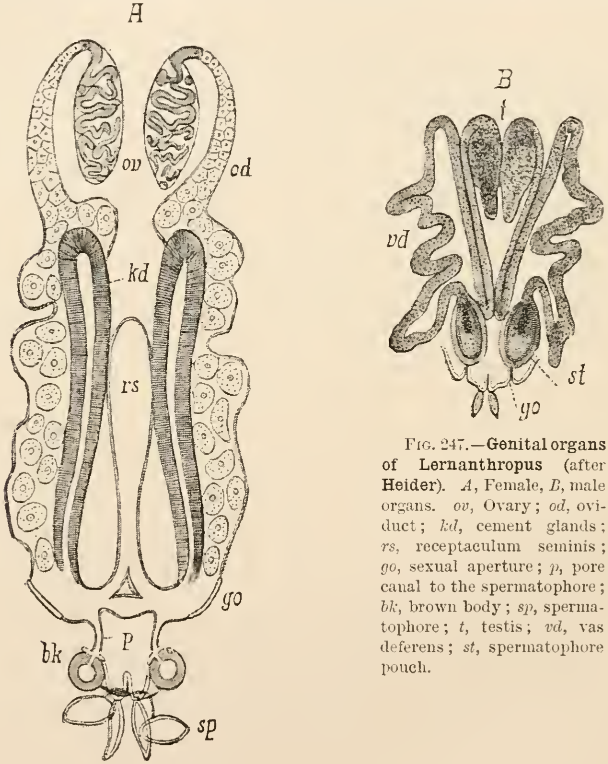

Fig. 247.—**Genital organs of Lernanthropus** (after **Heider**). *A*, Female, *B*, male organs. *ov*, Ovary ; *od*, oviduct ; *kd*, cement glands ; *rs*, receptaculum seminis ; *go*, sexual aperture ; *p*, pore canal to the spermatophore ; *bk*, brown body ; *sp*, spermatophore ; *t*, testis ; *vd*, vas deferens ; *st*, spermatophore pouch.

In the *Cladocera*, the ovaries and testes are simple paired tubes. The oviducts emerge dorsally into the posterior end of the brood cavity (see on Care of the Brood, p. 379). The vasa deferentia with the ductus ejaculatorius emerge by paired apertures on the ventral side of the limbless posterior division of the body.

In the *Ostracoda* the germ glands are paired, as also are the vasa deferentia and the oviducts. The testes often fall into several tubes. The ductus ejaculatorius with the sperm vesicle may be unpaired (*Cypridina*). The copulatory apparatus of the male is to some extent complicated (transformed hindermost limbs). In the female, two genital prominences corresponding with those of the male contain the receptacula seminis. In *Cypris* the ovarial tubes extend into the shell-fold.

Copepoda.—The germ glands are mostly unpaired, and placed symmetrically in the anterior trunk segment dorsally on the intestine. That they were originally double is occasionally apparent. In many parasitic *Copepoda* (Fig. 247) the germ glands are distinctly paired and not connected by any transverse bridge. In *Sapphirina* a transverse bridge occurs. The oviducts are paired, and generally branched. Their ends are glandular or provided with glandular invaginations (cement glands), whose secretion yields the material for the egg sacs. A receptaculum seminis common to the two oviducts is often found. The paired apertures lie in the first abdominal segment (sometimes at its posterior edge) either ventrally, laterally, or (rarely) dorsally. The sperm passages are paired or unpaired; in the latter case they are generally on one side. They are provided with a glandular division, which yields the envelope of the spermatophore, and often with a wider portion functioning as spermatophore pouch. The apertures in the genital segment are paired or unpaired; in the second case frequently asymmetrical.

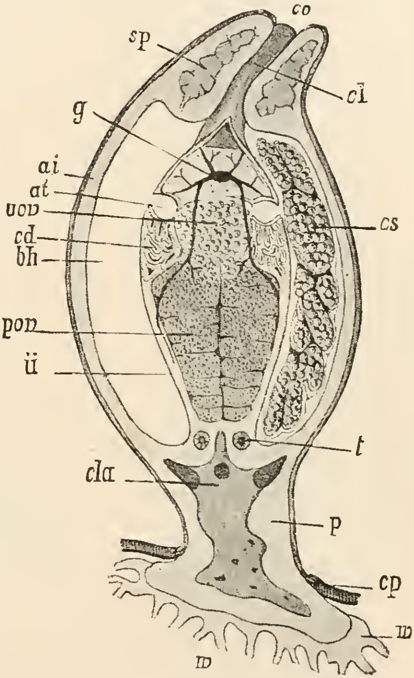

Fig. 248.—**Longitudinal section through a mature Sacculina carcini externa**, at right angles to the plane of symmetry (after **Delage**). *co*, Cloacal aperture; *sp*, sphincter of the cloaca (*cl*); *g*, ganglion; *ai*, outer integumental lamella, covering the brood cavity; *at*, female genital atrium, into which the unpaired portion (*uov*) of the ovary and the cement glands (*cd*) enter; *bh*, brood cavity, shown empty to the left, with egg sacs (*es*) containing the developing eggs to the right; *pov*, the paired part of the ovary; *ii*, inner integumental lamella covering the body proper or visceral sac; *p*, stalk entering the aperture in the shell carapace (*cp*) of the host; *w*, attachments of the roots on the stalk; *cla*, central lacuna of the stalk continued into the lacunæ of the outer integumental lamella, the roots, etc., representing the body cavity; *t*, testes.

Argulidæ.—Two pairs of testes occur in the caudal fin, and there are 2 vasa deferentia with common sperm vesicle. A glandular tube, coming from the anterior part of the body, enters each vas deferens. The two vasa deferentia unite under the intestine into a common ductus ejaculatorius, which opens at the end of the last thoracic segment on a papilla-like projection. The ovary is unpaired, and even from its first appearance asymmetrical; it lies in the thorax. The oviduct first appears paired, but it is afterwards atrophied on one side, and emerges at the base of the caudal fin. Two receptacula seminis, entirely separate from the female genital apparatus occur on the under side of the caudal fin.

Cirripedia.—The strikingly lobate ovaries are paired in the *Balanidæ*, and lie deep down in the shell ring (Fig. 207, p. 304) in that part of the body cavity which extends into the mantle fold. In the *Lepadidæ* (Fig. 205, p. 303) the ovaries, which are to some extent united, lie in the anterior cephalic portion of the body called the peduncle. In both the *Balanidæ* and the *Lepadidæ* the terminal division of the oviduct emerges on a projection on the basal joint of the anterior pair of tendril-like feet. This position deserves special notice, because the sexual apertures in no other Crustacean lie so far forward.

In the *Rhizocephala* (Fig. 248) the ovaries, in the shape of two lobate united masses, fill the greatest part of the visceral sac of the body which corresponds with the head of other *Cirripedes.* They open on each side into an atrium (*at*), into which the cement glands (*cd*) also enter, and which itself opens into the brood cavity (*bh*). The ovary in Sacculina is said at its first appearance to be unpaired.

The testes in the *Balanidæ* and *Lepadidæ* (Fig. 205, *t*) occur as two richly-branched tubes at the sides of the intestine and are continued as 2 vasa deferentia, which swell out into sperm vesicles before uniting at the base of the cirrus at the extreme posterior end of the body to form the common ductus ejaculatorius. The 2 testes of the *Rhizocephala* (Fig. 248, *t*) are simply tubular, and their vasa deferentia emerge at that part of the brood cavity where the visceral sac is produced into the stalk. See also below as to the sexual relations in the *Cirripedia.*

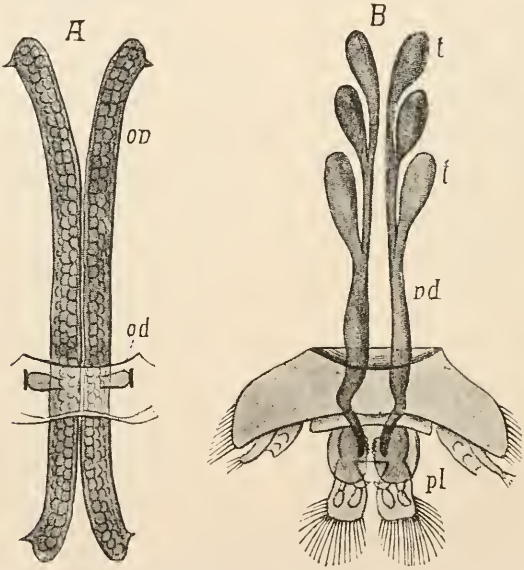

Fig. 249.—*A*, **female**, *B*, **male genital apparatus of Asellus aquaticus** (after **O. Sars**). *ov*, Ovary; *od*, oviduct; *t*, testicle lobes; *vd*, vas deferens; *pl*, 1st and 2d pairs of pleopoda.

There is much more uniformity in the genital organs of the *Malacostraca* than in those of the *Entomostraca.* While the two ovaries and the two testes remain separate in the *Leptostraca* and *Arthrostraca*, in the *Thoracostraca*, with few exceptions, they are joined above the intestine by an intermediate piece.

Leptostraca.—The ovaries and testes are long tubes which in the sexually mature animal run dorsally at the sides of the intestine from near the masticatory stomach to the last abdominal segment. The two short sperm ducts of the male emerge in the manner typical of the *Malacostraca* on a projection on the basal joint of the 8th pair of thoracic feet. The aperture of the oviduct also probably lies, as in other *Malacostraca*, in the third thoracic segment from the last.

Arthrostraca.—The testes and ovaries are nearly always simple paired tubes, which sometimes run through the largest portion of the thorax and abdomen, sometimes are limited to the thorax, or to one portion of the thorax. In most *Isopoda* the testis generally falls on each side into three pouches (Fig. 249, *B*), which, however, possess a common vas deferens. The oviducts open in the antepenultimate thoracic segment into the brood cavity, receptacula seminis often developing at their ends.

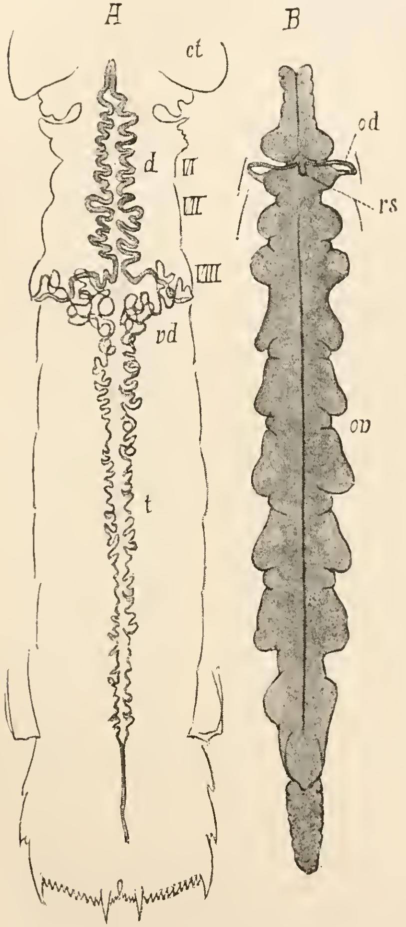

Fig. 250.—**Genital organs of Squilla mantis** (after **Grobben**). *A*, Male, *B*, female organs. *ct*, Posterior end of the cephalo-thoracic shield; *VI*, *VII*, *VIII*, the 3 hindermost free thoracic segments; *t*, testis; *vd*, vas deferens; *d*, appended glands; *ov*, ovary; *od*, oviduct; *rs*, receptaculum seminis.

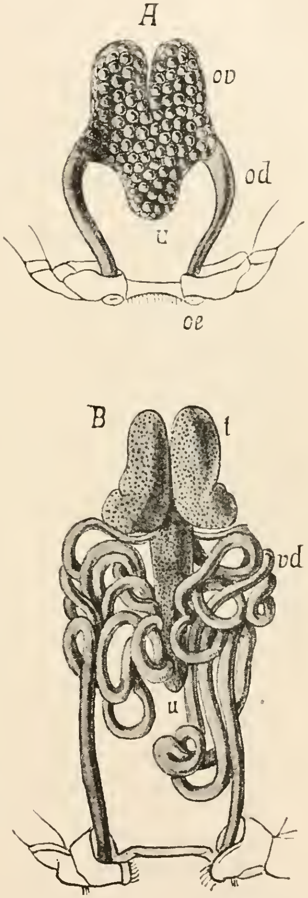

Fig. 251.—**Sexual organs of Astacus.** *A*, female, *B*, male organs. *ov*, Ovary; *u*, unpaired portion of the same; *od*, oviduct; *oe*, genital aperture; *t*, testes; *vd*, vas deferens (after **Huxley**).

The female genital apertures very often (*Isopoda, Anisopoda*) only appear at the time of the formation of the brood pouch. Peculiar phenomena appear at the time of reproduction in the *Oniscidæ.* The two receptacula (representing invaginations of the outer integument) are at first not in open communication with the ends of the oviducts. Only after sperm has, during copulation, entered the receptacula, do they pass into the oviducts by the bursting of their walls, and thus bring about the fertilisation of the eggs in the ovaries. The animal then casts its skin, and with the skin the receptacula seminis, so that the two genital apertures are no longer present. The fertilised eggs pass from the ovarium into the body cavity and thence through a newly-formed unpaired birth aperture in the last thoracic segment but one into the brood cavity. A new batch of eggs is fertilised later in the ovary by sperm left over from the first copulation, and this reaches the brood cavity in the same way. After this second batch of eggs has been developed in the brood cavity and the young that are hatched have left it, the animal moults, and then again appears as it was before copulation.

Thoracostraca.—The genital organs of the *Cumacea* and in some respects also those of the *Schizopoda* need more thorough investigation. The paired sexual glands of the Thoracostraca are united by an unpaired piece which lies in the thorax in the *Decapoda* and *Schizopoda*, and in the telson in the *Stomatopoda* (Fig. 250), and always above the intestine. This piece is wanting only in the *Cumacea* (?) and *Paguridæ*. Except in the *Stomatopoda* and *Paguridæ* where the ovaries and testes lie in the abdomen, the germ glands are entirely or for the greater part restricted to the thorax. They everywhere lie between the intestine and the heart. The testis on each side is a tube which either remains straight (*Stomatopoda*), or is coiled up in a complicated manner (*e.g.* in *Paguristes, Carcinus*), or is provided with simple lateral invaginations (*Palinurus*), or is much branched and carries small sacs at the ends of the branches (*Astacus*). It is enclosed in an envelope of connective tissue. The long and much coiled vasa deferentia run, like the oviducts in the female, posteriorly where the germ glands are in the thorax, and anteriorly where they are in the abdomen. They fall into two divisions, a proximal portion lying near the testes and a distal glandular portion often provided with small invaginations, this latter division being continued into the strongly muscular ductus ejaculatorius. This opens outwardly at the basal joint of the last pair of thoracic feet either on a slight-swelling (*Macrura*) or at the point of an elongated tubular penis (*Brachiura, Schizopoda*).

In the *Stomatopoda* there emerges at the point of the penis, besides the ductus ejaculatorius, the duct of a paired tubular accessory gland (Fig. 250, *A*, *d*) which lies in the free thoracic segments, and the two parts of which are connected anteriorly by an unpaired intermediate piece.

The ovaries agree in general with the testes in position and shape, but they are simpler inasmuch as they are simple tubes or vesicles. In *Squilla* they have segmental bulgings. The oviducts are shorter and not so much coiled as the sperm ducts. They emerge at the typical point in the antepenultimate thoracic segment, in *Squilla* immediately at the side of a median receptaculum seminis.

We cannot here enter on the subject of egg and sperm formation in the Crustacea. But the egg formation in the Cladocera, as it is peculiarly interesting, must be briefly described. Successive groups, each consisting of four germ cells, sever themselves from the germ layer when the production of summer eggs takes place, but only one cell out of each group becomes an egg, the others being used up as nourishment. In the production of winter eggs, however, only one cell out of every second group of germ cells becomes an egg, while the remaining 7 cells of the two groups serve as nourishment for the one egg.

XI. Sexual Dimorphism.

This is more or less marked in all Crustacea. There are indeed no outer or inner portions of the body which in some one species, genus, or order of Crustacea are not differently constructed in the two sexes, and these differences have great biological significance and are of great importance in classification. We can here only select the most important and most widely distributed.

The sexual differences are all to be ultimately explained as adaptations for ensuring reproduction and for preserving the young. Adaptations facilitating the copulation of the male and female are principally found in the body of the male. Adaptations for securing the favourable development of the eggs are met with in the female.

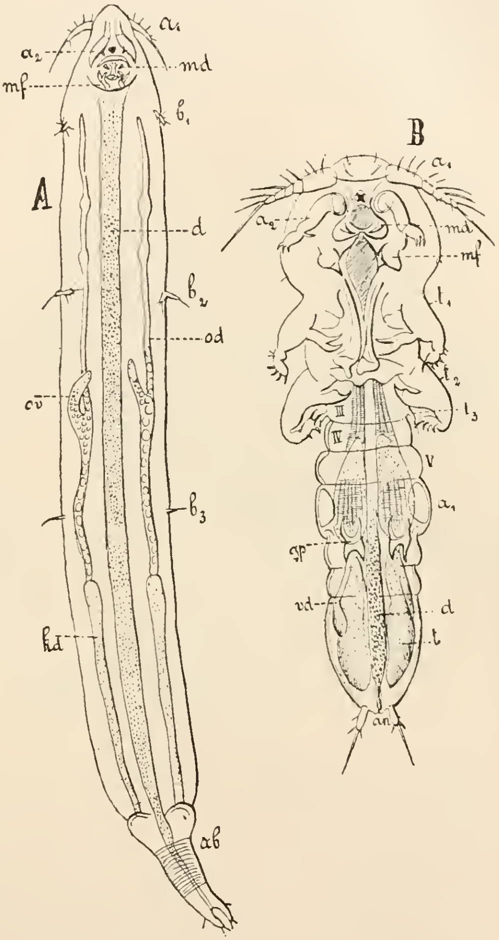

FIG. 252.—**Lernaeascus nematoxys.** *A*, Female, *B*, male, more highly magnified. a_1, Anterior; a_2, posterior antennæ; *md*, mandibles; *mf*, maxillipedes; b_1, b_2, b_3, t_1, t_2, t_3, thoracic feet; *od*, oviduct; *ov*, ovary; *kd*, cement gland; *ab*, abdomen; *d*, intestine; *III*, *IV*, *V*, thoracic segments; a_1, 1st abdominal segment; *gp*, genital plate; *vd*, vas deferens; *t*, testes (after Claus).

Male Sexual Characteristics.—(*a*) The males of the Crustacea are throughout smaller and often also more agile than the females. This distinction of size is specially remarkable in parasitic and attached Crustacea, where the minute males (as in the *Cirripedia* and *parasitic Isopoda*) are described as **dwarf males.** On the other hand, in all cases where the females are so deformed and degraded by parasitism as to be hardly recognisable or even altogether unrecognisable as Crustaceans, the males appear less degenerated; they are usually still able to move freely, are provided with distinct limbs, and show some resemblance to the nearest related free-living forms. This slighter degeneration on the part of the males may be considered as the **persistence of a larval stage,** the parasitic Crustacea undergoing, as we shall see, a striking metamorphosis. Free-living larval forms with Crustacean characteristics, however, bring about the infection of new hosts. The degradation and crippling of the body only take place after the larva has attached itself on its definitive host. In the males this degradation does not occur, or not to the same extent, because they are obliged to retain their power of free locomotion in order to ensure the possibility of copulation and of fertilisation of the females. Since, however, the sole work of the male consists in the seeking out of, and the fertilisation of the female, we often find (as in the parasitic *Cirripedia*) great degeneration of the parts not immediately connected with reproduction. The intestine is thus wanting in the dwarf male of the *Cirripedia* which on reaching its destination, *i.e.* the body of the female, there leads a semi-parasitic life. If the male does not reach this destination, he has failed in his life-work and perishes. To this subject of dwarf males we shall have to return (p. 382).

The accompanying figures (Figs. 252, 253, 254) illustrate the great sexual dimorphism found in certain parasitic *Copepoda* and *Isopoda*.

(*b*) The **olfactory** filaments (Riech- und Spür- fäden) on the anterior antennæ are always present in far greater numbers in the male than in the female.

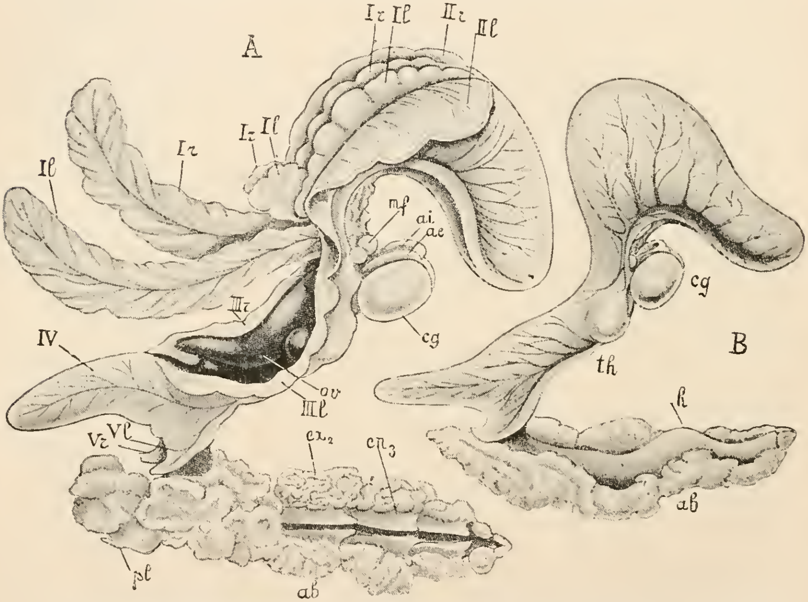

FIG. 253.—**Portunion Mænadis.** Adult mature female (after **Giard** and **Bonnier**). *A*, **With the brood cavity partly opened in the ventral median line and the brood lamellæ separated.** The abdomen (*ab*) is so placed that the ventral side is seen. *I r*, The anterior middle and posterior lobes of the first brood lamella on the right side; *I l*, the same of the first brood lamella on the left; *II r* and *II l*, 2d brood lamellæ (right and left): *III r* and *III l*, 3d brood lamellæ (right and left); *IV*, 4th brood lamellæ; *V r* and *V l*, 5th brood lamellæ (right and left); *pl*, pleural lamella of the 1st abdominal segment; *ex*$_2$, exopodite of the pleopod of the 2d abdominal segment; *en*$_3$, endopodite of the pleopod of the 3d abdominal segment; *ov*, ovary; *cg*, cephalogaster; *ae*, outer; *ai*, inner antennæ; *mf*, maxillipede. *B*, **Adult female, brood cavity not opened.** The abdomen *ab* is seen slantingly from above; *th*, thorax; *cg*, cephalogaster; *h*, cardial prominence.

(*c*) In the males of the most different divisions, apart from the actual copulatory organs, there are limbs transformed into "accessory organs of copulation" for the seizing, grasping, and holding fast of the female. Such are the posterior antennæ of *Branchipus*, the seizing hooks in the anterior pair of limbs of the *Estheridæ*, the adaptations for holding the female in the 2d antennæ or the maxillipedes of the *Ostracoda*, the anterior (seizing) antennæ of the *Copepoda*, etc. In the *Amphipoda* the seizing hooks on the anterior thoracic feet are more strongly developed in the male than in the female. In the *Anisopoda* (*Tanais dubius*) 2 forms of males have been observed, both of which seem to be peculiarly well organised for catching and holding the female. The one form may be called "scenters," the other "seizers." The former have numerous olfactory filaments on the antennæ, the latter much larger and very movable pincers on the chelate feet. In the *Decapodan* males, the most anterior pair or the two most anterior pairs of pleopoda seem transformed in order to assist in copulation. In the crayfish for example, they serve as tubes or channels for conducting the spermatophores away from the genital aperture to their destination. The other pleopoda which in the female carry the fertilised eggs are reduced in the male, or may be, as in the *Brachyura*, entirely wanting. In the *Decapodan* males also the chelæ of the chelate feet are more strongly developed than in the female.

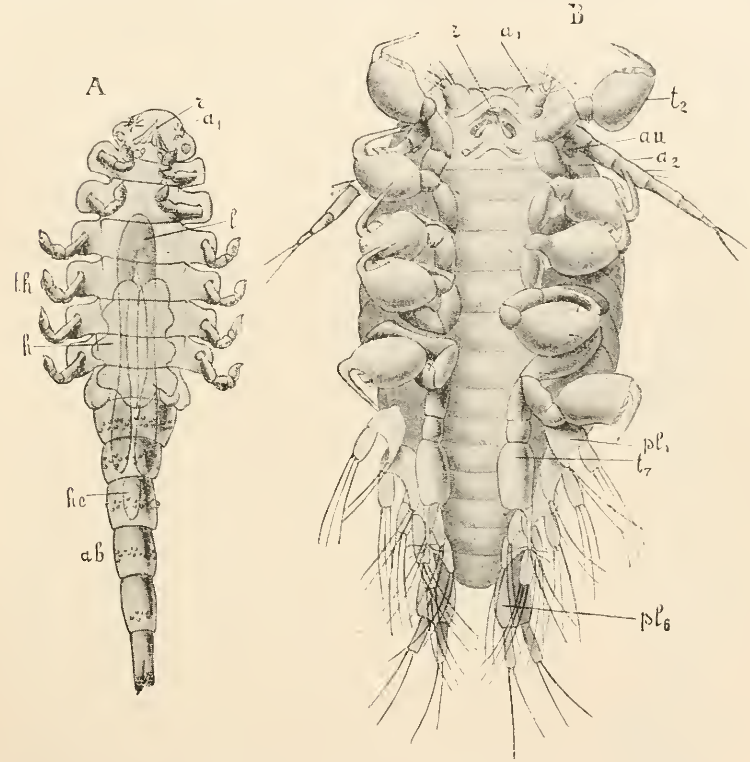

FIG. 254.—*A*, **Adult male of Cancrion miser (nearly related to Portunion,**[Fig. 253, after **Giard** and **Bonnier**). *r*, Rostrum; a_1, anterior antenna; *th*, thorax; *l*, liver; *h*, testis; *he*, heart; *ab*, abdomen. *B*. **Hatched embryo of Portunion Maenadis (after Giard and Bonnier)** from the ventral side. t_2, limb of the 2d; t_1, of the 7th thoracic segment; a_2, 2d antenna; pl_1, 1st; pl_6, 6th pleopod; *au*, eye.

Adaptations for the Care of the Brood.—It rarely happens in the Crustacea that the female simply lays the eggs, attaching them to some foreign object and leaving them to their fate. We find almost everywhere, on the contrary, that the females retain the eggs on or in their own bodies in such a way that they are protected and often also nourished by the mother body. The eggs develop under the protection of the mother body, till the larvæ or young Crustaceans are hatched, and even these occasionally remain for some time in their birthplace.

In the *Cirripedia* the eggs are concealed in the interior of the shell between the mantle and the body of the animal. In the *Rhizocephala* the integument splits into an outer lamella (mantle) and an inner lamella (wall of the visceral sac). Between the two a brood cavity arises (Fig. 248, p. 373), into which the eggs, emerging from the female atrium, enter, and in which they develop. The eggs are enclosed in a richly branched sac, formed of a chitinous membrane, and exactly repeating the form of the cement glands which enter the female atrium. The sac is in reality nothing but the inner cuticular lining of the cement glands which is ejected when the eggs are laid and becomes filled with the eggs as they leave the ovary. The Nauplii which develop out of the eggs in the brood cavity reach the exterior by means of its aperture called the cloaca. In the *Branchiopoda* there are various arrangements for the care of the brood. In the shelled forms, the eggs are concealed under the shell, either in appendages of certain pairs of limbs which are transformed into ovisacs or brood pouches (*Apus*), or on filamentous appendages of such limbs (*Estheridæ*). In the *Cladocera* the eggs develop in a brood cavity (Fig. 192, p. 289), which forms dorsally between the shell and the body, becomes entirely closed towards the exterior by special arrangements, and contains a fluid for the further nourishing of the brood. In some *Cladocera*, a saddle-shaped thickening of the dorsal integument of the shell (Ephippium) covers every one or two winter eggs, and is cast off with the eggs as a protection during winter. This ephippium is often provided with adaptations which facilitate its passive distribution in space. In the *Copepoda*, the eggs which emerge from the genital apertures reach the interior of ovisacs which stand out freely from the body (in the genital segment), and which are formed from the secretion yielded by the cement glands. Where the two genital apertures lie somewhat far apart laterally or dorsally in the double genital segment there is a pair of ovisacs; where they lie very near each other on the ventral side, one unpaired median ovisac is formed (Fig. 194, p. 290). These ovisacs are so characteristic of the *Copepoda*, that by this means the most deformed parasitic *Copepodan* females may be recognised (Fig. 255). In the *Notodelphydæ* alone the eggs pass into a brood cavity enclosed by the integumental folds. The female of the *Leptostraca* shelters the eggs and hatched larvæ between the lamellated thoracic feet. In the female of the *Arthrostraca*, *Schizopoda*, and *Cumacea* the brood lamellæ on the basal joints of the thoracic feet already described develop at the approach of sexual maturity. These brood lamellæ, by locking into one another from right and left, form the base of a brood cavity, whose cover is the ventral (sternal) integument of the thorax (Fig. 218, p. 318). The eggs reach this brood cavity and develop in it. The hatched young or larvæ often stay some time in it. The females of the *Decapoda* attach the emerging eggs to the pleopoda by means of the secretion of the cement glands already mentioned on the under side of the abdomen. In the *Brachyura*, whose shield-shaped abdomen is bent round on the sternal side of the cephalo-thorax, the abdomen is generally decidedly larger and broader in the female than in the male, and more adapted for covering and protecting the egg masses. The same difference, though not so pronounced, may be seen in the *Maerura* also.

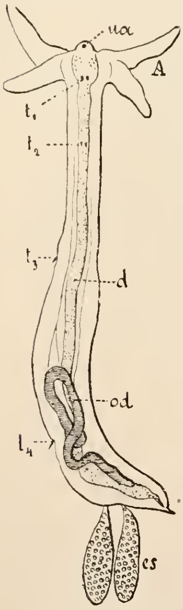

FIG. 255.—**Lernaeocera esocina, female.** *ua*, Frontal eye; t_1, t_2, t_3, t_4, rudimentary thoracic feet; *d*, intestine; *od*, oviduct; *es*, egg sacs; *A*, arm processes at the anterior end of the body (after Claus).

XII. Hermaphroditism in the Crustacea.

Hermaphroditism is a rare phenomenon in the Crustacea, and only found in attached and parasitic forms, viz. in the attached and parasitic *Cirripedia* and in parasitic *Isopoda*.[1] The sexual relations in these groups are very interesting and must be further briefly described.

The commoner *Balanidæ* and *Lepadidæ* are hermaphrodite. There are, however, *Lepadidæ* (*Ibla* and many species of *Scalpella*) in which, besides the hermaphrodite individuals, dwarf males occur. These latter live parasitically on the bodies of the hermaphrodite individuals, generally in a fold of the mantle at the closing edge of the scutum. In their structure and form they are nowise like the hermaphrodites. They do not advance beyond the so-called *Cypris stage*, their body is almost vermiform and possesses besides the antennæ only 4 pairs of reduced tendril-like feet. The oral limbs are wanting. A mouth is wanting, the enteric canal is rudimentary, and the testes unpaired. It is evident that these reduced dwarf males provide occasionally for the cross fertilisation of the hermaphrodite individuals.

There are again some species of *Scalpella* (*Sc. ornatum*, *regium*, *parallelogramma*, *nymphocola*), and further the genera *Cryptophialus* and *Alcippe*, in which dwarf males occur, but in which the individuals which correspond with the hermaphrodite individuals of the related *Cirripedia* are not hermaphrodite, but only female. Here, therefore, separation of the sexes prevails with marked dimorphism. The majority of the *Cirripedia*, however, seem to be hermaphrodite without dwarf males. The *Rhizocephala* are hermaphrodite with dwarf males, which remain at the *Cypris stage*.

The hermaphroditism of certain parasitic *Isopoda* is of another sort. The *Cymothoidea* are protandrously hermaphrodite, *i.e.* in youth they are male, later, the male copulatory segments are lost and the adult animals are exclusively female (Fig. 256).

The sexual relations in the *Entoniscidæ* (*Portunion*) are probably the following. These large, characteristically-deformed parasites (Fig. 253) are protandrously hermaphrodite, but there are, besides, small males (Fig. 254, *A*) which have remained in a larval stage, and besides these again other degenerate so-called complementary males. Out of several larvæ which reach the host, those which have the best place on its body and are best nourished probably develop into adults which function as females, the second-best nourished larvæ remain as males in a larval stage, and all the others become degenerate complementary males.

The Bopyridæ, which are parasitic in the branchial cavity of the *Carididæ*, are sexually separate and strongly dimorphic; the dwarf males live on the bodies of the females.

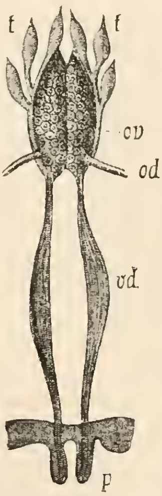

Fig. 256.—**Hermaphrodite sexual apparatus of a young Cymothoa œstroides** (after **P. Mayer**), somewhat diagrammatic. *t*, Testes; *ov*, ovary; *od*, oviduct; *vd*, vas deferens; *p*, penis.

The origin of all these peculiar sexual relations is still very uncertain. Most free living Crustacea are sexually separate, and so are also the free living forms related to the hermaphrodite Crustacea. From this, and from the fact that hermaphrodites are found among the parasitic and attached Crustacea, we may, with some probability, conclude that hermaphroditism in the *Cirripedia* and *Isopoda* is an acquired condition, perhaps brought about by the small

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[1] The *Apusidæ* (*Phyllopoda*) have also lately been shown to be hermaphrodites, with the occasional presence of males.

chance of fertilisation, which the attached or parasitic mode of life offers to sexually separate animals. To explain the occurrence of a hermaphrodite condition in general, we must assume (an assumption not without foundation) that the rudiments of the germ glands are indifferent, that in one case, under certain unknown circumstances, they may develop as testes, in another as ovaries, and in others again produce ovaries as well as testes.

In the *Cirripedia*, the attached and parasitic modes of life are evidently extremely old. If the view that they are descended from *Copepoda*-like forms is correct, then the ancestors of the *Cirripedia*, when first the attached or parasitic modes of life appeared, were probably sexually separate, and dimorphic with small, free-moving males, as indeed is still the case in many parasitic *Copepoda*. The attached and parasitic modes of life then became more and more pronounced in the female, and caused the appearance of hermaphroditism. The males, in the meantime, who had also taken on the Cirripede character, remained as dwarf males, and so the possibility of occasional cross-fertilisation was preserved. In most *Cirripedia* the males have probably in time disappeared, and the purely hermaphrodite condition has become fixed. In others, the dwarf males proving under certain conditions sufficient for ensuring fertilisation, have apparently led to the disappearance of hermaphroditism and the reappearance of sexual dimorphism.

In the *Isopoda* the sexual relations have probably developed in quite another way. How protandrous hermaphroditism arose in the *Cymothoidea* is indeed, at present, uncertain. But we can perhaps imagine the rise of the sexual relations in the *Cryptoniscidæ* and *Entoniscidæ* in this way; these animals were originally, like the *Cymothoidea*, protandrously hermaphrodite, then in time some of the larvæ developed only to the male stage and became larval or degenerate males.

In the gill-inhabiting *Bopyridæ* the male stage, in the originally hermaphrodite individuals, must have been suppressed, as the dwarf males sufficed.

In the Amphipodan species *Orchestia*, the curious fact has been established that a certain part of the germ layer of the testes of the male produces eggs, while the other parts produce spermatozoa. The eggs, however, never, or only in exceptional cases, reach the exterior, and in any case do not develop further. The above fact, which does not stand alone, is at present unexplained.

XIII. **Parthenogenesis—Cyclic Reproduction.**

Parthenogenesis occurs in the Crustacea only in the *Phyllopoda*, viz., in *Estheria* and *Apus* (see note, p. 381) among the *Branchiopoda* and in the *Cladocera*. The males are much rarer than the females, and in the *Cladocera* appear only periodically in autumn.

The thin-shelled summer eggs develop parthenogenetically, and in many *Phyllopoda* in summer there is a succession of generations of females multiplying parthenogenetically. The larger hard-shelled winter eggs, on the contrary, which are supplied with more nutritive yolk and are laid in autumn, require fertilisation.

XIV. **Ontogeny.**

We can here present only a selection of the observations on the ontogeny of the Crustacea, which are so numerous and have such an important bearing on general morphological and biological questions. We shall first briefly describe the development of the outer body form of some few Crustaceans which go through a long process of metamorphosis, and then give a sketch of the development of their inner organisation.

A. **The larval history of the Crustacea—The Development of Apus** (Order **Phyllopoda**, Family **Branchiopoda**).

1st Larval Stage, *Nauplius.*—Out of the egg is hatched an oval larva narrowing like a pear posteriorly, with a median frontal eye and three pairs of limbs, the most anterior of which is rod-shaped, while the two posterior are biramose. Its form and its setæ are illustrated in Fig. 257, *A*.

On the dorsal side of the body the **dorsal shield** has begun to form. The anus lies in an indentation of the posterior margin of the body. This first stage is called the *Nauplius* larva : it is met with in essentially the same form as the first product of the egg in many Crustaceans ; we shall therefore enumerate its general characteristics. **Body unsegmented with median frontal eye, with dorsal shield and frontal sensory organs (filaments, etc.) with 3 pairs of limbs, the first of which is simply rod-shaped,** *i.e.* **consists of a single row of joints, while the 2 posterior are biramose,** *i.e.* **consist of a protopodite, endopodite, and exopodite (shaft, inner and outer branch). In all Crustaceans the first pair of limbs of the Nauplius become the anterior antennæ, the second the posterior antennæ, the third the mandibles of the adult animal.**

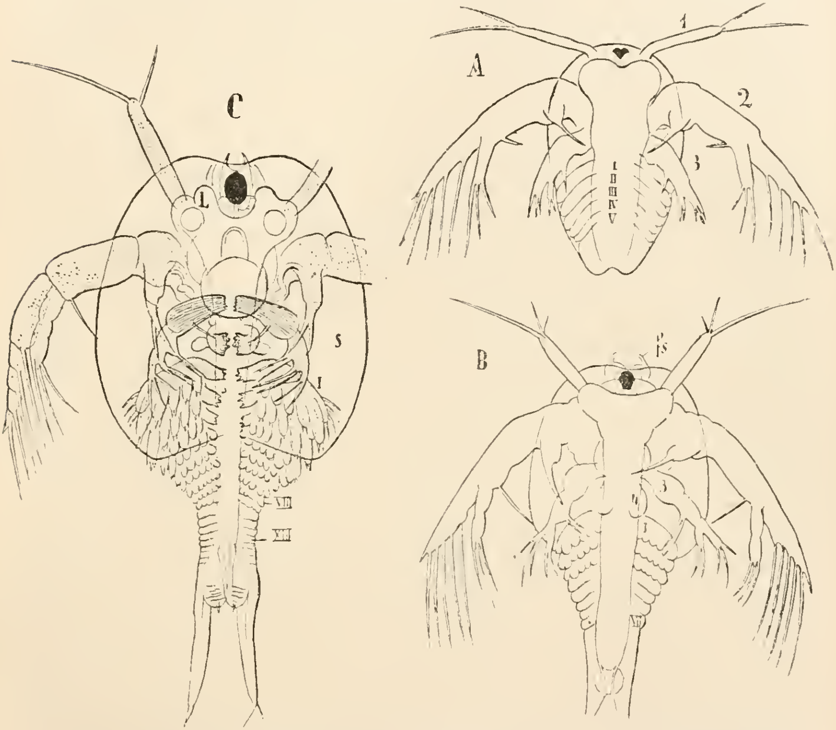

Fig. 257.—**Larvæ of Apus** (after **Claus**). *A*, **Nauplius**, just hatched, with the rudiments of the 5 anterior trunk segments I-IV. *B*, 2d larval stage, with the rudiments of the anterior maxillæ and the first 7 trunk segments. *C*, 4th larval stage. *L*, Liver ; *s*, shell ; *fs*, frontal sensory organ.

The *Nauplius* of *Apus* (Fig. 257, *A*) is distinguished from the typical *Nauplius* larva only by the fact that in the posterior third of the larval body, in front of its posterior end, the rudiments of the 5 anterior trunk segments (*I-V*) and their limbs can be recognised under the integument.

2d Larval Stage.—The *Nauplius* casts its skin and the larva in the 2d stage (Fig. 257, *B*) shows considerable modifications. The anterior body is broadened, the posterior body elongated in the shape of a cone. There are two frontal projecting stylets (frontal sensory organs). The dorsal shield has increased in size. On the basal joint of the 3d pair of limbs (mandibular limbs) a masticatory process has formed. Behind the mandibular limbs are the rudiments of the first pair of maxillæ (4). The 5 anterior segments of the trunk can be more clearly distinguished, and also the rudiments of the 3d and 4th pair of trunk limbs, the latter as transverse ridges. Later a 6th segment arises, and behind it the rudiments of the 2 subsequent segments. The bulgings at each side of the anus have become elongated into considerable furcal processes.

3d Larval Stage.—This is entered on at the 2d moult. There are 6 anterior pairs of lobate trunk limbs, whose size and degree of differentiation decreases from before backward; these already clearly show the characteristic form of the Phyllopodan swimmerets, with their endites, exopodites, and branchial sacs. Behind the 6 anterior trunk segments 2 more, and later 3 more, can be distinguished, and behind the anterior maxillæ the posterior have begun to form. The dorsal shield at first covers only the two anterior trunk segments.

The **4th Larval Stage** appears with 7 anterior pairs of lobate trunk limbs (Fig. 257, *C*). Three to four anterior segments are covered by the dorsal shield. The 8th and 9th pairs of limbs show the beginning of lobate formations; the 10th to 13th pairs of trunk limbs just arising. Rudiments of the paired eyes are visible. The rowing antennæ (2d antennæ) are provided with large jaw hooks.

5th Larval Stage.—The 9 anterior pairs of trunk feet are lobate, the 10th is in the act of forming a lobe, the 11th, 12th, 13th, and 14th pairs of feet are forming. Behind these are to be seen the rudiments of 6 new segments. Locomotion, hitherto caused by the 2 anterior pairs of limbs, is now chiefly produced by the trunk feet (swimmerets).

The mandibular foot is, as compared with the earlier stage, very much reduced, its principal part now being the masticatory process.

Further Larval Stages.—Frequent moults follow. New swimmerets are continually formed behind those already developed, and become differentiated from before backward. The mandibular foot is more and more reduced, till nothing remains but the masticatory process. The rowing limbs of the larvæ (2d antennæ) also become reduced. The dorsal shield continues to widen. The form of the adult animal develops very gradually.

From this larval history we see, 1st, that the body and its appendages in general become differentiated quite gradually from before backward, that new segments and limbs progressively, though also occasionally irregularly, form behind those already developed, and that these differentiations originate in the most posterior region of the body.

2d. That there occur deviations in details from this manner of formation. The maxillæ are an instance of **belated** appearance in the order of the limbs from before backward. This fact is of importance because in the adult *Phyllopoda* as compared with other Crustaceans the maxillæ are very much simplified.

3d. The mandibles, which in the adults are masticatory ridges without feelers, are in young larvæ well developed biramose limbs.

4th. The posterior antennæ, which are reduced in the adult, are, as large biramose rowing arms, the chief organs of locomotion in the young larva.

Development of Cetochilus (Order **Copepoda**, Family **Calanidæ**).

1st Larval Stage. Typical Nauplius (Fig. 258, *A*).—At the basal joint of the 2d antenna there is a masticatory process characteristic of most Crustacean *Nauplii.* The mouth is overhung by an enormous upper lip, which is also characteristic of many other *Nauplius* larvæ. The anal aperture is not yet formed.

2d Larval Stage.—The body, and especially the posterior division, has grown longer. Anteriorly there is a small shell-fold. At the end of this stage the first pair of maxillæ appear as small biramose feet behind the pair of mandibular feet.

3d Larval Stage. Metanauplius (Fig. 258, *B* and *C*).—Behind the first pair of maxillæ the 2d, and behind these the 2 anterior pairs of trunk limbs, are forming, all as biramose feet. The dorsal shield covers the anterior part of the body as far as and including the 2d maxillar segment. Masticatory ridges have developed on the basal joints of the maxillipedes

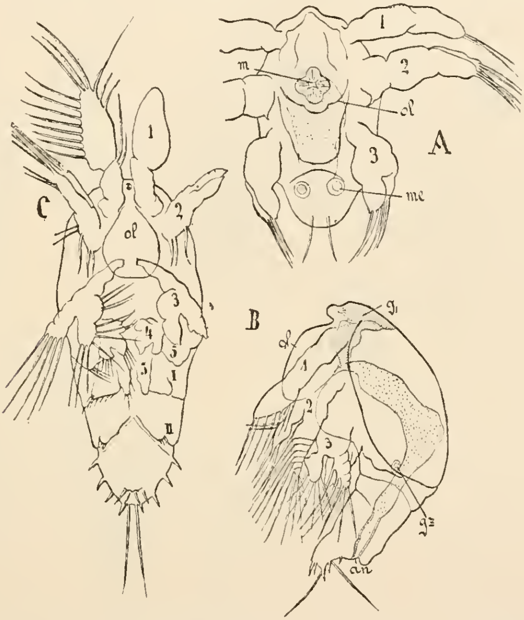

Fig. 258.—**Larvæ of Cetochilus septentrionalis (after Grobben).** *A*, **Nauplius**; *B*, **Metanauplius** with the rudiments of the first 2 thoracic limbs from the side. *C*, **older Metanauplius.** *ol*, Upper lip; *m*, mouth; *g*, brain; *gz*, genital cells; *an*, anus; *me*, primitive mesoderm cells; *5*, the two maxillipedes of the left side (exo- and endopodite of the posterior maxillæ).

Further Larval Stages.—During several moults a third trunk segment forms.

1st Cetochilus Stage.—The furcæ at the end of the body are completed. A 4th trunk segment and the 3d trunk limbs begin to form.

From what we find in other *Copepoda,* the only parts needed to complete the form of the adult animal are the remaining trunk segments and the 2 posterior trunk feet, all of which form during successive moults. The 2 pairs of maxillipedes which are separately inserted on the body, and are characteristic of the adult *Copepoda* in reality only correspond with the branches of the 2d pair of maxillæ from which they come, and thus strictly speaking represent but one pair of extremities.

We thus again see that in the *Copepoda* also the body with its limbs becomes progressively differentiated from before backward. Inasmuch as all the limbs of the adult animal are fully and typically developed, we find in this case, during the development, no reduction of limbs once (*i.e.* in larval stages) strongly developed.

Development of Sacculina (Order **Cirripedia**, Sub-order **Rhizocephala**).

The comparison of the process of development in free-living *Entomostraca* with that in the parasitic forms is very instructive. Let us take that Crustacean form which in an adult hermaphrodite condition is the most degraded and deformed, viz. *Sacculina* (Figs. 208, 248). Although the adult animal cannot be recognised as a Crustacean, the series of larval forms through which it passes during its individual development most clearly proves it to be such, and related to the *Cirripedia*.

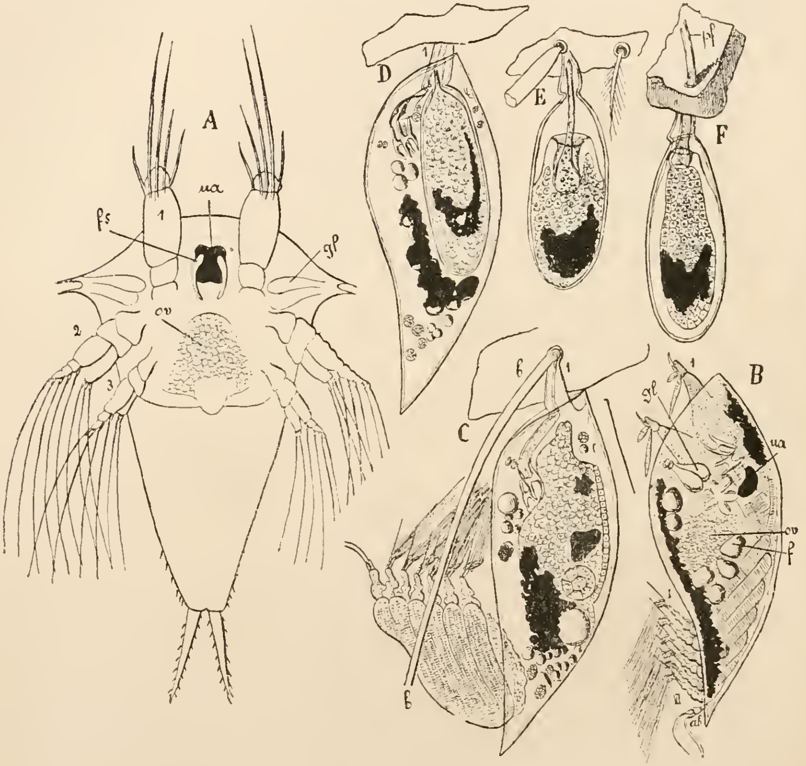

Fig. 259.—**Various larval stages of Sacculina Carcini.** *A*, **Nauplius** after the first moult. *B*, **Cypris stage** from the side. *C*, The same, 3 hours after the larva has by means of its adhering antennæ attached itself to a seta of the host. *D*, **Formation of the Kentrogon larva.** *E*, The same completed, the *Cypris* larval shell thrown off. *F*, The arrow has bored through the chitinous carapace of the host. The contents of the sac begin to pass into the body cavity of the host through the arrow. *fs*, frontal sensory organ; *ua*, Nauplius eye; *gl*, glands of the frontal horns; *ov*, rudiment of the ovary; *f*, fat globules; *b*, seta of the host, to which the parasite has attached itself by means of its adhering antennæ; *pf*, arrow of the *Kentrogon* stage; *ab*, abdomen (after **Delage**).

Nauplius Stage (Fig. 259, *A*).—A typical *Nauplius* with its 3 characteristic pairs of limbs is hatched from the egg. The shield-like dorsal integument forms on each side anteriorly a process (frontal horn) at whose base glands emerge. There are 2 frontal filaments (frontal sensory organs) and an unpaired frontal eye. On the under side of the head is a median projection of considerable size in the place of the large upper lip of other *Cirripede* larvæ. At the posterior end of the body are 2 separate jointed caudal processes. Mouth, intestine, and anus are wanting. Near the *Nauplius* eye is a cerebral ganglion. About the middle of the body lies a mass of cells, the rudiments of the ovary. The *Nauplius* now moults 3 times and undergoes during these processes a series of transformations preparatory to

The **Cypris Stage** (Fig. 259, *B*), which it enters after its 4th moult. In this stage we find a laterally compressed shell entirely enclosing the body, and consisting of 2 lateral valves which pass into each other, in the dorsal middle line, without articulating. The body consists of 3 regions, the large head, the trunk, and a rudimentary terminal portion (the abdomen). The shell arises from the head. The head contains the rudiment of the ovary, and carries the *Nauplius* eye, the frontal filaments and one pair of antennæ which have proceeded from the anterior uniramose pair of limbs of the *Nauplius*. The **two pairs of typical biramose limbs of the Nauplius (2d pair of antennæ and pair of mandibular feet) have disappeared.** The trunk consists of 6 segments, which have formed during the last *Nauplius* stages behind the head portion, and it has 6 pairs of typical biramose limbs which cause the swimming movement of the larva. The short abdomen carries one pair of short appendages provided with setæ. Mouth, intestine, and anus are wanting. The larvæ still feed at the expense of the nutritive yolk derived from the egg, which is thus gradually absorbed.

The Kentrogon Stage.—After a free life of at least 3 days the *Cypris-like* larva fixes itself by means of one of its two antennæ to the base of a seta on the back or on a foot of a very young crab. It then throws off the whole trunk, so that only the head is retained (Fig. 259, *C*, *D*). The organs retained in the head become indistinct and, to a certain extent, fuse into a spherical mass which surrounds itself with a new hollow cuticle under the old one. The shell is then thrown off, and another new cuticle forms round the sac-shaped body within the old one, and in a crater-like depression of this new cuticle a hollow arrow-like process is formed (Fig. 259, *E*). The crater-like depression is then evaginated, the hollow arrow or borer is in this way pushed forward through the antennæ and pierces it and the soft chitinous cuticle at the base of the seta of the host, and thus penetrates the body of the latter (Fig. 259, *F*). Through this hollow arrow the whole contents of the pouch now pass over into the body cavity of the host, and after becoming surrounded with a new cuticle are known as

"**Sacculina Interna.**"—All the organs of the adult *Sacculina* are formed out of the cell masses which have in this way passed over through the arrow. Among others the testes are now first developed, and are thus, as compared with the ovaries, very late. The *Sacculina interna* lies on the abdominal intestine of the host, and feeds by means of numerous root-like processes proceeding from its surface and penetrating the viscera of the host. As the *Sacculina* increases in size it exercises pressure on the musculature and integument of the host, which die away on the under side of the abdomen in the immediate neighbourhood of the parasite, thus allowing the latter to pass out, while the roots (now proceeding from a stalk) remain inside the host.

Sacculina Externa.—The cloaca, till now closed, opens, and at its edge dwarf males are always found; these have been shown to be animals which have remained at the *Cypris-like* larval stage, but can be distinguished from the female *Cypris-like* larvæ by the fact that they develop no arrow.

The attached *Cirripedia* (*Lepadidæ* and *Balanidæ*) like the *Sacculina* pass through a *Nauplius* and a *Cypris* stage in the course of their developments. These larvæ differ from the corresponding larvæ of *Sacculina* not only in the possession of an enteric canal, but in a few other points as well. The **Nauplius larva** of the *Cirripedia* is characterised by a dorsal shield with frontal horns and posterior pointed processes, and by a large upper lip. Frequent moults lead to the **Cypris-like larva** (Fig. 260); this has a bivalve shell with shell muscles; its anterior antennæ have become adhering antennæ. The posterior antennæ and mandibular feet of the *Nauplius* larva have disappeared, and so has the upper lip. By the side of the median eye a paired compound eye has arisen. Behind the mandibular feet of the *Nauplius* simple anterior and perhaps also posterior maxillæ have begun to form. The trunk consists of 6 segments with 6 pairs of biramose feet serving for swimming. The abdomen has 2 furcal appendages. A cement gland opens on the 2d joint of the adhering antenna, which is provided with a sucking disc.

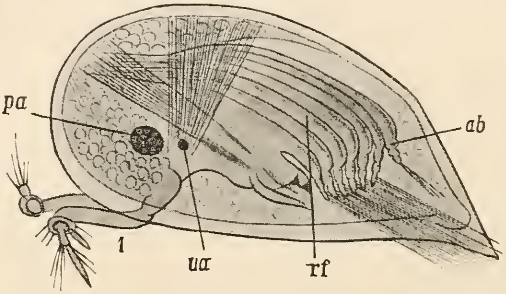

Fig. 260.—**Cypris-like larva of Lepas fasciculata** (after Claus).

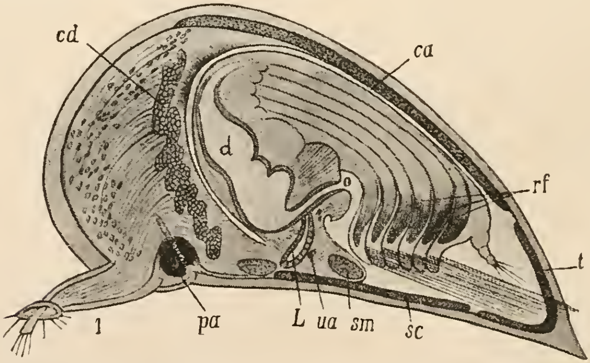

Fig. 261.—**Pupa of Lepas pectinata**, in optical section (after **Claus**). In Figs. 260 and 261, the same letters are used: *pa*, paired eye; *ua*, unpaired Nauplius eye; *rf*, trunk feet, in Fig. 261 with the tendril-like feet beginning to form inside; *1*, anterior (adhering) antennæ; *L*, liver; *sm*, occlusor muscle of the scuta; *ab*, abdomen; *ca*, carina; *t*, tergum; *sc*, scutum; *cd*, cement gland.

The *Cypris-like* larva attaches itself by means of its adhering antennæ. A pupa stage follows (Fig. 261), during which the organs of the adult *Cirripede* form under the larval skin. Within the maxillæ and the 6 pairs of trunk feet of the *Cypris-like* larva the mouth parts and the 6 pairs of tendril-like feet of the adult *Cirripede* begin to form. In the *Lepadidæ* the head grows out anteriorly into the stalk which carries the minute adhering antennæ, and under the Cypris shell the 5 shell pieces form on the mantle-fold. The Cypris shell is thrown off, and the paired eyes disappear.

The history of the development of the attached and parasitic *Cirripedia* is in many respects exceedingly interesting. The *Cypris-like* larva shows, apart from the absence of posterior antennæ and mandibular feet, a distinctly *Entomostracan* character. Its 6 typical biramose feet recall the swimmerets of the *Copepoda*. The remarkable transformation of the free-swimming *Cypris-like* larva into the attached sexual animal must be referred to its adaptation to an attached mode of life; this adaptation consists in the formation of a hard shell or framework serving for protection, the transformation of the swimmerets into tendril-like feet suited for bringing food within reach, and the reduction of the paired eyes which are of no great use to the adult animal. A commencement of this adaptation to the attached mode of life may perhaps be seen even in the *Cypris* stage, viz., in the degeneration of the posterior antennæ and mandibular feet, which in the *Nauplius* larva had played an important part, especially as organs of locomotion, whereas in the *Cypris-like* larva the trunk feet serve that purpose. The transformation of the *Cypris-like* larva into the parasitic *Sacculina* involves far more radical changes than those which take place in the development of the *Lepadidæ* and *Balanidæ*. The development of *Sacculina* may be described as a strikingly retrogressive metamorphosis. To explain the reappearance of the typical *Nauplius* and *Cypris-like* larvæ in the course of development, notwithstanding the degradation of the adult animal, it is necessary not only to emphasise the power of inheritance but to remember that free-moving young forms are extremely useful to parasites for the infection of new hosts and the maintenance of the race. Nevertheless, even in the free-swimming larvæ of *Sacculina*, we recognise distinct signs of degeneration such as the absence of an alimentary canal. This degeneration could take place without damage to the maintenance of the race, because the adult *Sacculina*, in consequence of its exceedingly favourable conditions of nutrition, can give its eggs for their development so much nutritive yolk that the larvæ proceeding from them are under no necessity of obtaining food from without. The occurrence, at first sight so remarkable, of an endoparasitic stage in the development of the *Sacculina* is not difficult to understand, for by passing through such a stage the parasite avoids the danger of being thrown off by the moulting of the host.

Larval History of the Euphausidæ (Order **Schizopoda**, Fig. 262).

1. **Nauplius Stage.**—Typical.

2. **Metanauplius Stage.**—The masticatory ridge of the mandible develops, while the mandibular foot itself is reduced. The upper and under lips form. Behind the mandibles the rudiments of the 2 pairs of maxillæ and of the 1st pair of thoracic feet (maxillipedes) appear as buds. The cephalothoracic shield is distinctly developed, and the paired eyes first appear.

3. **Calyptopis Stage** (somewhat corresponding to the *Protozoœa* stage of *Penæus*) (*B*, *C*).—The thorax and abdomen are demarcated, and the latter already elongated. Segmentation appears in the thorax, and later in the abdomen. No new extremities except the last pair of pleopoda (uropoda) begin to form.

4. **Furcilia Stage.**—The paired eyes become stalked. The most anterior pairs of thoracic and abdominal feet begin to form in succession from before backward.

5. **Cyrtopia Stage.**—The antennæ are transformed and no longer serve for locomotion. The posterior pairs of thoracic and abdominal feet and the gills appear.

6. **Post-larval Stages.**—The adult animal is gradually formed, and the caudal fin definitely developed. It is hardly necessary to remark that all the thoracic feet

and pleopoda are originally biramose and in this animal retain this character during life. No great importance should be attached to the names of the developmental stages (*Calyptopis, Furcilia, Cyrtopia*); they are referable to a time when the larvæ so named were thought to be different genera. We thus again see, from the larval history of the *Euphausidæ*, that the body with its limbs is differentiated from before backward. We notice, however, special and important exceptions to this rule. In the first place the rudiment of the last pair of pleopoda appears before those of the other pleopoda, before even those of the thoracic feet. This is noteworthy on account of the special form of and the important part played by these pleopoda as part of the caudal fin in the older stages of development and in the adult. We further note that although the thorax becomes segmented sooner than the abdomen, and although on the thorax as on the abdomen the extremities become differentiated in succession from before backward, the rudiments of the extremities on the thorax and the abdomen are almost simultaneous and sometimes they even occur earlier on the abdomen.

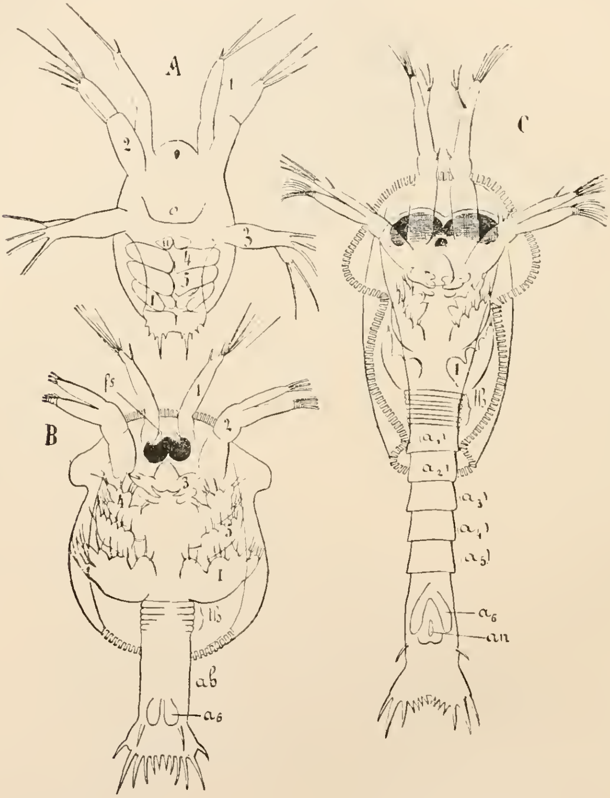

FIG. 262.—**Larvæ of Euphausia.** *A*, **Nauplius**, last form before moulting (after **Metschnikoff**). *B*, **Protozoæa.** *C*, **the same somewhat older** (after **Claus**). *th*, Thoracic segments ; *ab*, abdomen ; (a_1-a_6), abdominal segments ; *an*, anus ; *fs*, frontal sensory organ ; 1-5, limbs of the head ; a_6, 6th pair of pleopoda.

Larval history of Penaeus (Order **Decapoda**, Sub-order **Macrura**, Family **Carididæ** (Shrimps), Figs. 263 and 264).

1. **Nauplius Stage.**—A typical unsegmented **Nauplius** (Fig. 263, *A*) is hatched from the egg. The body possesses no dorsal shield; it carries 2 setæ posteriorly.

2. **Metanauplius Stage.**—The dorsal shield begins to form. The 3d pair of Nauplius limbs (mandibular limbs) shows the rudiments of the masticatory ridge. Behind this appear the rudiments of the 4 subsequent limbs (maxillæ and 2 anterior pairs of maxillipedes).

3. **First Protozoæa Stage** (Fig. 263, *B*).—The cephalothoracic shield has grown large. The posterior division of the body elongates till it is as long as the anterior part. The 2 pairs of maxillæ and the 2 anterior pairs of maxillipedes have developed and are capable of functioning; the latter are biramose limbs with endo- and exopodites. The division which follows behind these is divided into 6 segments without any trace of extremities, and these segments are the rudiments of the 6 posterior thoracic segments (III-VIII). These are followed by the posterior body which is not yet segmented and shows no trace of extremities. The mandibular feeler has disappeared. The posterior body ends with two furcal processes. Near the median eye the paired eyes appear.

4. The **Second Protozoæa stage** (Fig. 264, *A*) is very similar to the first, but on the abdomen the rudiments of the 5 anterior abdominal segments (a_1-a_5) are visible. Behind the 2d pair of maxillipedes on the first of the 6 newly formed thoracic segments the rudiments of the 3d pair of maxillipedes appear (III).

5. **First Zoæa Stage.**—The paired eyes stand out as stalked eyes. The 3d pair of maxillipedes has also become biramose. On the 5 subsequent pairs of thoracic segments the rudiments of the 5 pairs of "ambulatory feet" appear (Fig. 264, *B*, *IV-VIII*). On the segments of the abdomen also formations appear which are probably the rudiments of the pleopoda (a_1-a_6). In any case the beginnings of the last pair of pleopoda which are destined to form with the telson the caudal fin, are distinctly visible on each side as bi-lobed formations under the integument.

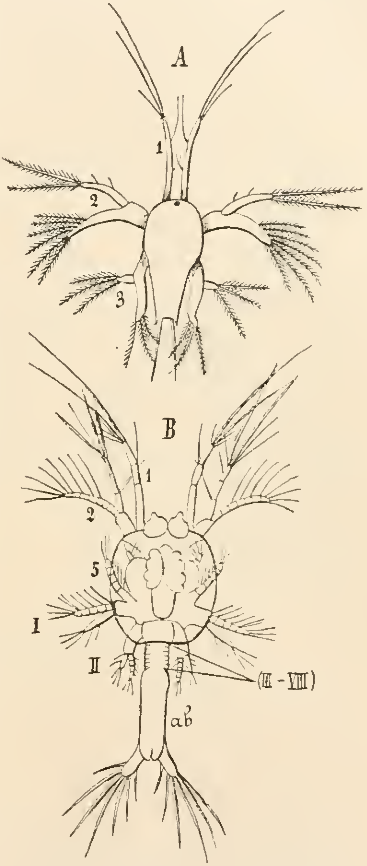

Fig. 263.—**Young larva of Penaeus** (after **F. Müller**). *A*, **Nauplius**; *B*, **Protozoæa**. III-VIII, Rudiments of the 3d-8th trunk segments. *ab*, Abdomen; *1-5*, limbs of the head; *I*, *II*, of the thorax. In all subsequent figures the head limbs are denoted by Arabic, the thoracic limbs by Roman numerals, the abdominal limbs (pleopoda) by a_1, a_2 etc., the telson by *t*, the exopodite by *ex*, and the endopodite by *en*.

6. **Second Zoæa Stage** (Fig. 264, *C*).—The last pair of pleopoda project freely. On the two pairs of maxillæ the small fan-plates (exopodites) have formed. The 5

posterior pairs of thoracic feet (ambulatory feet) project freely as doubly-tipped protuberances. The formations on the abdomen of the 1st *Zoæa* stage, which were indicated as the rudiments of pleopoda, are no longer to be seen. The cephalothoracic shield has a pointed process projecting anteriorly in the middle line. The animal still moves chiefly by means of the 2 pairs of antennæ.

7. **Mysis or Schizopoda Stage** (Fig. 264, *D*).—This is so called because all the thoracic feet are developed, like those of the *Schizopoda*, as long biramose limbs (with exo- and endopodite), and here also serve for swimming. The branchial appendages of the thoracic feet appear. The pleopoda grow further during this period, the most anterior pair first, then the 2d and then the others almost simultaneously. The feelers undergo important transformations, which bring them nearer the adult form. Alterations likewise appear in the cephalothoracic shield. The auditory sac forms at the base of the antennæ. The mandible receives a feeler. The jaws approach their definitive form. By degrees, through several moults, the larvæ reach

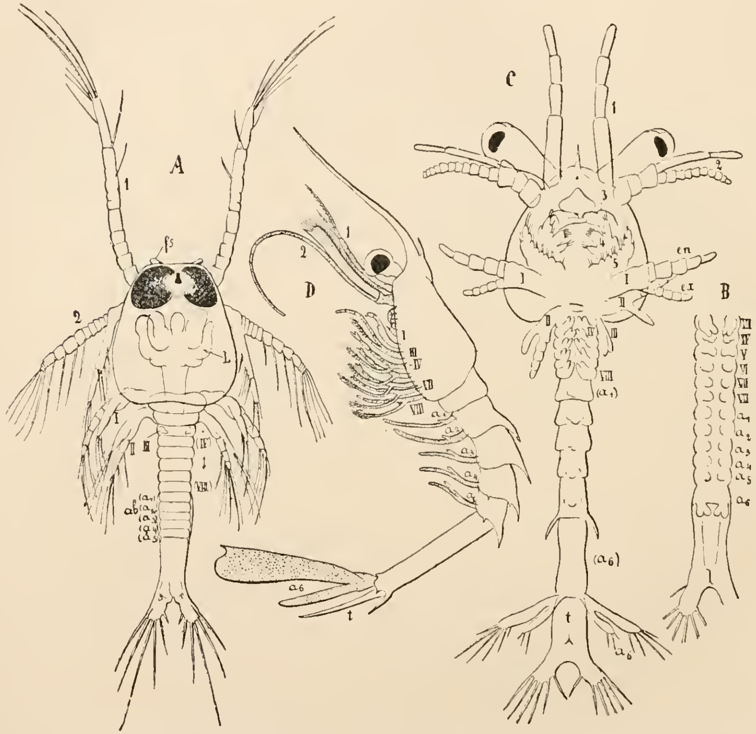

Fig. 264.—**Older larvæ of Penaeus.** *A*, **Older Protozoæa,** dorsal view. *B*, **6 posterior thoracic segments, and abdomen, with the rudiments of the feet of a somewhat older larva.** *C*, **Further advanced Zoæa.** *D*, **Mysis stage of a Penaeus,** from the side. *fs*, Frontal sensory organ; *L*, liver; *ab*, abdomen; *IV-VIII*, thoracic segments; (a_1-a_6), abdominal segments; *t*, telson. In *C* to the left, the 3d thoracic foot (3d maxillipede) is covered by the 2d (after **Claus**).

8. The **Penaeus form,** the exopodites of the thoracic feet becoming more or less reduced and the pleopoda developing further.

The *Penaeus* development also shows us that the body with its appendages becomes differentiated from before backward. But here also the last pair of pleopoda advances more rapidly than the others.

Larval history of the Stomatopoda (Fig. 265).

Unfortunately we do not know the whole series of larval forms in any of the *Stomatopoda*. They belong to two types, one of which is called the *Erichthus*, the other the *Alima* type. We shall only consider the first.

A. **Youngest known Erichthoid larva** (*A*).—Three regions can be distinguished in the body, an anterior, a middle, and a posterior. The anterior corresponds with the head, and from it arises as a fold of the integument a large dorsal shield which covers the second region as well. The head carries besides a median eye the two large stalked eyes, the two pairs of antennæ, the pair of mandibles and the two pairs of maxillæ. The second region consists of 5 segments, corresponding with the 5 anterior thoracic segments, and carries 5 pairs of biramose swimmerets (*I-V*), the last 3 of which decrease in size from before backward. The 5 pairs of limbs answer to the 5 pairs of oral limbs in the adult *Stomatopoda*. The third region consists of 3 short limbless segments (also covered by the dorsal shield) corresponding with the 3 posterior thoracic segments, and a very large caudal plate, also devoid of appendages.

B. **In a somewhat older 2d larva** a new segment (the most anterior abdominal segment) with one pair of limbs has formed in front of the caudal plate. The 2d pair of thoracic feet shows alterations preparatory to its transformation into large seizing feet.

C. **In a third larva** (*B*) 2 new segments with the rudiments of their limbs, and in older larvæ all the abdominal segments with their pairs of limbs excepting the 6th, have begun to form in front of the caudal plate, while the 3 posterior thoracic segments are still limbless.

D. **In a fourth Erichthoid larva** the 2 anterior pairs of thoracic feet have lost their exopodites, but on the other hand the rudiments of epipodites (gills) appear on them. The three subsequent pairs of thoracic feet are reduced, and the last three thoracic segments are still limbless. On the 6th abdominal segment the rudiments of the limbs (uropoda) appear.

E. **In the subsequent stages**, the 3rd, 4th and 5th pairs of thoracic limbs are completely reduced, or else are represented only by small sac-like prominences (*C*).

F. There now follows, after various preparatory intermediate stages, **the completely developed Erichthus larva.** (*D*) The 3d, 4th, and 5th pairs of thoracic limbs again appear in their definitive form, so that now the 5 anterior trunk limbs are developed as seizing or oral limbs. On the last three thoracic segments the rudiments of the biramose ambulatory limbs appear. By this time, not only the full number of segments, but the full number of limbs of the adult animal is reached.

In this larval history of the *Stomatopoda* we note

(1) That **the segments of the body become differentiated from before backward.**

(2) That **the limbs also as a general rule follow the same order.** We observe this principally in the case of the abdominal limbs, since in the youngest *Erichthoid* larva the 5 anterior thoracic limbs are already developed. Of the pleopoda, the last (uropoda) appeared last, in opposition to the *Decapoda*, in which this latter takes precedence of all the others and even of some of the thoracic limbs.

3. **The last three** weakly developed thoracic limbs (ambulatory limbs) form the chief exception to the rule stated under (2), in that they first appear after the pleopoda.

4. It is a striking fact that the 3d, 4th, and 5th pairs of trunk limbs which are early developed as biramose rowing feet become completely reduced, and are then again formed in their definitive shape in the oldest *Erichthus* stage.

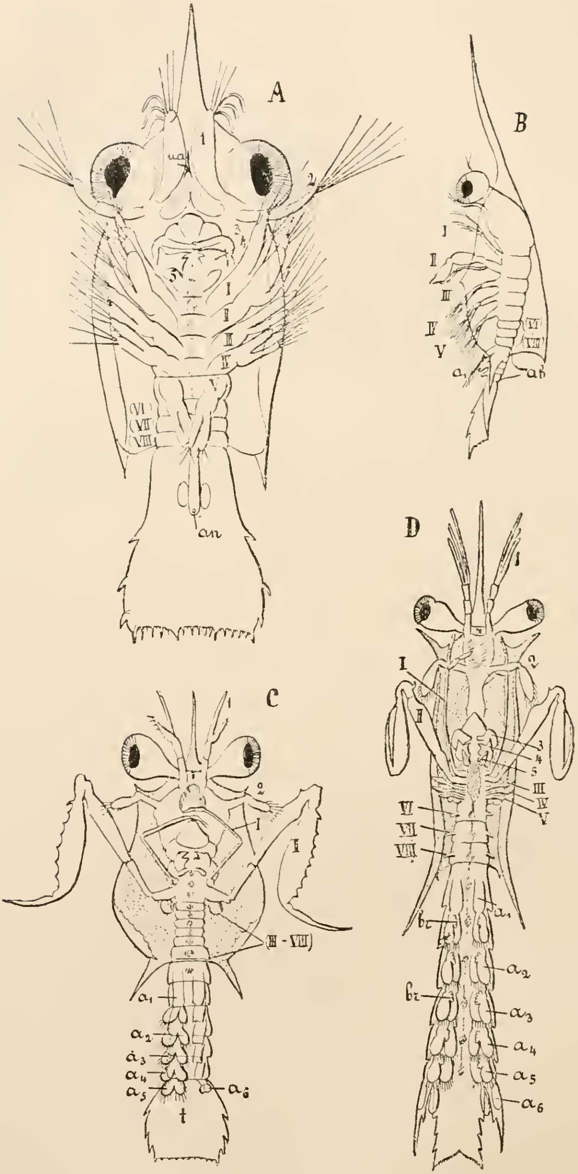

FIG. 265.—**Stomatopodan larvæ of the Erichthus type.** *A*, **Youngest known Erichthoid larva.** *B*, **Somewhat older larva,** from the side. *C*, **Young Erichthus larva** (*Zoœa*). *D*, **Older Erichthus larva** with complete number of limbs. *an*, Anus; *ua*, nauplius eye; *br*, rudiments of the gills on the pleopoda; *ab*, abdomen. The Roman numerals in brackets denote the corresponding limbless thoracic segments. *I-V*, Oral feet; *VI-VIII*, ambulatory feet; *t*, telson (after **Claus**).

Development of Palinurus and Scyllarus (Decapoda, Macrura, Fam. Loricata).

The early larval development is carried on within the shell; during this development 2 stages, a *Nauplius* stage and a very important further stage which might be called the **embryonic Phyllosoma stage**, are passed through. The characteristics of this latter stage are as follows: There are 2 pairs of antennæ, mandibles, and 2 pairs of maxillæ. The thoracic limbs have all begun to form, *i.e.* 3 pairs of maxillipedes and 5 pairs of ambulatory limbs. The 2 most posterior (ambulatory limbs) are only present as minute buds. The 6 anterior are biramose, but the exopodites of the 2d and 3d pairs of maxillipedes are degenerated even during embryonic life. There are two stalked lateral eyes, and the median *Nauplius* eye. In the body 3 regions are to be distinguished. (1) Head with dorsal shield; (2) thoracic region, in which the segmentation is indicated; (3) a distinctly segmented but limbless abdominal region ending in a fork.

Before the larva is hatched, however, in addition to the 2 posterior pairs of ambulatory feet which remained undeveloped, the 1st pair of maxillipedes disappear, and the 2d pair of maxillæ and the 2d pair of antennæ degenerate.

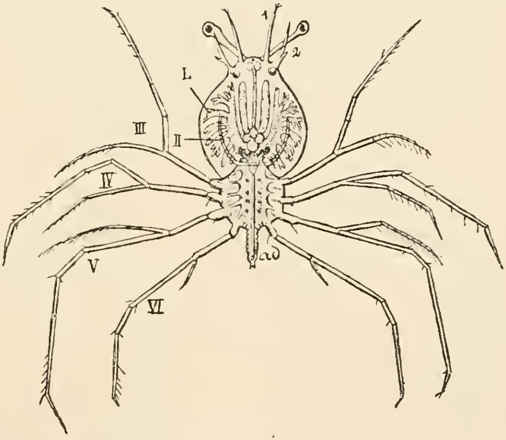

Fig. 266.—**Phyllosoma of Palinurus** (after **Claus**). *ad*, Abdomen; *l*, liver.

In the larva hatched from the egg the above-mentioned regions of the body can be recognised—it is much flattened dorso-ventrally (like a leaf), and as transparent as glass; it is called the **younger Phyllosoma** (Fig. 266).

The **older Phyllosoma larva** is distinguished from the younger by the following characteristics. The 1st pair of maxillipedes has formed anew, and the 2 posterior pairs of ambulatory feet have developed. The 2 posterior maxillipedes again develop exopodites, and on the ambulatory limbs the rudiments of the gills appear. The abdomen is more elongated and shows the rudiments of the pleopoda. The larva thus already has, apart from its strange form, typical Decapodan characteristics. Its transformation into the sexual form has not been observed.

In the development of the Loricata we note:—

1. That during the processes which go on in the last part of embryonic life the body with its extremities becomes differentiated typically from before backward.

2. That before the hatching of the *Phyllosoma* larva certain extremities or parts of **extremities degenerate, to appear anew on the older Phyllosoma larva**; this

is especially the case with the 1st maxillipedes, and the rudiments of the last 2 ambulatory feet. The *Phyllosoma* shows in a specially striking manner the character of a pelagic larva.

Development of the Brachyura.

A very characteristic **Zoæa larva** (Fig. 267) is hatched from the egg. Its dorsal shield is marked by the possession of long spine-like processes, among which a frontal, 2 lateral and 1 dorsal are never wanting. All the head limbs are present. Of the thoracic limbs we find only the 2 anterior pairs of maxillipedes ; the other thoracic limbs, as well as that part of the thorax to which they belong, are wanting or are only found in their first rudiments. The abdomen is segmented, and ends in a fork, but has no appendages.

FIG. 267.—**Zoæa of Maja,** after its moult (after **Claus**). *h*, Heart.

In the **later Zoæa stages** the 3d pair of maxillipedes appears, the 5 ambulatory feet arise as uniramose limbs (without exopodites), and the pleopoda begin to form. The *Zoœa* swims principally by means of the 2 biramose anterior pairs of maxillipedes, and also by means of the abdomen which, in comparison with that of the adult, is elongated and well developed.

The older *Zoœa* changes into a **Megalopa larva** (Fig. 268).

This larva, but for the more strongly developed abdomen and the pleopoda, already resembles the sexual form. The maxillipedes and ambulatory feet appear as in the adult condition, and it must be specially remarked that the ambulatory feet are never biramose, and that the **Brachyura thus do not pass through any Schizopoda stage.**

Through many moults the *Megalopa* is gradually transformed into the sexual form.

We need say only a few words about the **development of the other Malacostraca.** The *Leptos-*

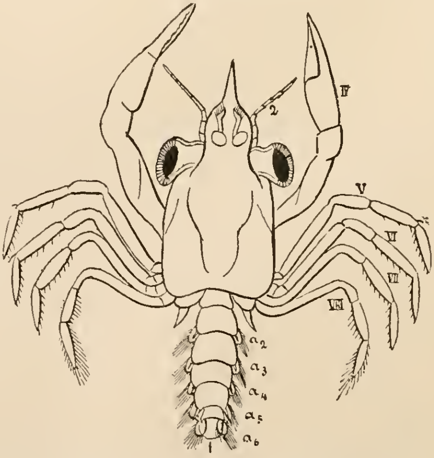

FIG. 268.—**Megalopa larva of a Portunus with abdomen straightened out,** dorsal aspect (after **Claus**).

traca (*Nebalia*), the *Amphipoda*, and a few *Decapoda* (*e.g.* the *Cray-fish*), leave the egg in a form like that of the sexually ripe animal. On the other hand in the *Isopoda*, *Mysidæ*, and *Lophogastridæ* among the *Schizopoda* and the *Cumacea*, the young form hatched from the egg may be very little developed, and may even resemble a maggot-shaped *Nauplius* or *Metanauplius*; but there are no early free-swimming larval forms, as the young undergo their metamorphoses in the brood pouch of the mother. The development of the parasitic *Isopoda* is interesting, since here the free-moving young or larval forms which go in search of hosts, resemble the typical *Isopoda* in form and development of the body and limbs much more distinctly than do the sexually mature animals.

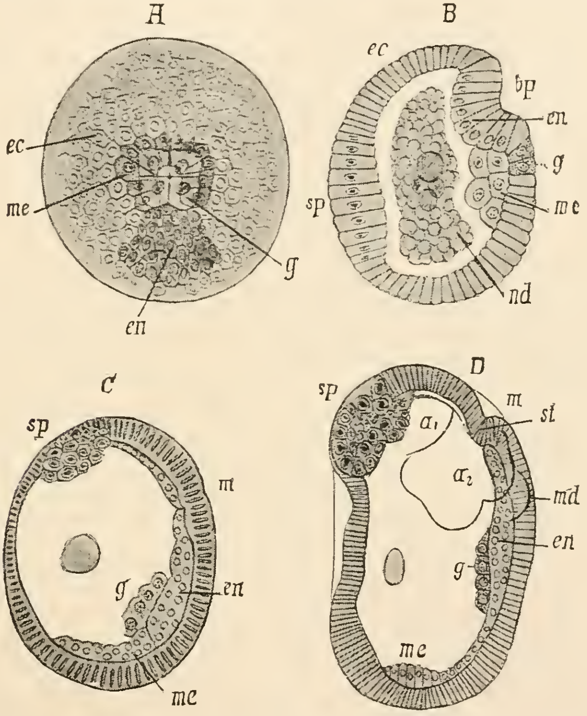

FIG. 269.—**Moina rectirostris. Four early stages of development.** *A*, **Blastosphere,** seen from the vegetative pole. *B*, **Gastrula stage.** *C*, **somewhat older stage,** with neural plate, closed blastopore and sexual cells sunk below the surface; *D*, **Nauplius stage,** *B*, *C*, *D*, in optical longitudinal section. In *C*, *D*, the neural plate, and in *D*, the rudiments of the *Nauplius* limbs are projected on to the section. *ec*, Ectoderm; *me*, mesoderm; *g*, primitive sexual cells; *en*, endoderm; *sp*, neural plate; *bp*, blastopore; *nd*, nutritive yolk; *m*, mouth; *st*, stomodæum; a_1, anterior; a_2, posterior antennæ; *md*, rudiments of mandible (after **Grobben**).

B. The Arrangements of the Germ Layers and the Development of the Inner Organs

may here be described by means of a few examples.

I. Moina rectirostris (Order, Phyllopoda; Sub-order, Cladocera; Fig. 269).

The segmentation of the mesolecithal egg is superficial, and somewhat unequal. In the 32 blastomere stage a blastomere lying at the vegetative pole is distinguished by a specially large nucleus. This divides, and as the **primitive sexual cell** produces the rudiments of the **germ glands.**

A blastomere in contact with this sexual cell yields the **endoderm,** and the blastomeres, which surround the primitive sexual cell, and the primitive endoderm cell, yield the **Mesoderm** (except the sexual organs and nervous system). In a later stage (Fig. 269, *A*) we find 4 genital cells, 32 endoderm cells, and 12 mesoderm cells; all the remaining blastomeres represent the ectoderm. First the 12 mesoderm cells sink down, then the **endodermal plate becomes invaginated** (*B*). In place of the gastrula mouth, which probably closes, the definitive mouth appears later. The genital cells increasing in number to 8, then sink down (*C*). Nutritive yolk remains in the segmentation cavity. Two paired frontal groups of cells appear as rudiments of the **neural plate.** Later on this plate consists of several layers and yields anteriorly the **brain,** and posteriorly the **retina.** The œsophageal commissures and the ventral chord arise in situ as thickenings of the ectoderm. The mesoderm spreads itself out on the inner side of the ectoderm, on the surface of the rudiments of the genital glands, and around the mid-gut which is at first solid: this mid-gut alone proceeds from the endodermal invagination. The **shell gland** is of mesodermal origin and only opens secondarily at the point of the 2d maxilla. The compound eye is from the first paired.

II. **Cetochilus septentrionalis** (Order, **Copepoda**).

The segmentation is total and yields a blastula with a small segmentation cavity. Under the blastomeres at a certain stage 2 symmetrically placed cells can be distinguished as **primitive mesoderm cells** and a few others also symmetrically placed as **endodermal cells.** The dividing mesoderm cells sink deeper inwards. In still later stages we can recognise at the posterior end of the mesoderm, on each side, a large primitive mesodermal cell. The endoderm also becomes invaginated into the segmentation cavity. The gastrula mouth closes in a median line from before backward. The dividing mesoderm cells fill the segmentation cavity. The **stomodæum** and **proctodæum** arise by means of ectodermal invaginations. At a later (*Nauplius*) stage there arises at each side behind the *Nauplius* eye an **ectodermal thickening** connected with the brain, which severs itself from the integument but degenerates later. These are to be considered as the rudiments of the **paired compound lateral eyes** with their optic ganglia, which are wanting in most *Copepoda.* A pair of mesoderm cells lying on the ventral side of the intestine represent the rudiments of the **sexual glands.** The 2 cells move higher on the 2 sides of the intestine, and become surrounded with smaller mesoderm cells, which yield the rudiments of the **ducts,** which at first are solid. In the 1st *Cetochilus* stage the paired genital rudiments fuse to form an unpaired dorsal sexual gland. The **heart** develops out of a paired rudiment of mesoderm cells.

III. **Branchipus** (*Phyllopoda*).

In the hatched *Nauplius* larva under the cuticle, the segments of the first maxillæ and the first two trunk segments, with their limbs, have already begun to form. An elongated portion follows, in which the segmentation of the mesoderm streaks has begun. This does not reach as far back as into the anal segment. The two mesoderm streaks unite posteriorly directly in front of the anal segment to form a ventral plate which forms a **budding zone.** Its cells rapidly increase, and as the development of the larva progresses new mesoderm segments continually become demarcated from the budding zone and spread out under the ectoderm to the dorsal middle line. But this segmented germ streak merely represents the **parietal layer** of the mesoderm; the **visceral layer** never becomes segmented, and differentiates quite apart from the parietal layer. (In the anal segment on each side there lie 2 large cells, which, however, do not divide and do nothing to increase the budding zone by contributing cells.)

The cell material of the mesoderm segments, which are successively formed at the anterior end of the budding zone, begins to group itself into three divisions, and this group is the more distinct the further the segment is removed from the budding zone, *i.e.* the older it is. The dorsal division yields the rudiment of the cardial chamber of the segment and that part of the dorsal longitudinal musculature which also belongs to it; the lateral division yields the musculature of the limbs, the ventral the segmental division of the ventral musculature as well as the neurilemma of the ganglia. The **limbs** begin to form as outgrowths and bulgings of the ectoderm, into which cell-growths of the mesoderm penetrate. The **ventral chord** becomes differentiated from before backward. In each segment in which a pair of limbs begins to form an ectodermal thickening appears on each side of the ventral median line. The two thickenings in a segment represent the rudiments of the double ganglion, which at first are not united by a transverse commissure. These rudiments free themselves from the ectoderm at a later stage. We thus find in an older *Branchipus* larva the whole ventral chord from back to front in all stages of differentiation. Posteriorly, where new pairs of ganglia are continuously formed with the new segments, these are still ectodermal thickenings. In the **formation of the heart** (many-chambered dorsal vessel) only one longitudinal row of perpendicularly arranged muscle cells on each side takes part. The two rows grow together in such a way as to form a hollow tube. The heart becomes differentiated from before backward. In many larval stages a greater or smaller number of segmental cardial chambers are already developed anteriorly and already pulsate, while posteriorly new cardial chambers are in process of formation.

The rudiments of the **compound eye** appear in the *Metanauplius* larva on each side as a hypodermal thickening, which is then said to divide into two layers, a superficial layer which yields the cornea and crystalline cone cells, and a deeper layer which yields the retinulæ with the rhabdoms. Another ectodermal thickening connected with the first and belonging to the secondary brain chiefly yields the material for the optic and the retinal ganglia.

IV. **Astacus fluviatilis** (Figs. 270-280).

The segmentation is superficial, and leads to the formation of a spherical blastosphere (blastula), in which the central nutritive yolk, which is divided in radially arranged yolk pyramids, is enveloped all round by the blastoderm as by an epithelium.

Stage A. At one point of the blastosphere the constitution of the blastoderm undergoes a change. The cells at this part are longer and stand closer together. This part corresponds with the future ventral side and is symmetrical; it can be denominated the ventral plate. This ventral plate consists of the following portions: the 2 **cephalic lobes**, the 2 **thoraco-abdominal rudiments**, and farthest back, the unpaired median **endoderm disc** (Fig. 271). The whole ventral plate is of one layer except at one point between the endodermal disc and the thoraco-abdominal rudiments. Large cells have sunk down inwards from the blastoderm as the **primitive mesoderm cells** (*B*, *M*). With the exception of the endoderm disc, which becomes invaginated later, and the primitive mesoderm cells, the ventral plate and the whole remaining blastoderm represents the ectoderm. The latter yields at a later stage the sides and back of the thoracic shield, but in the early stages of development is nothing more than a sac surrounding the yolk.

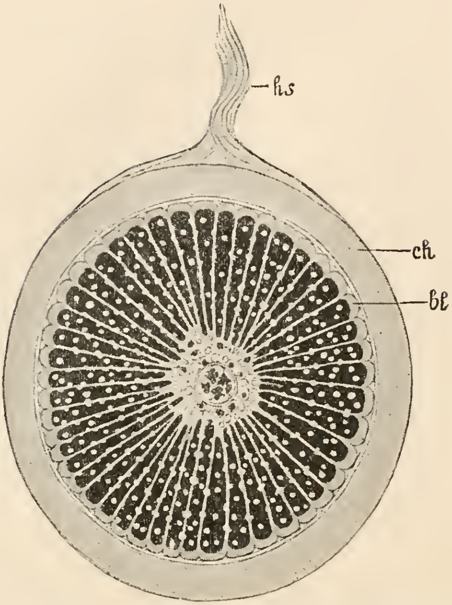

Fig. 270.—**Astacus fluviatilis, section through an egg, after completed formation of blastoderm.** *ch*, Chorion; *hs*, stalk of attachment; *bl*, blastoderm cells. The nutritive yolk is black in this and the following Figs. (after **Reichenbach**).

Fig. 271.—**Astacus fluviatilis, part of the surface of an egg with embryo beginning to form.**—Stage **A.** *K* Cephalic lobes, with the rudiment of the eye; *TA*, thoraco-abdominal rudiments; *BM*, formative zone of the mesoderm; *ES*, endoderm disc (after **Reichenbach**).

Stage B. Embryo, with semicircular gastral furrow.—Only the ventral plate alters. At the anterior edge of the endoderm disc a semicircular furrow, or a fold projecting inwards, appears.

Stage C. Embryo, with circular gastral furrow.—The thoraco-abdominal plates unite in the middle line. The semicircular furrow has become a furrow round the whole circumference of the endoderm disc and is thus circular. The middle part of the endoderm disc sinks down, so that it now becomes a depression with a somewhat raised floor (gastrula invagination). This depression represents the rudimentary midgut, and the outer edges of the original circular furrow are the edges of the blastopore or gastrula mouth. In front of the anterior edge of the blastopore lie the primitive mesoderm cells in active growth, and giving off cells towards the centre of the blastosphere (Fig. 275).

Stage D. The primitive mouth is in the act of closing.—In the centres of the two cephalic lobes are the rudiments of the eyes. Between the cephalic lobes and the thoraco-abdominal rudiments the first traces of the mandibles and antennæ appear. The primitive mouth closes from before backward, its lateral edges growing together in the middle line. The cells of the primitive intestine begin to consume nutritive yolk.

Stage E. Embryo, with mandibles beginning to form.—In the middle of the thoraco-abdominal disc the (ectodermal) rudiments of the anus and hind-gut (proctodæum) appear in the form of an anal pit. The mesodermal elements spread out below the ectoderm.

Stage F. Embryo in the Nauplius stage (Figs. 272 and 276).—The 3 most anterior pairs of extremities (*Nauplius* extremities) can be distinctly made out. Between the anterior antennæ the first (paired) traces of the brain appear, and immediately behind there is a pit-like depression, the ectodermal rudiments of the mouth and fore-gut (stomodæum). In the posterior antennal and the mandibular segments the rudiments of ganglia appear as ectodermal thickenings in the same way as in the formation of the brain. The thoraco-abdominal ridge, surrounded by a deep furrow, projects anteriorly. The anus has moved forward on it and reaches the inner side of its anterior edge, *i.e.* the later ventral side of the end of the body. The ectoderm and mesoderm form a budding zone on the thoraco-abdominal ridge, and from this time new

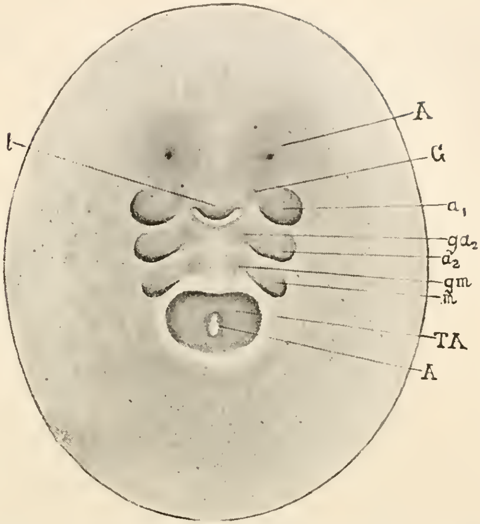

FIG. 272.—**Astacus fluviatilis, embryo in the Nauplius stage.**—Stage **F.** *A* (above), Rudiment of eye; *l*, upper lip; *G*, cerebral ganglion; a_1, anterior antennæ; ga_2, ganglion of the segment of the 2d antennæ (a_2); *gm*, ganglion of the segment of the mandibles (*m*); *Ta*, thoraco-abdominal rudiments; *A*, (below) anus (after **Reichenbach**).

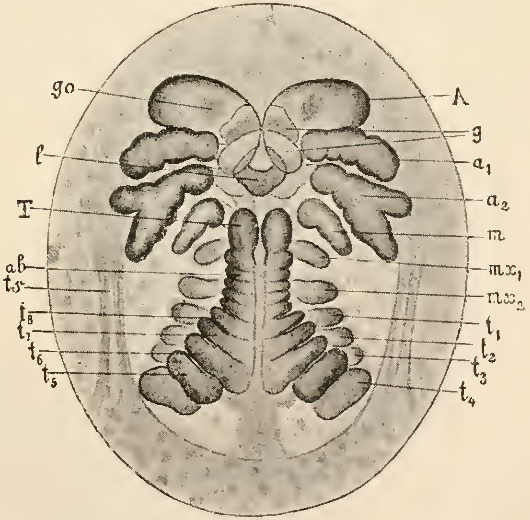

FIG. 273.—**Astacus fluviatilis, embryo with thoracic feet beginning to form.**—Stage **H.** *A*, Eyes; *g*, brain and ganglia of the anterior antennæ (a_1); a_2, 2d antennæ; *m*, mandible; mx_1, mx_2, anterior and posterior maxillæ; t_1-t_8, thoracic feet, of which t_1-t_3 are maxillipedes; *ts*, rudiment of thoracic shield; *ab*, abdomen, bent back on the anterior portion of the thorax; *T*, telson; *l*, upper lip; *go*, ganglion opticum (after **Reichenbach**).

segments with the rudiments of their extremities are continually differentiated anteriorly (but apparently posteriorly, since the rudiments of the thoraco-abdomen are bent forward). At this (*F*) stage the rudiments of the maxillar segments and of the first maxillipedal segment are already present. The hind-gut has become longer, and with its blind end touches the primitive enteric sac (mid-gut). On each side the thoraco-abdomen is bordered by a curved integumental wall, the rudiment of the cephalo-thoracic shield.

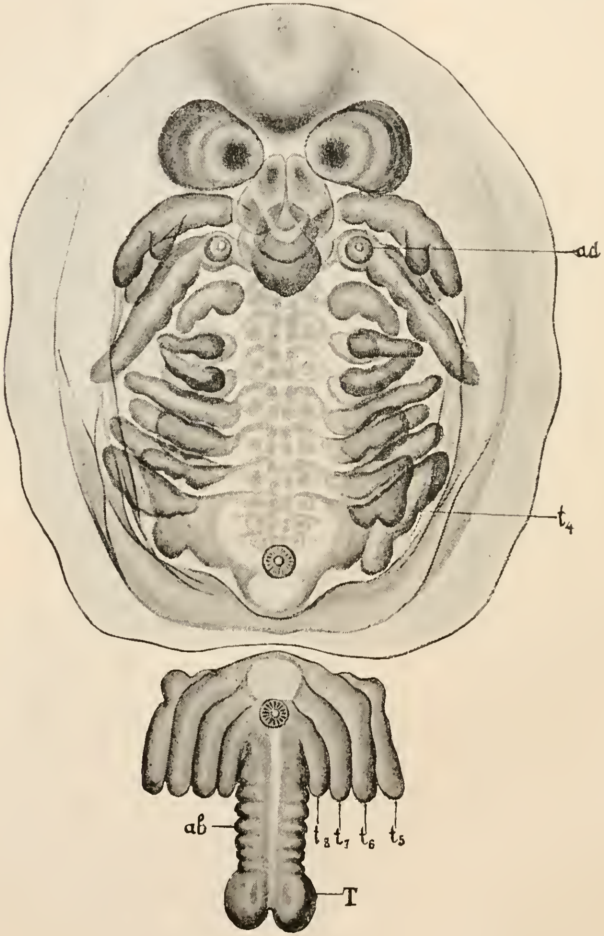

Fig. 274.—**Astacus fluviatilis, embryo with the rudiments of all the limbs.**—The thoraco-abdomen, with the last 4 pairs of thoracic feet cut off and laid back. *ad*, Antennal glands; t_4-t_8, 4th-8th pair of thoracic feet (ambulatory feet); t_4, chelate feet; *ab*, abdomen; *T*, telson (after **Reichenbach**).

Stage G. Embryo with rudiments of maxillipedes (Fig. 277).—The thoraco-abdomen elongates in a longitudinal direction and shows at the **end which is**

directed forwards (telson) **a deep indentation.** The budding zone, from which new segments have formed, borders directly on this indentation. The penultimate abdominal segment (6th) appears, and thus precedes in order of development a large number of segments which lie in front of it. The rudiments of its limbs are already visible.

Stage H. (Fig. 273 and 278) **Embryo with rudiments of ambulatory feet.—All the segments** of the Crustacean body are formed ; they have developed in succession from the budding zone in front of the telson, so that the anterior and most differentiated are the oldest and the posterior least developed are the youngest (with the exception of the 6th abdominal segment). The budding zone itself has been exhausted in the formation of the segments. The rudiments of the eyes project as spheres. The ambulatory feet have developed. The telson appears deeply forked. The abdomen has become slender, and is so bent forward along the thorax that the telson almost touches the upper lip. The hind-gut has opened into the mid-gut, the epithelial cells of the latter having for some time become swollen by assimilating yolk, and being at this stage columnar. The yolk between the mid-gut and the ectoderm is absorbed, and the wall of the mid-gut is almost in contact with the cephalothoracic ectoderm. The ventral chord with its ganglia differentiates from before backward, having arisen out of paired lateral strands, and a middle strand formed by invagination. The lateral strands are ectodermal thickenings with segmental swellings, which sever themselves from the ectoderm in order from before backward (*cf.* also Fig. 279).

Stage J. Embryo with rudiments of abdominal feet.—The cephalothoracic shield has developed greatly, its lateral parts project freely as rudimentary branchiostegites.

Stage K then follows, with developed eye-pigment and the rudiments of the gills. Thereupon the young Crustacean, which is already tolerably similar in appearance to the adult, is hatched from the egg. The fusing of the anterior thoracic ganglia to form the infra-œsophageal ganglion has begun. The forked telson has become a round plate, and the abdomen resembles that of the adult. The liver is formed almost exclusively by processes of folding of the wall of the mid-gut (*cf.* Figs. 274 and 280).

FIGS. 275-280.—**Astacus fluviatilis. Median longitudinal sections through embryos at different stages of development.** In Figs. 275, 276, 277, and 279 only the ventral side of the embryo is depicted, in Figs. 278 and 280 the whole embryo in longitudinal section. In Fig. 280 the position of the embryo is the reverse of what it is in the other figures (all Figs. after **Reichenbach**

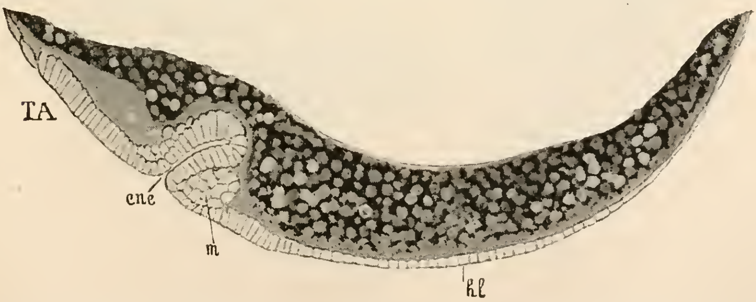

FIG. 275.—**Stage C.** *TA*, Thoraco-abdominal rudiments ; *ene*, endodermal invagination (gastrula invagination) ; *m*, mesoderm ; *hl*, cephalic lobes.

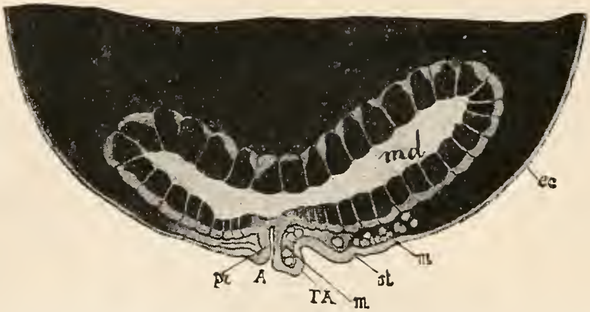

FIG. 276.—**Nauplius Stage. Stage F.** *md*, Mid-gut, the endoderm cells have assimilated nutritive yolk; *pr*, proctodæum (hind-gut); *A*, anus; *TA*, thoraco-abdominal rudiment; *m*, mesoderm; *st*, beginning of invagination of the stomodæum; *ec*, ectoderm.

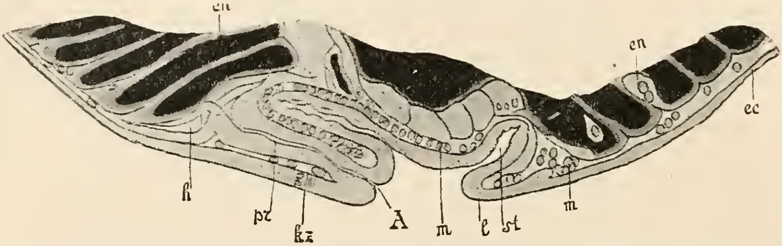

FIG. 277.—**Stage G.** *en*, The endodermal cells laden with yolk; *h*, rudiment of heart; *pr*, proctodæum; *kz*, germ zone; *A*, anus; *m*, mesoderm; *l*, upper lip; *st*, stomodæum; *ec*, ectoderm.

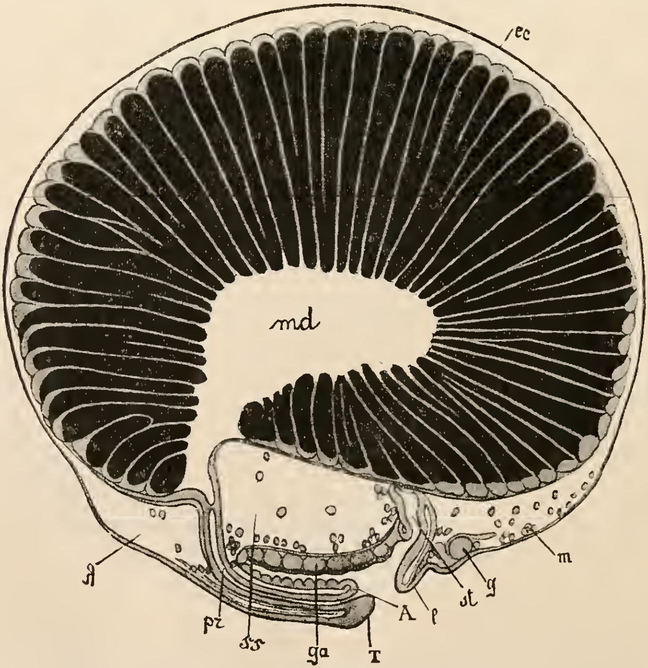

FIG. 278.—**Stage H.** Lettering the same. In addition: *ss*, sternal sinus; *ga*, ganglia of the ventral chord; *T*, telson; *g*, supra-œsophageal ganglion.

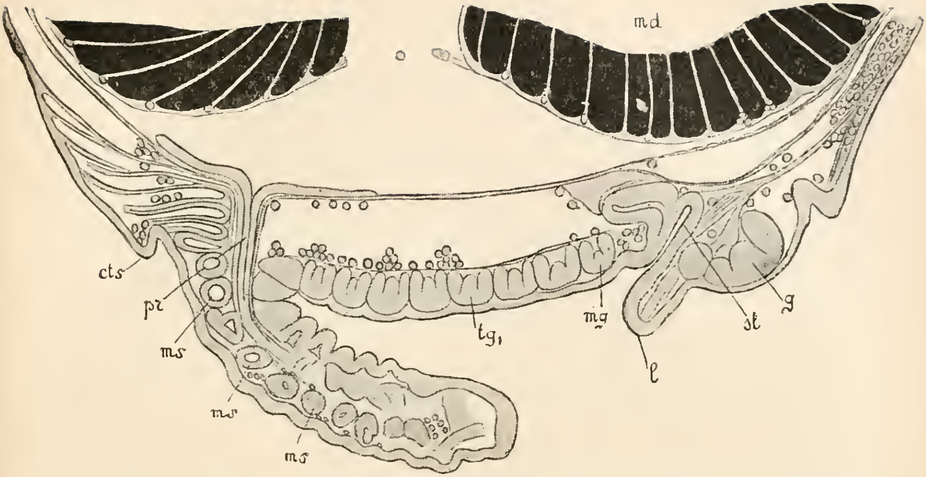

FIG. 279.—**Stage J.** Section not quite median. Lettering as before. In addition: *cts*, cephalothoracic shield; *ms*, mesoderm segments; tg_1, 1st thoracic ganglion (of 1st maxillipede); *mg*, mandibular ganglion.

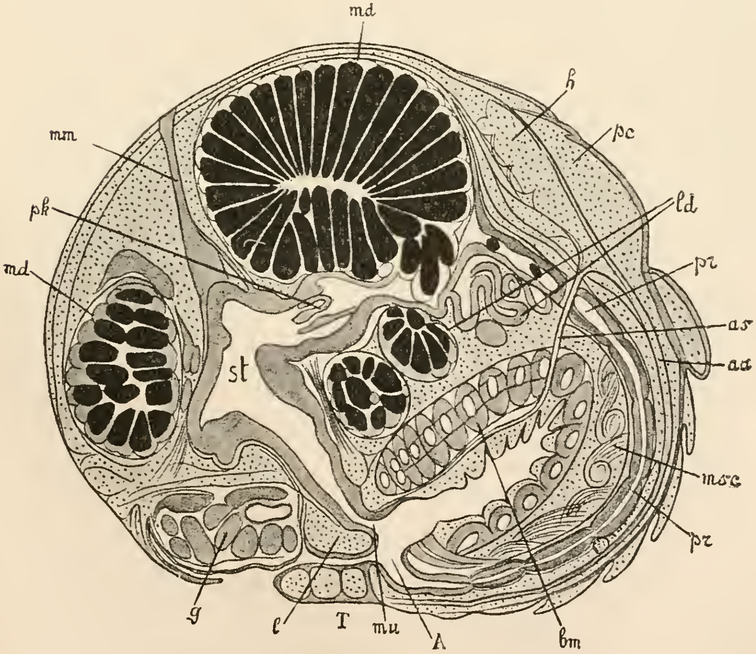

Fig. 280.—**Ripe embryo.** Lettering as before. *mu*, Mouth; *bm*, ventral chord; *msc*, musculature; *aa*, arteria abdominalis; *as*, arteria sternalis; *ld*, diverticula of the mid-gut (hepatopancreas); *h*, heart; *pc*, pericardium; *md*, extensions of the mid-gut; *mm*, muscles of the masticatory stomach; *pk*, pyloric valve.

Development of the eye.—Each eye consists of three elements : (1) a hypodermal layer, (2) an ectodermal invagination, and (3) a nerve mass.

The hypodermal layer becomes many-layered ; some of its elements combine to form groups, each of which consists of 8 cells, 4 of which (Semper's cells) secrete a cuticular corneal facet, while the 4 others produce the crystalline cone.

The ectodermal invagination (optic fold) deepens in the *Nauplius* stage and is constricted off in stage (G) as a solid mass of cells. This mass develops into a fold, opens outward and upward, with an outer and inner wall several layers thick. The outer wall becomes connected with the layer of the crystalline cones, its cell elements form groups of 6 to 8 and become the retinular cells. The inner wall yields the nervous connections of the retinular layer with the ganglion opticum.

The **ganglion opticum** arises like any other ganglion of the central nervous system as an ectodermal thickening.

Between the hypodermal layer and the optic fold, mesodermal elements penetrate and grow, uniting to form a fenestrated mass which secretes a large quantity of pigment.

XV.—The morphological significance of the most important Crustacean larval forms, and the Phylogeny of the Crustacea.

That the Crustacea form a single class is evident to the student of comparative anatomy and ontogeny. It is probable that they can ultimately be traced to one racial form. Basing our conjectures for the present simply on the **comparative anatomy** and **classification** of the group, we feel justified in describing this racial form as follows.

The original Crustacean was an elongated animal, consisting of numerous and tolerably homonomous segments. The head segment was fused with the 4 subsequent trunk segments to form a cephalic region, and carried a median frontal eye, a pair of simple anterior antennæ, a second pair of biramose antennæ and 3 pairs of biramose oral limbs, which already served to some extent for taking food. From the posterior cephalic region proceeded an integumental fold which, as dorsal shield, covered a larger or smaller portion of the trunk. The trunk segments were each provided with one pair of biramose limbs. Besides the median eye there were 2 frontal sensory organs. The nervous system consisted of brain, œsophageal commissures and segmented ventral chord, with a double ganglion for each segment and pair of limbs. The heart was a long contractile dorsal vessel with numerous pairs of ostia segmentally arranged. In the racial form the sexes were separate, the male with a pair of testes, the female with a pair of ovaries, both with paired ducts emerging externally at the bases of a pair of trunk limbs. The excretory function was carried on by at least 2 pairs of glands, the anterior pair (antennal glands) emerging at the base of the second pair of antennæ, the posterior (shell glands) at the base of the second pair of maxillæ. The mid-gut possibly had segmentally arranged diverticula (hepatic invaginations).

This conjectural racial form shows a considerable correspondence with the *Annelida*, and this correspondence would be increased if it could be satisfactorily proved that the biramose limbs of the Crustacea with its exo- and endopodite answered to the dorsal and ventral parapodia,[1] and the epipodial gills of the Crustacea to the dorsal gills (of the dorsal parapodia) of the *Annelida*. The setiparous glands of the *Annelida* would correspond with the segmental leg glands of certain Crustacea (*Phyllopoda*).

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[1] It must here be remembered that the question whether in the *Polychæta* the uniserial or the biserial arrangement of the parapodia is the original is not yet satisfactorily settled.

The proof of the homology of the antennal and shell glands of the oviducts and vasa deferentia with Annulate nephridia would also be of the greatest importance.

Among the now living Crustacea there are two orders of the *Entomostraca*, viz., the *Phyllopoda* (the *Branchiopoda* especially) and the *Copepoda*, whose organisation best recalls that of the racial form, the former in the rich homonomous segmentation of the trunk and the structure of the nervous system and the heart; the latter in the form of the limbs, especially the oral limbs, which still most clearly show their original biramose character. The *Cladocera* and perhaps the *Ostracoda* might be derived from animals like the *Branchiopoda* by the shortening of the body and the reduction of the number of segments. The ancestors of the *Cirripedes* are probably nearly related to the immediate progenitors of the *Copepoda*.

At first sight the results of research in **comparative ontogeny** do not seem to harmonise with the view just stated. Out of the egg of the *Entomostraca* and many *Malacostraca* the unsegmented *Nauplius* larva is hatched with only 3 pairs of extremities, without a heart, and without a segmented ventral chord. On account of this the Crustacean racial form was formerly universally held to be a *Nauplius*-like animal. It was assumed that from this racial form the Crustaceans of to-day developed phylogenetically through a series of gradual transformations, in a manner similar to that in which they develop ontogenetically at the present time from the *Nauplius* by a series of metamorphoses.

We consider these views incorrect, both for general and special reasons.

General Reasons.—(1) We know of no animal form which in an adult sexually mature condition resembles a *Nauplius*. (2) We are not justified, without further proof, in concluding that the early larval stages of an animal form closely resemble the ancestors of that form.

Special Reasons.—The assumption of a racial form like a *Nauplius* leaves the problem of the rise of the typical Crustacean organisation, of the segmentation of the body, the segmented ventral chord, and the segmented dorsal heart quite unexplained. It must also be emphasised that the ducts of the sexual organs, except in one single case, emerge in regions of the body which in the *Nauplius* are not at all developed.

On the other hand, the **Nauplius, as characteristic larval, not racial form of the Crustacea,** is explained without difficulty by the assumption of a Crustacean racial form resembling the *Annelida*. Just as the racial form of the Crustacea is to be traced back to the *Annelida*, so is the larval form of the Crustacea to the larval form of the *Annelida*. We have already mentioned the tendency in the animal kingdom to shift back to earlier stages of development the characteristics of the adult animal. Hence in the Crustacea, Crustacean characteristics (such as limbs and dorsal shield) appear as early as in the larva which corresponds with the *Trochophora* of the *Annelida*. The method of moving by means of the limbs makes the old method needless, so that the ciliated circles of the *Trochophora* larva are no longer produced.

In all Crustacea the 3 pairs of *Nauplius* limbs become the 3 most anterior extremities of the adult animal (2 pairs of antennæ and the mandibles). The fact that, in the *Nauplius*, just these pairs of limbs appear first can again be explained without difficulty. As in the *Annelida* so in the Crustacea also, the body with all its organs becomes differentiated from before backward. At the posterior end of the body a growing or formative zone continually constricts off new segments anteriorly. It is thus evident that the most anterior extremities must appear first. But why just the 3 most anterior, and neither more nor less? A natural answer may perhaps also be found to this question. In a young larva which, like the *Nauplius*, is hatched early from the egg, only a few of the organs most necessary for independent life and independent acquisition of food can be developed. The 3 most anterior pairs of limbs which serve for swimming may be described as such most necessary organs. The 3d pair perhaps belongs to this category, because as mouth parts, generally provided with masticatory processes, they serve not only with the others for locomotion, but also for conducting food to the oral aperture. Where the egg is provided with a somewhat richer supply of nutritive yolk, the larva which hatches from it may, as a *Metanauplius*, be provided with the rudiments of other limbs.

The *Nauplius*, however, as **typical Crustacean larva**, certainly shows many primitive Crustacean characteristics, such as the dorsal shield, the median eye, the frontal sensory organs, the special form of the posterior antennæ and mandibles which, like the extremities which follow them, are developed as typical biramose limbs.

The Nauplius is thus to be traced back to a Trochophora larva, in which we already find Crustacean characteristics; it is unsegmented, contains the rudiments of the anterior cephalic portion of the adult Crustacean with the mouth, and the rudiments of the most posterior end of the body with the anus. Between the two lies an embryonic formative zone, from which, in the further development of the larva, the rest of the body begins to form and becomes differentiated, as in the Annelida, from before backward. The Nauplius is a typical Crustacean larva; the ancestors of the Crustacea did not as yet possess a typical Nauplius larva, still less did they come from a Nauplius-like racial form.

As for the *Malacostraca*, the testimony of comparative anatomy is unequivocal, that the *Leptostraca* not only stand nearest to the common racial form of this whole sub-class, but also retain many primitive characteristics of the common racial form of all Crustacea. The *Leptostraca* appear as genuine *Malacostraca*, first on account of the formation of the regions of the trunk, which consists of a thorax of 8 segments and an abdomen; the latter, although it has one more posterior segment than the typical Malacostracan abdomen, still carries the same number of pleopoda. Both the oral and thoracic limbs show the typical Malacostracan character. The intestine proves itself to be a Malacostracan intestine by its masticatory stomach, and the special form of its hepatic glands, and the apertures of the genital organs have the position which is characteristic of the *Malacostraca*. On the other hand, by the possession of a bivalve shell-fold, the simultaneous development of the 8 free thoracic segments and their appendages, by the rich segmentation of the nervous system, and the elongated heart with many pairs of ostia, the *Leptostraca* show themselves to be very primitive *Malacostraca*, whose ancestors must have been racially related to the *Phyllopoda*.

The relationships of the other orders of *Malacostraca* are, according to the present state of our knowledge, to be considered as follows: the *Stomatopoda* form an order standing quite by itself, which, though showing further and somewhat peculiar development (*e.g.* in the possession of gills on the pleopoda, sexual organs in the abdomen, numerous hepatic appendages, special form of the thorax and its extremities) has still retained, in many points of its organisation, primitive characteristics, as, for instance, the elongated dorsal vessel with many pairs of ostia, and the shell-fold which leaves several thoracic segments free.

Of the other *Malacostraca*, the *Schizopoda*, and especially the *Euphausidæ* have, for the most part, retained characteristics belonging to the common racial form of the *Malacostraca*. Of these the chief are the special form of the biramose thoracic feet, their epipodial appendages which function as gills, the dorsal shell, etc. The *Arthrostraca* have evidently a common origin with the *Schizopoda*. Among the former the *Anisopoda* must occupy the most primitive place, as well on account of the occurrence of a small dorsal shell as of that of small exopodites on the second and third pairs of trunk feet (*Apseudes*).

The *Arthrostraca* are otherwise characterised by degeneration of the shell-folds, transformation of the stalked eyes into sessile eyes, and disappearance of the exopodites on the thoracic feet.

The difference in the position of the heart in the *Amphipoda* and *Isopoda* is to be explained, as already pointed out, by the fact that in the former only a thoracic portion, and in the latter only an abdominal portion of the primitive elongated dorsal vessel has been retained, in both cases, clearly in connection with the localisation of the respiration. The *Cumacea* stand nearest to the *Schizopoda*, but exhibit a few Isopodan characteristics. It is pretty certain that the *Decapoda* come from *Schizopoda*-like ancestors; the *Macrura*, and especially the *Carididæ*, appear to be the most original forms, while the *Brachyura* and *Anomura* appear as one-sidedly, but very highly, developed branches of the order.

We are again met by the question, what is the phylogenetic significance of the various larval forms of the *Malacostraca?* Just as the *Nauplius* larva, which is characteristic of the whole class of the Crustacea, was held to be a stage of development repeating the common ancestral form, so a further developed Malacostracan larva, the so-called *Zoæa*, was considered to be a larva characteristic of the *Malacostraca*, and assumed to correspond with one of their racial forms.

These *Zoæa* larvæ have been already thus characterised: a large cephalothoracic shield, 2 compound stalked eyes, a median *Nauplius* eye, head with 5 pairs of limbs, only the most anterior part of the thorax with thoracic feet (2-3) in a rudimentary condition, the remainder of the thorax wanting, or else rudimentary and limbless. Abdomen with full number of segments but without appendages. Tail bifurcated.

Those investigators who wished to find in this *Zoæa* larva a larval form corresponding more or less with the racial form of the *Malacostraca* had to assume that in the *Malacostraca* now living the last 5 or 6 thoracic segments are new formations, since they are wanting in the racial form. When therefore the structure and systematic position of the *Leptostraca* were better appreciated, and the larval history of the *Euphausidæ* and the *Carididæ* better and more completely understood, these authors were obliged to take refuge in the following explanation. The earliest ancestors of the *Malacostraca* possessed the full number of trunk segments and the full number of thoracic feet, but a later form lost the last 5 or 6 trunk segments with their appendages, while, however, they were still retained by the larva. Finally these segments and their appendages again appeared (in the living *Malacostraca* known to us or in fossil forms). In support of these very forced views the larval history of certain *Stomatopoda* was cited; in these the 3d, 4th, and 5th pairs of thoracic feet are present in the young larva, but disappear later, to be finally reformed. In the larvæ of *Sergestes* also, the last 2 pairs of thoracic feet are reduced and appear again later.

So many objections, however, can be brought against this assumption that it must necessarily be relinquished.

In the first place it must be pointed out that of all the manifold known forms of Crustacea, and especially in that series (which indeed is not without gaps) beginning with the *Phyllopoda* and ending with the *Brachyuran Decapoda*, of which *Branchipus*, *Nebalia*, *Euphausia*, *Penaeus* are the most important, there is nothing to give the slightest indication that whole regions of the body with their extremities can disappear and reappear again later, or that between already existing segments new segments with their limbs can be intercalated.

We must therefore ask, to what extent the *Zoæa* larva above characterised is distributed among the *Malacostraca*. In its typical form it is found only in the *Brachyura* and (though slightly deviating in form) in the *Stomatopoda*. This fact alone warns us to be careful, since the *Brachyura* are decidedly the most recent and most specialised *Decapoda*, and in their development the *Schizopodan* stage with the characteristic biramose thoracic feet does not once occur. The larval history of the *Euphausidæ*, *Stomatopoda*, and *Carididæ*, the early developmental processes in the *Loricata* which take place within the egg, and the so-called direct development of so many *Malacostraca* show that the Malacostracan body becomes gradually differentiated in the typical manner (as in the *Entomostraca*) from before backward. The larval history of *Penaeus* shows further that, with the exception of the 6th pair of pleopoda, the extremities also begin to form and differentiate from before backward. In the *Euphausidæ* the extremities of the posterior thoracic region differentiate almost simultaneously with those of the abdomen from before backward.

It is of the greatest importance for the comprehension of the typical *Decapodan Zoœa*, and especially of that of the *Brachyura*, to bear in mind the established fact that in that larva, in spite of the apparent absence of the thoracic region comprising the 4th to 8th thoracic segments, the thoracic ganglionic mass through which the sternal artery runs has already begun to form.

Not less important also is the fact that the *Stomatopodan* larva possess an elongated dorsal vessel with many pairs of ostia, while the *Decapodan Zoœa* and the other *Thoracostracan* larvæ which resemble it possess a compact thoracic heart, generally with 1 or 2 pairs of ostia. These facts sufficiently show how varied are the *Thoracostracan* larvæ which have been artifically combined into a *Zoœa* group.

In all future attempts to understand the morphology of Crustacean larval forms the following considerations will probably have to be taken into account.

The grade of development and physiological importance of a section of the body or of a pair of limbs in the adult animal may be recognised by the earlier or later appearance of their rudiments; *e.g.* the extraordinarily early appearance of the last pair of pleopoda in the *Thoracostraca*, *i.e.* of that pair of pleopoda which in the adult differs so strikingly from the others, forming together with the telson the caudal fin, which is the chief organ of locomotion. A contrast to this is afforded by the late appearance of the reduced maxillæ of the adult *Phyllopoda* and *Cirripedia*.

Not only the special form of the adult animal, however, but also that of one or more of its larval stages may have some influence on the early processes of development, *i.e.* when these larval stages are not merely phases of development, but animals feeding themselves and leading an independent life and playing an important part in the life economy of the species, more or less like adult animals though unable to reproduce themselves. Such larvæ show throughout their organisation independent adaptation to the special conditions of their existence, and it is the first and chief object of the preceding developmental stages **to prepare their organisation, not that of the adult animal.** From this point of view we shall perhaps some day be able to explain the *Brachyuran Zoœa* with its reduced thorax and failing 4th to 8th ambulatory feet, which in the adult animal are the only organs of locomotion, but in the *Zoœa* are perhaps useless or even a hindrance. The larvæ lead a marine life, and their organisation is no doubt more or less adapted to this life. We see, therefore, how important it is to ascertain what are the functions of the different parts of each larva, in order to arrive at any sure conclusion as to the significance of the changes it undergoes.

One of the most important and most interesting problems of ontogeny is the reduction and subsequent reappearance of the same portions of the body, of which the larval history of the Malacostraca yields us so many examples. (Compare especially the larval history of the *Stomatopoda* and *Loricata*.) For the solution of this problem also the above points of view may prove of service. In the *Stomatopoda* the last 3 pairs of thoracic feet, the so-called ambulatory feet, like the 5 pairs of ambulatory feet in the *Brachyura*, first appear at the end of larval life. The 5 anterior pairs, however, develop during the first period of larval life (youngest known *Erichthoid* larva) partly to disappear in the 2d period and finally to reappear in their definitive form. The developmental history of the *Loricata* shows similar phenomena. The first attempt, later frustrated, to form all or most of the typical Malacostracan extremities, which we here observe is no doubt to be ascribed to the force of heredity. The temporary disappearance of some of the extremities is most probably a phenomenon of adaptation to the special conditions of existence of the larva, so different from those of the adult. If, however, these first fruitless and useless attempts were in the course of time to become gradually weaker, and finally entirely cease, then we should meet in the *Loricata* and *Stomatopoda* with phenomena quite similar to those in the Brachyuran development, where the formation of the last 5 thoracic segments, and their extremities occurs so extraordinarily late. In this way, also perhaps we can explain the fact that the Brachyuran ambulatory feet appear in their definitive form and not as biramose feet.

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First Appendage to the Class of Crustacea.

The Trilobites, Gigantostraca, Hemiaspidæ and Xiphosura.

I. The Trilobites.

These extinct Articulata are found only as fossils, and only in palæozoic formations.

Body (Fig. 281). The integument of the upper side was hard; but on the under side soft. The body falls into 3 divisions, cephalic shield, thorax, and caudal shield (pygidium). Each of these divisions is again divided by 2 almost parallel longitudinal dorsal furrows (the thorax most distinctly) into an arched middle area (rhachis) and 2 lateral areas (pleura). The cephalic shield is unsegmented, semicircular, or crescent-shaped, with the rounded part to the front; it generally carries 2 large **compound eyes**. The occurrence of simple eyes is very doubtful. The thorax consists of a varying (usually rather large) number of freely moving segments. The **caudal shield** seems composed of a varying number of segments more or less completely fused together. Nearly all (or all ?) *Trilobites* were able to roll up their bodies like woodlice, so that the anterior edge of the cephalic shield and the posterior edge of the caudal shield touched one another.

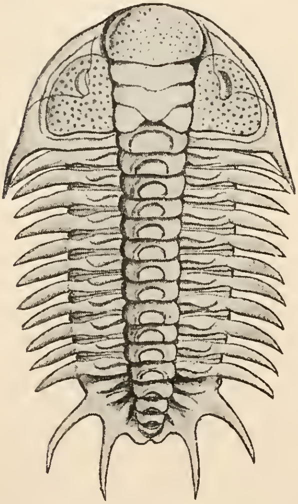

Fig. 281.—**Cheirurus Quenstedtii**, dorsal view.

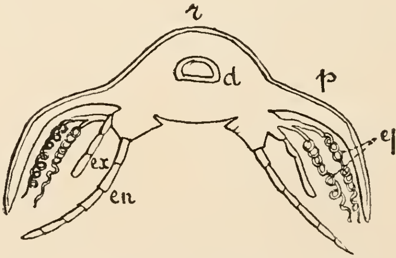

Fig. 282.—**Restored trunk segment of a Trilobite**, transverse section (after **Walcott**). *r*, Rhachis; *p*, pleura; *ep*, epipodial appendages; *en*, endopodite; *ex*, exopodite; *d*, intestine.

Limbs (Fig. 282).—These are retained only in rare cases. They are slender and long, and more or less like one another, segmentally repeated from the cephalic shield to the end of the caudal shield. Under the cephalic shield there are 4 pairs of limbs reckoned as maxillipedes, the most posterior of these being more developed than the rest; the most anterior is inserted **behind the upper lip.** The limbs of the trunk and pygidium are biramose with long endopodite and short exopodite, and with bifurcated epipodial appendages on the basal joint, which may be either filamentous or ribbon-shaped, simple or spirally twisted; these may safely be assumed to be gills. These gills also seem to occur on the limbs of the pygidium, but in a reduced condition. The enteric canal runs through the body in a straight line to the end of the caudal shield. In front of the mouth, at the lower and anterior edge of the cephalic shield, is found a shell-piece which is called the upper lip.

In some of the genera of *Trilobites* a pretty complete series of successive stages of development (larval stages) has been discovered. In the youngest stages the cephalic shield is present, but the trunk is still quite incomplete. The development of the latter generally occurs in such a way that the pygidium takes precedence of the thorax, and that new segments continually become differentiated at the anterior end of the pygidium. In other words, the thorax differentiates in the order from before backward.

The available material suffices to show: (1) that the *Trilobites* are Arthropoda, and (2) that they are most nearly related to the Crustacea. Their Crustacean character is unmistakably supported by the fact that the trunk feet are biramose, and carry epipodial appendages. A closer comparison with distinct orders of Crustacea, however, cannot be carried out, because in the *Trilobites* no limbs have been found placed in front of the mouth, and comparable with the anterior antennæ. Whether these were entirely wanting, or rudimentary, or not capable of petrifaction, is quite uncertain. Should they still be found, then the 5 cephalic limbs could without difficulty be referred to the 5 typical limbs of the Crustacean head, and the *Trilobites* might then be regarded as original *Entomostraca*, to be derived from the same racial form as the *Phyllopoda*. We are prevented from comparing them with the *Malacostraca* on account of the different segmentation of the body and the inconstant number of the segments which does not agree with that of the *Malacostraca.*

The *Trilobites* were marine. *Agnostus* (with only 2 thoracic segments), *Trinucleus*, *Olenus*, *Paradoxides*, *Conocephalites*, *Sao*, *Calymene*, *Asaphus*, *Bronteus*, *Phacops*, *Cheirurus*, *Acidaspis*, *Lichas*, *Proetus*, *Harpes*.

II. The Gigantostraca (Merostomæ, Eurypteridæ).

These are also extinct. They lived during the palæozoic epoch.

Body (Fig. 283).—The elongated scale-covered body of these, the largest of all Arthropoda, falls into head (cephalothorax ?), thorax, and abdomen. The unsegmented head is relatively small, and carries 2 compound lateral eyes, and very near the median line 2 ocelli. The thorax and abdomen each consist of 6 segments. The 6th abdominal segment is followed by a caudal stylet or a fin-shaped terminal segment.

Extremities.—The division described as the head carries 6 pairs of extremities, composed of simple rows of joints, and thus not biramose. The anterior pair lies in front of the mouth, and in *Eurypterus* is a small finely jointed pair of feelers, while in *Pterygotus* it is a pair of long chelate limbs, with powerful pincers. The basal joints of the five subsequent pairs of limbs are inserted round the mouth, and have masticatory ridges directed inwards, which, in *Pterygotus*, are specially strongly developed on the last pair.

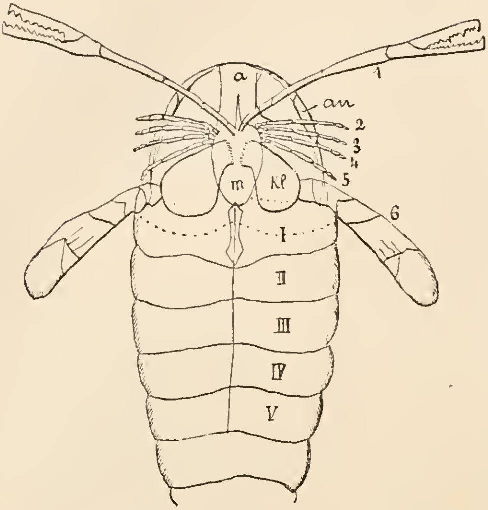

Fig. 283.—**Pterygotus osiliensis.** Upper Silurian. Under side restored, and smaller than natural size (after **F. Schmidt**). *a*, Epistoma; *me*, metastoma; 1-6, feet; 1, chelicer; 6, rowing foot with large masticatory ridge, *kl*; *I-V*, ventral plates; *au*, eye.

The last pair of cephalic limbs is much more strongly developed than the rest; they are oar-shaped, and evidently served as swimming feet. On the under side of the thorax of 6 segments are found 5 plates (leaf-like limbs) consisting of 2 lateral halves; these overlap like tiles, and cover leaf-like gills. The most anterior largest plate is called the operculum. The abdomen is devoid of limbs. Behind the mouth is a large oval plate, the metastoma.

The systematic position of the *Gigantostraca* is not clear. In the number and position of the cephalic feet they agree with the *Xiphosura*. The leaf-like limbs of the thorax also somewhat recall those of *Limulus*, and above all the operculum in the 2 groups seems to be homologous. Their relation to the other Arthropoda, especially to the Crustacea and the *Scorpionidæ*, whom they resemble in appearance, has often been pointed out, but nevertheless is not clear, because the morphological significance of the limbs, and especially of those which lie in front of the mouth, is not known with anything like certainty. Our knowledge of the structure of the *Gigantostraca* and *Trilobites* has during the last decade received such unexpected additions through palæontological investigations (*e.g.* discovery of the limbs of *Trilobites*) that we may hope for further advance.

Eurypterus, *Pterygotus.*

III. The Hemiaspidæ.

These are extinct palæozoic forms apparently related to the *Xiphosura* and perhaps forming a sort of connecting link between them and the *Gigantostraca.*

The body falls into 3 regions: a head of considerable size covered by a shield, a thorax consisting of 5 or 6 free (rarely fused) rings, and an abdomen consisting of 3 or more segments, and followed by a strong caudal stylet. The cephalic shield often has 2 compound lateral eyes, ocelli are wanting. Two dorsal longitudinal furrows give the thorax an appearance like that of the *Trilobites*. The extremities are unknown.

Bunodes, *Hemiaspis*, *Belinurus*.

IV. The Xiphosura (Pœcilopoda, Limulidæ).

The **body**, which is covered by a hard and thick chitinous carapace falls into 2 principal divisions, the cephalic shield (cephalothorax) and the hind body (abdomen). The hind body is followed by a large and long **post-anal caudal spine** which can move independently of the body. The cephalothorax is very large, almost crescent-shaped, with 2 lateral horns directed backwards. On its dorsal side are the 2 compound lateral eyes, and in front of them, nearer the median line, 2 ocelli. The flat segmented abdomen, which articulates with the cephalothorax, is almost hexagonal.

The upper side of the cephalothorax is arched, and the under side is concave.

Limbs (Fig. 284).—There are 7 pairs of limbs on the cephalothorax. The most anterior lie in front of the mouth; they are small and end in pincers. They are innervated from the anterior part of the œsophageal commissure, and (if a comparison with Crustacea is allowed) should perhaps correspond with the 2d pair of antennæ, while limbs corresponding with the anterior antennæ are wanting. The 1st pair of limbs, which are called **cheliceræ**, are followed by 5 strong long pairs of limbs, also ending in pincers. They arise at the sides of the slit-like oral aperture, and each has a masticatory ridge on the basal joint. The masticatory ridges of the 4 anterior pairs of feet are armed with spines, those of the 5th pair, however, have a sharp cutting inner edge. The 5th pair of feet is further distinguished by a different formation of the terminal joint and by an appendage on the basal joint, which has been considered to be an exopodite. Behind the mouth there are two stylet-shaped processes, the **chilaria**.

The 7th pair of limbs of the cephalothorax, which arises at its posterior edge, is quite differently formed from the preceding, and agrees far more with the abdominal limbs. It is called the **operculum**, and consists of 2 plates, which are united in the middle line, and cover the subsequent abdominal limbs. The latter, of which there are 5 pairs, are leaf-like, and shaped like the operculum. In all the leaf-like feet 2 rows of areas are marked by sutures, an outer row of large areas (exopodites) and an inner row of smaller areas (endopodites). The last areas or joints project freely. The leaf-shaped abdominal feet on each side carry on the upper surface (*i.e* on the surface turned to the body) a **gill** consisting of numerous integumental folds, arranged like the leaves of a book.

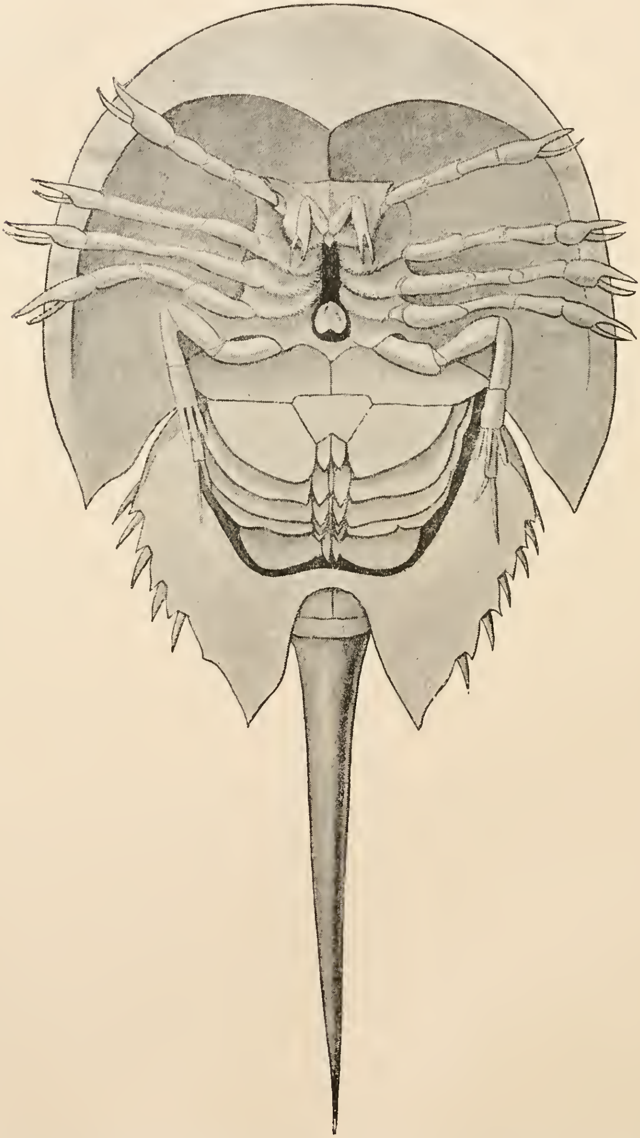

Fig. 284.—**Limulus polyphemus**, young specimen from the ventral side (after **Packard**).

The leaf-like feet serve for swimming as well as for breathing. A sternal endoskeleton is present.

Nervous System.—The central nervous system consists of a ganglionic mass lying in the cephalothorax and surrounding the œsophagus; it is continued into the abdomen as a ganglionic ventral chord. The circular ganglionic mass of the cephalothorax is found to consist of the brain, which lies in front of the œsophagus, and gives off nerves to the lateral eyes and the ocelli, and of 7 postoral pairs of ganglia with their transverse commissures, these ganglia lying near each other. The latter yield the nerves for the cephalothoracic limbs. The ventral chord of the abdomen consists of 6 ganglia, the last of which is the largest. The nerves to the leaf-like feet are given off by these latter.

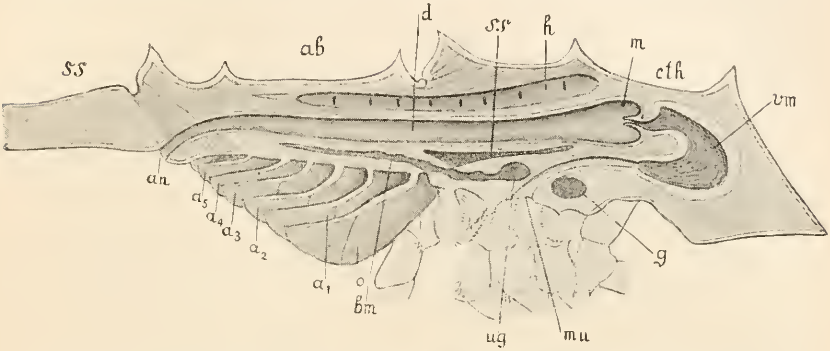

Fig. 285.—**Median longitudinal section through a young Limulus polyphemus** (after **Packard**). *cth*, Cephalothorax; *ab*, abdomen; *ss*, caudal spine; *vm*, anterior stomach; *m*, stomach; *h*, heart; *ss*, sternal cartilaginous endo-skeleton; *d*, intestine; *g*, brain; *ug*, infra œsophageal ganglionic mass; *bm*, ventral chord; *o*, operculum; a_1-a_5, gill carrying abdominal appendages; *mu*, mouth; *an*, anus.

The **compound eye** of *Limulus* (Fig. 286) deserves special description. The chitinous carapace is thickened over each of the two compound eyes; outwardly its surface is smooth, but inwardly, by the formation of conical processes, it pushes in the subjacent hypodermis to form towards the interior an equal number of papillæ; each of these chitinous cones may be considered as a single lens. A completely separate retinula probably consisting of 10 cells, with rhabdom, pigment, and nerve, corresponds with each of these single lenses. The retinulæ lie

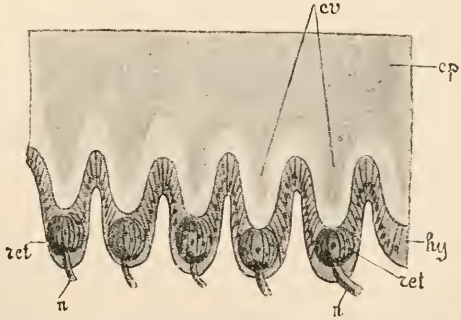

Fig. 286.—**Part of a section through the eye of Limulus.** *cp*, Chitinous carapace; *cv*, papilla-like thickenings of the same over each single eye; *hy*, hypodermis; *ret*, retinulæ; *n*, nerves of the single eyes.

in the hypodermis. The compound eye of *Limulus* is thus seen to be composed of numerous independent unilaminate single eyes crowded together. Each single eye corresponds with the unilaminate eye of certain *Myriapoda* and *Scorpionidæ*, and the whole compound eye corresponds with the sum of the eyes on one side of these Arthropoda, except that the chitinous carapace in *Limulus* forms a thickening common to all the single eyes.

Enteric Canal.—From the large mouth a long œsophagus rises upward and forward, to enter a muscular masticatory- or fore-stomach placed in the anterior part of the cephalothorax; the chitinous intima of this stomach projects in numerous longitudinal folds into its lumen. The fore-stomach is followed by a long straight mid-gut widened at its commencement; this runs through the cephalothorax and abdomen and opens externally at the base of the caudal spine through a ventral anal aperture of the short hind-gut. The mid-gut receives the 4 ducts of 2 pairs of hepatopancreatic glands which branch freely in the cephalothorax. All through the intestine, except in the mid-gut, a chitinous intima is found.

Circulatory System.—The heart is an elongated dorsal vessel provided with 8 pairs of ostia which can be closed by valves.

Sexual Organs.—The sexes are separate. The male, which is smaller than the female, is further distinguished externally by the fact that the most anterior or the two anterior postoral pairs of limbs do not end in pincers, but in claws.

The 2 **ovaries** are tubes forming a network of branches, those of the two sides communicating with each other at various points. The two oviducts form a sac-like wider portion before they emerge. The female sexual apertures lie on the inner side of the opercular plates (the side turned to the body), at their bases, to the right and left of the median line. The two **testes** consist of a large number of vesicles dispersed throughout the body and attached to sperm ducts which branch and anastomose freely. The male apertures have the same position as the female.

Coxal Glands.—On each side of the cephalothorax lies a red gland of considerable size whose outer aperture has only been found in young animals on the basal joint of the fifth pair of limbs. It is uncertain whether these coxal glands correspond with the shell glands of the Crustacea (which also emerge on the 5th pair of extremities, *i.e.* on the 2d maxillæ). We have no right to assume that the 5th pair of extremities of *Limulus* answers to the 2d pair of maxillæ of the Crustacea; it is indeed improbable that this is the case.

Ontogeny.—The 6 anterior pairs of limbs appear first and simultaneously, then follow the 7th pair (operculum) and the 8th (first gill-carrying abdominal limbs). On the cephalothorax there are indications of segmentation. The young *Limulus* hatched from the eggs shows a complete rudimentary cephalothoracic shield, the segmentation having then entirely disappeared. The abdomen, on the contrary, appears distinctly formed of 8 segments, but these are not movable upon each other.

The caudal spine is still a very short and simple plate. The 2 compound eyes and the 2 ocelli are already present. Behind the 1st pair of abdominal feet the rudiments of the 2d are visible. At this stage the larva has the appearance of a *Trilobite*, and this similarity is increased by two dorsal longitudinal furrows. The gradual transition from the *Trilobite* stage to the *Limulus* stage is brought about by the appearance in order from before backward of the abdominal leaf-like feet. The leaf-like feet become biramose. Gills develop on them; in the *Trilobite* stage rudiments of gills were found only on the most anterior pair of abdominal feet. The abdomen loses its segmentation. The caudal plate elongates by degrees into the caudal spine.

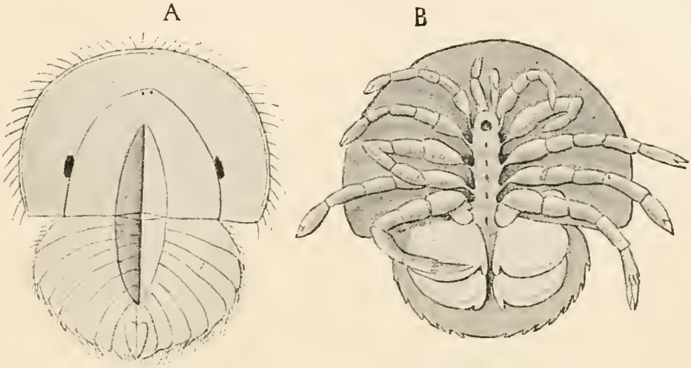

Fig. 287.—**Limulus polyphemus in the so-called Trilobite stage.** *A*, Dorsal side; *B*, ventral side (after **Kingsley**).

Systematic position.—The relationship of the *Xiphosura* to the Crustacea is in any case very distant, since it is at present impossible to homologise the extremities of *Limulus* with typical Crustacean extremities, or to compare in detail the segmentation of *Limulus* with that of any Crustacean. The biramose character of the leaf-like feet and of the 6th pair of thoracic feet is the only specific Crustacean characteristic shown by the *Xiphosura*, if we leave the gills out of consideration. The relation between the *Xiphosura* and the fossil *Hemiaspidæ* and *Gigantostraca* is evidently much closer. The *Xiphosura*, *Hemiaspidæ*, and *Gigantostraca* are themselves again perhaps racially connected with the *Trilobites*. In any case, however, in the present state of science, it seems probable that all these groups are only connected at their roots with the Crustacea. The relations of the *Gigantostraca* and *Xiphosura* to the *Arachnoidea*, especially to the *Scorpions*, which is assumed by some observers, will be discussed later.

Single genus **Limulus.**—Marine, *L. moluccanus*, Molucca, Sunda Islands; *L. polyphemus*, East coast of North America.

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Second Appendage to the Class of the Crustacea

The Pantopoda (Pycnogonidæ).

The body, in comparison with the long and slender limbs, is extremely reduced, and falls into three divisions—proboscis or beak, trunk, and hind-body. The **proboscis** articulates with the most anterior trunk segment. At its point lies the mouth surrounded by three lips, and it contains internally the greater part of the fore-gut ("fish trap" apparatus). It consists of three pieces lying side by side longitudinally, an upper median piece and two lower lateral pieces. The **trunk** consists of 6 segments, the three anterior of which are always fused together; it has lateral outgrowths on to the ends of which the limbs are hinged. The **hind-body** is unsegmented, short, truncated, and devoid of limbs.

Extremities.—7 pairs of extremities occur typically. The first extremities (1), the cheliceræ, are innervated from the brain, and in the young animal end in pincers; in the adult they are often reduced or altogether wanting. The following extremities (2-7) are innervated from the ganglia of the ventral chord, 2 and 3 from the most anterior ganglion, which consists in the larva of two separate ganglia.

The 2d pair of extremities is generally shorter than those which follow, and in several genera is wanting. The 3d pair of extremities is developed in the males of all *Pantopoda*, and functions in them as egg-carriers. In several genera it is wanting in the females. The extremities 4-7 are never absent, they consist of nine joints, and end in claws, and are in comparison with the body exceedingly long, giving the animal a spider-like appearance. All the extremities are uniramose.

The **nervous system** in the adult animal consists of a supra-œsophageal ganglion, an œsophageal commissure, and a ventral chord. The latter has 4 or 5 pairs of ganglia, from which arise the nerves for extremities 2-7; it ends posteriorly with one or two pairs of reduced ganglia, the last of which gives off nerves to the abdomen.

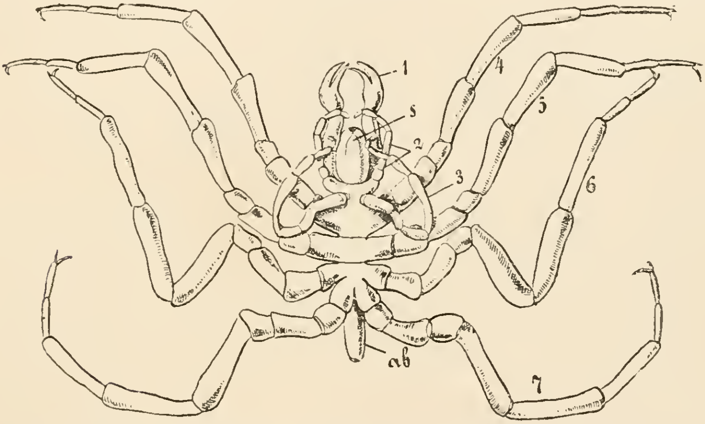

Fig. 288.—**Nymphon hispidum**, male, ventral side (after **Hoek**). The setæ are omitted. 1-7, Limbs; (1, cheliceræ; 3, egg-carriers); *s*, proboscis; *ab*, abdomen.

Since the most anterior ganglion of the ventral chord consists of 2 or 3 pairs of ganglia, distinct in the larva, the complete number of the pairs of ganglia in the ventral chord is 8, 7 of which belong to the trunk and 1 to the abdomen. According to this the number of trunk segments and also of pairs of limbs must originally have been 8. From the supra-œsophageal ganglion the nerves for the eyes arise, and also those for the first pair of limbs and some of those for the proboscis. Some of the other proboscis nerves have their roots in the anterior portion of the first ventral ganglion. The nervous system of the proboscis with its ganglion is very complicated.

Four **eyes**, each with a cuticular lens and a retina surrounded by pigment, lie on a prominence on the dorsal side of the first trunk segment.

The **enteric canal** has 3 divisions: fore-gut, mid-gut, and hind-gut. The **fore-gut**, placed in the proboscis, has a complicated inner framework and a "fish trap" apparatus. The straight **mid-gut** is provided with **long cœca which project into extremities 1, 4, 5, 6, 7,** sometimes as far as the terminal joint.

The anus lies at the end of the hind-body. **Special respiratory organs are wanting.** The **heart** has 2-3 pairs of ostia; its dorsal wall is formed by the dorsal integument.

The **sexes** are separate. The sexual glands are paired tubes, which extend through the trunk at the sides of and above the intestine, and are connected behind the heart by an unpaired piece. They give off accessory tubes into the extremities 4-7, which emerge on the 2d joints. In the male, however, the genital apertures are wanting in the 4th pair of extremities, and generally also in the 5th. In *Pycnogonum* and *Rhynchothorax* only one aperture is found on each side in the females, and this is in the 7th pair of extremities. In the males, in the fourth joint of extremities 4-7 **cement glands** (coxal glands?) are found, whose secretion glues the eggs which issue from the female genital apertures into balls, which are carried about by the male on the 3d pair of extremities, transformed into egg-carriers.

We find glands which are considered as **excretory organs** in the 2d and 3d pairs of extremities, emerging on the 4th or 5th joints.

Ontogeny.—Most *Pycnogonidæ* pass through a more or less complicated metamorphosis. The youngest unsegmented larva carries 3 pairs of extremities, corresponding with extremities 1, 2, and 3 of the adult. The first ends in a claw. In spite of the agreement in the number of extremities this larva shows no near agreement with the *Nauplius* larva, and the extremities themselves, since they all consist of only one row of joints, do not show the character of the *Nauplius* limb. In the next stage new segments appear at the posterior end of the body and differentiate in the order from before backward. The enteric cœca at first do not project into the extremities.

The cause of the entrance of enteric cœca and lateral tubes of the sexual glands into the interior of the limbs must be sought in the extraordinary reduction of the trunk and in the great longitudinal development of the limbs.

The *Pantopoda* seem to occupy an isolated position among the Arthropoda. On account of the want of a typical *Nauplius* or *Zoœa* larva we are not justified in placing them near the Crustacea, and they show no evident relation to any other class of Arthropoda. Many zoologists consider the *Pantopoda* to be related to the spiders, and establish the following homologies for the limbs. Extremity 1 = cheliceræ or falces; extremity 2 + the paired piece of the proboscis = lower jaw and pedipalps; extremities 3-6 = the 4 pairs of legs of the spider. Extremity 7 is wanting in the adult spiders, but it is pointed out that in a few *Arachnoidea* the rudiments of paired extremities temporarily appear on the abdominal segments during embryonic development. On the other hand it must be remarked that the connection of the two paired pieces of the proboscis of the *Pantopoda* with the second extremity, and the homology of the two parts taken together with the lower jaw and pedipalp of the *Arachnoidea*, is by no means proved. The inner organisation and the development give little footing for a special comparison of the *Pantopoda* with the *Arachnoidea*, since the cœca of the mid-gut have no great morphological significance.

The *Pantopoda* are exclusively marine. *Nymphon, Pallene, Phoxichilidium, Ammothea, Pycnogonum. Collossendeis gigas* is a gigantic form in the deep seas.

The longest extremity sometimes measures 30 cm., while the whole body only attains a length of 8 cm.

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In these works further bibliography is given.

CHAPTER VI

The second division of the Arthropoda.—Organisation and Development of the Air-breathing Articulata (Tracheata).

Systematic Review.

Class I. **Protracheata (Onychophora).**

Body vermiform. A pair of preoral feelers at the point of the head. In the oral cavity a pair of horny jaws, at the side of the mouth oral papillæ (slime papillæ), numerous pairs of short almost truncated limbs. Respiration through tubular tracheæ, whose outer apertures are scattered over the whole body. Numerous segmentally arranged pairs of nephridia. Coxal glands on the legs. Heart a long dorsal vessel with numerous pairs of ostia.

Class II. **Antennata (Myriapoda and Hexapoda).**

One pair of preoral feelers, 3 pairs of oral limbs. Trunk either homonomously segmented with numerous pairs of jointed legs, or heteronomously segmented with the limbs limited to the three segments of the anterior region of the trunk, the thorax; the posterior region, the hind-body, being limbless. The head everywhere distinctly marked off from the trunk. Respiration by means of tubular tracheæ, whose outer apertures (stigmata) are segmentally arranged. The heart in the homonomously segmented *Myriapoda* is a long dorsal vessel, supplied with many segmentally arranged pairs of ostia; it runs through the trunk longitudinally: in the *Hexapoda* it is restricted to the abdomen.

Class III. **Chelicerota sive Arachnoidea.**

No preoral limbs comparable with the antennæ of the *Antennata* or *Protracheata*. Several anterior body segments (7, including the frontal lobes) are fused to form an unsegmented region, called the cephalothorax. This carries 6 pairs of extremities, the most anterior of which lies in front of the mouth. The two anterior pairs are developed as oral limbs. The first are called the jaw-feelers (chelicerræ), and the second jaw-palps (pedipalps). The 4 remaining pairs of extremities are jointed legs, generally long. Abdomen segmented or unsegmented, or fused with the thorax, with no developed limbs. Respiration either exclusively through book-leaf tracheæ, or at the same time through book-leaf and tubular tracheæ, or exclusively through tubular tracheæ. Number of stigmata limited, at the most 4 pairs. The stigmata almost always lie in the abdomen. Heart, seldom wanting, restricted to the abdomen.

CLASS I. The Protracheata (Onychophora).

An accurate knowledge of the organisation of the only genus belonging to this division, *Peripatus*, is of the greatest importance, because it combines unmistakable Annelid with unmistakable Tracheatan characteristics. Of all living Arthropoda, *Peripatus* has perhaps best preserved the original organisation of the ancestors of the *Tracheata*.

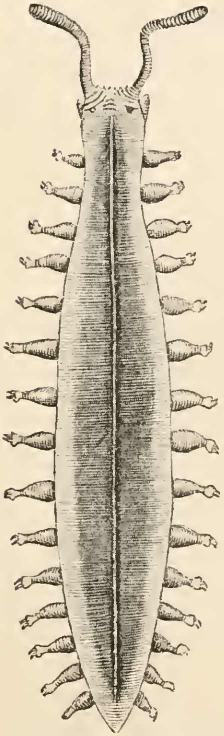

FIG. 289. — **Peripatus Novæ Zealandiæ** (after Sedgwick).

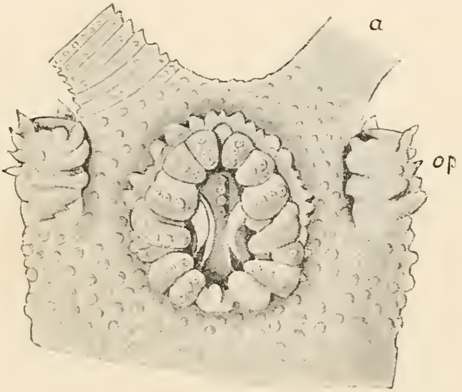

FIG. 290.—**Peripatus Edwardsii,** Head from the under side. *a*, Basal portions of the antennæ; *op*, oral papillæ. The figure shows also the papillæ surrounding the entrance to the oral cavity, and the jaws within the same.

Body.—The soft-skinned body is long and in appearance strikingly recalls certain *Annelida*, *e.g. Hesione.* The body is slightly flattened dorso-ventrally, with arched dorsal side and tolerably flat ventral side. The integument is transversely ringed. The limbs are the only external indications of segmentation. The head is fairly distinct from the trunk. Over the whole body are scattered the wart-like papillæ, each of which carries a hollow spine at its point. On each side of the head dorsally there is an eye, and in the middle of the ventral side is the mouth. The anus lies terminally at the posterior end of the body.

Extremities.—The head carries anteriorly and dorsally two ringed and somewhat slender antennæ. In the buccal cavity on each side lies a sickle-shaped jaw, consisting of two chitinous plates toothed along their inner sharp edges. On each side of the mouth arises a short ringed process beset with papillæ. This process is called the oral or slime papilla. The trunk carries a varying number (14 to 42, according to the species) of similarly formed limbs. These extremities are placed laterally at that part where the arched dorsal side bends in to meet the flat ventral side. Each extremity is truncated, with transverse rows of papillæ, which give it a ringed appearance, and each falls into two parts, a larger proximal conical leg and a smaller, narrower, distal foot, ending in two chitinous claws.

Integument.—The body epithelium (hypodermis) is externally covered by a delicate chitinous cuticle. The spines on the papillæ and claws on the feet also belong to the cuticular formation secreted by the hypodermis. Under the hypodermis lies a peculiar subepithelial layer, formed of fibres running in various directions.

Musculature (Fig. 291).—*Peripatus* has a strongly developed dermo-muscular tube, which consists of the following layers: (1) an external layer of circular muscular fibres; (2) a double layer of fibres crossing each other diagonally; (3) internally a strong longitudinal layer, consisting of various bundles, whose arrangement on a transverse section of the body is shown in Fig. 291. In addition to these layers there are numerous sagittal or transverse muscle fibres corresponding with the dorso-ventral or transverse muscle fibres of the *Annulata*. Some of these fibres run through the body cavity in such a way as to divide it into a median and two lateral divisions, the former containing the heart, the intestine, and the sexual organs, the latter the longitudinal trunks of the nervous system and the segmental organs. The musculature of the extremities chiefly proceeds from the layer of diagonal fibres and the sagittal musculature. Special muscles serve for moving the jaws, claws, etc.

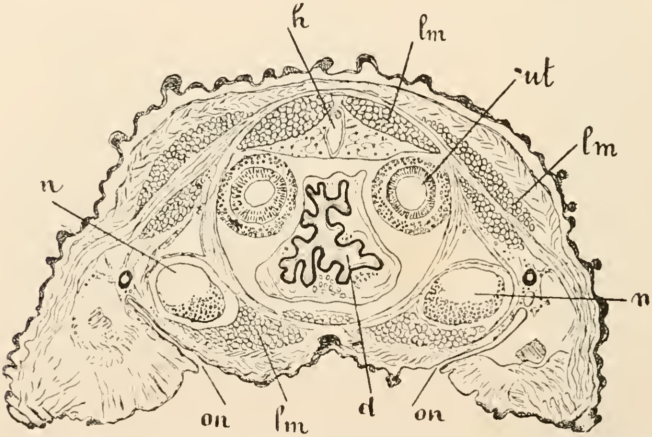

Fig. 291.—**Transverse section through the antepenultimate segment of a female Peripatus Edwardsii** (after **Gaffron**). *n*, Longitudinal trunks of the nervous system; *h*, heart (contractile dorsal vessel); *lm*, longitudinal muscles; *ut*, uterus; *d*, intestine; *on*, outer apertures of the nephridia.

None of the muscle fibres of Peripatus, except those of the jaw muscles,[1] are transversely striated.

The **alimentary canal** runs nearly straight through the body.

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[1] This exception, however, does not hold good for P. Leuckartii.

It falls into the following divisions: buccal cavity, pharynx, œsophagus, mid-gut or stomach-intestine, and rectum. The **buccal cavity**, in whose base the mouth proper lies, arises ontogenetically by the growing together of a row of papillæ surrounding the mouth; the mouth and jaws are thus enclosed within a circular wall. In front of the mouth, within the buccal cavity, lies a median prominence, the tongue. At the back of the buccal cavity, where it passes into the pharynx, *i.e.* at the posterior edge of the mouth, is an invagination directed backwards, into which the unpaired terminal portion of two **salivary glands** enters; these glands are long tubes running through the greater part of the body longitudinally in the lateral divisions of the body cavity. At the anterior end, near the bend towards the common terminal division, each salivary gland has a cœcal vesicular appendage. The **pharynx,** which reaches to the region between the first and second pair of legs, possesses a very thick muscular wall: its lumen in a transverse section is Y-shaped. The **œsophagus** is shorter. Its wall, which consists of an outer longitudinal and an inner circular muscular layer, is much thinner than that of the pharynx. These three divisions are lined by the chitinous cuticle.

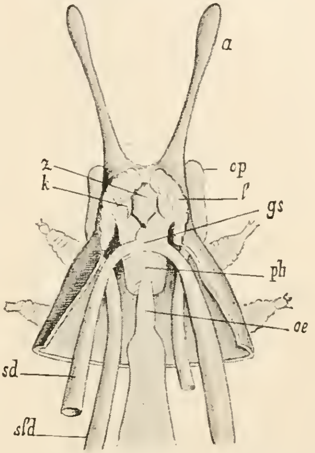

Fig. 292.—**Anterior end of the body of Peripatus capensis**, ventral side, laid open (after **Balfour**). *a*, Antenna; *z*, tongue; *k*, jaw; *dg*, salivary gland; *gs*, common terminal portion of the two salivary glands; *ph*, pharynx; *œ*, œsophagus; *l*, the lip papillæ surrounding the buccal cavity; *op*, oral or slime papillæ; *sld*, duct or reservoir of the slime glands.

The **stomach-intestine** stretches from near the two pairs of legs almost to the end of the body. Its wall is in folds, and its muscular layer (outer circular and inner longitudinal, *i.e.* the reverse of what obtains in all anterior sections of the canal) is exceedingly thin. It is nowhere fastened to the body wall by mesenteries. The **rectum,** which is distinctly separated from the mid-gut, is considerably narrower, with a tolerably well-developed muscular wall.

An **endothelium** (peritoneal epithelium) covers the outer muscular wall of the enteric canal and the other organs lying in or forming the boundary of the body cavity.

The **nervous system** of *Peripatus* (Fig. 293) consists of a large **brain** placed in the head in front of and over the pharynx (supraœsophageal ganglion), and of **two ventral longitudinal nerve trunks** proceeding from the brain, which run far apart in the lateral divisions of the body cavity to its posterior end. In each segment, *i.e.* in each part of the body corresponding with a pair of extremities, the longitudinal nerves are connected by several transverse commissures (9-10 in

Peripatus capensis). The longitudinal trunks show slight segmental swellings corresponding with the extremities; they are also provided with a continuous layer of ganglion cells. At the posterior end of the body they pass over into each other above the rectum by means of a connecting portion in which the layer of ganglion cells is wanting. Numerous nerves go off laterally from the longitudinal trunks along their whole course; these diverge at regular intervals and more or less correspond with the transverse commissures. Each extremity is supplied with two such lateral nerves. The nerves for the jaws diverge at the points where the longitudinal trunks enter the brain; rather farther back (or at the posterior end of the œsophageal commissure) arise the nerves for the oral papillæ. Besides small nerves, the **brain** gives off strong nerves to the antennæ. From its lower portion two more nerves arise which run to the tongue and the dorsal wall of the pharynx, and unite at the commencement of the œsophagus into an unpaired mediodorsal nerve forming a **sympathetic nervous system.**

The two **eyes** correspond to some extent in their structure

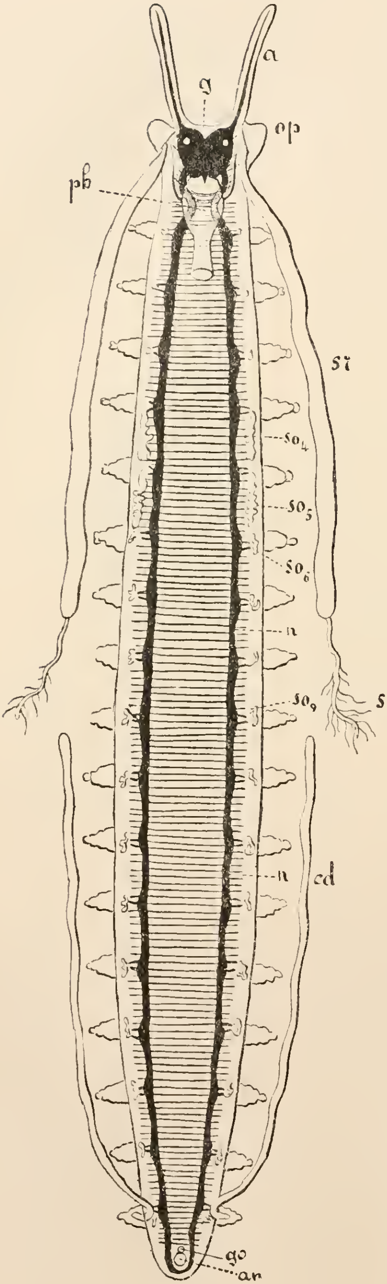

FIG. 293.—**Anatomy of Peripatus capensis** (after **Balfour**). The enteric canal behind the pharynx is cut off and removed. *g*, Brain; *a*, antenna; *op*, oral or slime papillæ; *sd*, slime glands; *sr*, slime reservoir, which at the same time acts as duct to the glands; so_4, so_5, so_6, so_9, nephridia of the 4th, 5th, 6th, and 9th pairs of limbs; *cd*, elongated coxal gland of the last pair of feet; *go*, genital aperture; *an*, anus; *ph*, pharynx; *n*, longitudinal trunk of the nervous system.

with the *Alciopidan* eye of the *Chætopoda* described on p. 230. But the space containing fluid between the lens and the rod layer is wanting. The *Peripatus* eye proceeds ontogenetically from a hollow invagination of the cephalic ectoderm near the rudiments of the brain. The invagination closes and becomes the optic vesicle. The connection with the brain is said to arise later by the growing out of the optic nerve from the brain.

The **circulatory system** consists of a **contractile dorsal vessel** or **heart** running through the body from the first segment to the last but one. This heart is supplied with paired ostia arranged segmentally and provided with valves. It lies in a pericardial sinus imbedded on its ventral side in a tissue comparable with the fat body of the *Insecta.* This sinus is incompletely separated from the underlying body cavity by a horizontal septum. The septum, which is formed of endothelium and muscle fibres running transversely, is fenestrated on both sides of the middle line. A median longitudinal nerve runs on the dorsal wall of the heart, as in the *Iulidæ.* Besides the heart a very fine medio-ventral longitudinal vessel is said to occur.

Excretory organs (nephridia). Each trunk segment of Peripatus is provided with a pair of nephridia. The nephridia lie in the lateral divisions of the body cavity and emerge on the under side of the extremities near their bases. Each nephridium (Fig. 294) consists of the 3 following parts:—(1) a **terminal vesicle** which opens outwards through the external aperture; (2) a looped **nephridial canal** bent back upon itself, which ends in (3) a **funnel** opening into the body cavity and placed near the terminal vesicle. We here find then the typical structure and arrangement of an Annulatan nephridium. In the 4th and 5th segment the nephridial canal is distinctly longer and forms many loops. The nephridia of the first three trunk segments are much smaller than the others; their canal is short and without loops. According to the species, the nephridia are apparently wanting in the penultimate or antepenultimate segment, *i.e.* the last or penultimate limb-bearing segment. It has, however, been proved that **the ducts of the sexual organs which emerge here are transformed nephridia. Transformed nephridia are also found in two so-called anal glands, which open in the last body segment (the anal segment without extremities) near the anus.** These glands are wanting in the adult female,

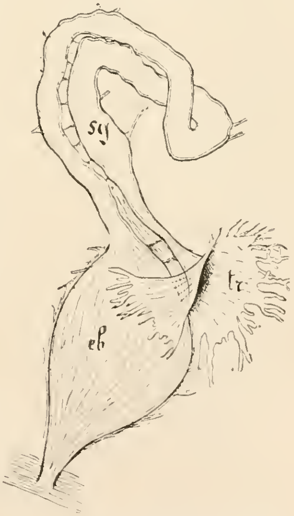

FIG. 294.—**A nephridium of Peripatus Edwardsii** (after Gaffron). *tr*, Funnel; *sg*, looped canal, or nephridial duct; *eb*, terminal vesicle of the nephridium.

but appear temporarily in the course of development. It has also been ontogenetically proved **that the salivary glands are the transformed nephridia of the segment carrying the oral papillæ which has fused with the head**; this is of extreme importance. Two blindly ending canals which open into the oral cavity near the base of the jaws have been pointed out as **nephridia of the jaw segment reduced to their ectodermal portion.**

Respiratory Organs.—It is a fact of great importance that *Peripatus* possesses the respiratory organs which are characteristic of the *Tracheata*, and which occur only in them. They consist of long, very fine, and thin chitinous tubes filled with air and widely dispersed through the body; in *Peripatus* they are not branched; they emerge united into tufts at the base of a flask-shaped depression of the integument. The outer aperture of such a depression may be called, as in the *Tracheata*, the **stigma.** In *P. Edwardsii* the stigmata occur in great numbers and quite irregularly all over the surface of the body. In *P. capensis*, on the contrary, at least some of the stigmata show a definite arrangement, viz. in longitudinal rows—on each side two, one dorsally and one ventrally. The stigmata in a longitudinal row are, however, more numerous than the pairs of legs.

Leg Glands (coxal glands) and Slime Glands.—In *Peripatus capensis*, in both sexes, there are paired glands emerging on the under side of the extremities, and only wanting in the first pair of trunk limbs. Every such **coxal gland** consists of a sac lying in the lateral division of the body cavity, and of a duct. The coxal glands of the last pair of feet are extraordinarily long in the male, and stretch far forward to near the middle of the body (Fig. 293, *cd*). In *P. Edwardsii* leg glands occur only in the males, not in each segment, but only in a certain number of segments lying in front of the genital segments; one, two, or three glands may occur in each limb.

There are two largely-developed thickly-branched **slime glands** (Fig. 293, *sd*), which must be considered as transformed leg glands, reaching far back into the body cavity. Their ducts run forward to emerge at the ends of the oral papillæ. When the animals are irritated, these glands forcibly eject a secretion consisting of a tangle of viscid threads.

Sexual Organs.—The sexes are separate. The best known sexual organs are those of *P. Edwardsii.* Those of other species seem in many points to be differently formed. (1) **Female sexual apparatus** (Fig. 295). This is as a rule paired. The two lateral halves, however, are connected at two points; first, where the ovaries pass into the uteri, and second, to form the unpaired terminal division (vagina) leading to the exterior. The two **ovaries** are imbedded in a common envelope of connective tissue, and suspended to the pericardial septum in the median line by a ligament consisting of two muscles. They lie in the posterior portion of the body cavity. They are continued into the two **uteri**, which, close to the ovary, are united by an unpaired portion;

separating again and winding about the intestine, they run first forwards then outwards, and finally backwards towards the median line, where they reunite to form the unpaired **vagina**, whose outer aperture lies ventrally between the penultimate pair of legs. Each uterus has in the part nearest the ovaries two appendages, a **receptaculum seminis** and **receptaculum ovorum.** The former is a sac opening into the uterus by means of two canals which unite at their mouths.

This peculiar method of junction of the receptaculum seminis and the uterus is explained by ontogeny. The receptaculum is originally only a U-shaped loop of the uterus. The two limbs of the loops unite at a later stage (Fig. 295, *rs*), fuse together at their ends, and open into each other, the partition wall disappearing. The limbs of the U-shaped bend thus become the two connecting canals, and the median piece (the bend of the U) becomes the sac of the receptaculum seminis. The receptaculum ovorum, which enters the part of the uterus lying between the ovary and receptaculum seminis, consists of a funnel, which enlarges at its free edge into a blindly-closed sac of connective tissue filled with fertilised eggs.

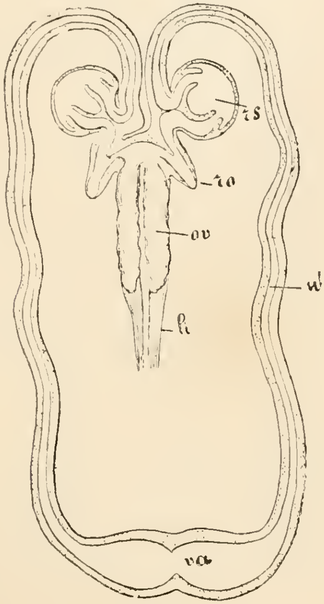

FIG. 295.—**Female sexual organs of an older embryo of Peripatus Edwardsii** (after **Gaffron**). *li*, Ovarial ligament; *ov*, ovarium; *ro*, funnel portion of the receptaculum ovorum; *rs*, receptaculum seminis; *ut*, uterus; *va*, vagina.

FIG. 296.—**Male genital apparatus of an adult Peripatus Edwardsii** spread out (after **Gaffron**). *t*, Testis; *vs*, vesicula seminalis; *vd*, vas deferens; *de*, ductus ejaculatorius.

Peripatus is viviparous. The eggs develop in the uterus, in which all stages of development are met with, the youngest embryos close to the ovary, the oldest near the vagina. The younger embryos are fastened in a peculiar manner to the wall of the uterus, in the older embryos this placenta-like connection ceases, but they lie in a closed sac formed by the epithelium of the uterus. The position of the embryo in the uterus is externally marked by constrictions of that organ. As the embryos cannot travel along the uterus, the latter itself grows at the part nearest to the receptaculum seminis, while its last chamber shortens and degenerates; in this way space is provided for the attachment of new embryos to its wall. In copulation, which probably takes place only once, the semen enters the receptaculum seminis. The eggs from the ovary which have reached the receptaculum ovorum pass thence into the uterus.

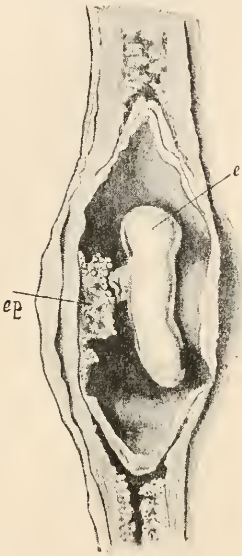

Fig. 297.—**Part of a uterus of Peripatus Edwardsii**, longitudinal section to show a brood cavity, and the embryo (*e*) contained in it with its placenta (*ep*), (after **v. Kennel**).

In other species of *Peripatus* either the receptaculum seminis or the receptaculum ovorum may be wanting, and the eggs, which from the first have been better provided with nutritive yolk, do not attach themselves to the wall of the uterus.

2. **Male genital apparatus** (Fig. 296).—This is paired, with the exception of the terminal portion, which opens outwardly at the same place as the vagina in the female. Each of the two tubular testes is continued into a short **vas efferens**, which opens like a funnel into a **vesicula seminalis.** From this again arises a fine coiled **vas deferens**, which, united with its companion, enters a long coiled terminal portion, the tubular **ductus ejaculatorius.** In the proximal part of the latter an envelope of complicated structure is secreted round the masses of spermatozoa, and a **spermatophore** is formed.

Ontogeny.—The development of *Peripatus Edwardsii* is complicated by the attachment of the embryos to the uterus wall, the latter undergoing considerable changes and forming a closed **brood chamber** (Fig. 297) round each embryo. In the case of each embryo an umbilical **cord** and **placenta** are formed, serving for its nourishment. Attached by the cord the embryo projects freely into the brood chamber. The side of the embryo turned away from the navel cord (which is a process of the dorsal side of its future head) becomes the ventral side. Around the embryo an envelope yielded by itself and called the **amnion** is formed, and is attached to the inner surface of the uterus. As the embryo grows older, it gradually curls up within the brood cavity.

In Peripatus all those parts of the body which are metamerically or segmentally repeated (the mesoderm segments, extremities, nervous system, coxal glands, etc.) develop and differentiate in the manner universally characteristic of the segmented animals, *i.e.* progressively in order from before backwards.

The **Mesoderm** is differentiated into two ventral symmetrical mesoderm streaks, which unite posteriorly (at the edge of the blastopore) in a median zone, and in this zone, throughout embryonic development, active processes of growth go on. Besides this the cell material of the two mesoderm streaks themselves increases by a continuous process of division. Segmental cavities appear in the mesoderm streaks in continuous succession from before backward, and these separate into mesoderm segments or mesoderm sacs with walls, which are at first unilaminar. The further differentiation of these mesoderm sacs occurs in such a way that each falls into three cavities, one of which becomes the nephridial funnel (Fig. 299, *A-C*) while the others disappear as distinct cavities, and the cell material of their walls yields the mesodermal portions (endothelium, muscles, connective tissue) of the trunk and of the extremities.

The **extremities** arise as outgrowths of the body wall. The first pair of rudimentary extremities, after the antennæ, develop into the jaws; the second into the oral papillæ (Fig. 298). The two segments corresponding with them fuse with the primitive head segment to form the later secondary head.

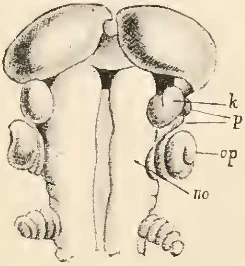

FIG. 298.—**Embryo of Peripatus Edwardsii, with growths beginning round the jaws.** Anterior end of the body from the ventral side (after **v. Kennel**). *k*, Jaws; *p*, papillæ, embracing the jaws laterally; *op*, oral papillæ; *no*, nephridial aperture of the segment of the oral papillæ.

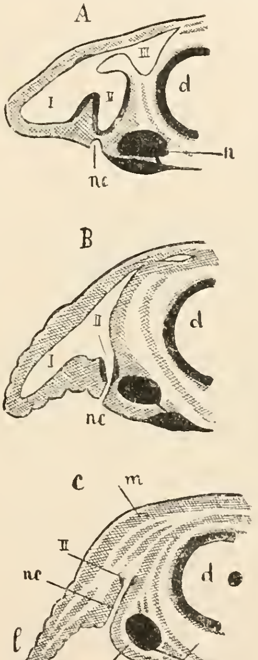

FIG. 299.—*A*, *B*, *C*, **Diagrams to elucidate the development of the nephridia of Peripatus Edwardsii** (after **v. Kennel**). Only one side of the body is represented in the transverse section. *I*, *II*, *III*, The three divisions into which each mesoderm sac falls; *II*, the division which forms the rudiment of the funnel. In *A* the rudiment of the nephridial canal (*nc*) has appeared as an invagination of the ectoderm, in *B* it has united with the funnel rudiment (*II*); *m*, mesoderm; *lb*, body cavity; *n*, longitudinal trunks of the nervous system; *d*, intestine.

The pharynx and œsophagus (stomodæum) and the hind-gut (proctodæum) form by invaginations of the ectoderm which open later into the endodermal mid-gut. The buccal cavity arises by the growing up of a rampart round the oral region, and in this cavity the jaws come to lie.

While the **coxal glands** (including the slime glands), which proceed exclusively from ectodermal invaginations, are clearly dermal glands, the **nephridia** (and the salivary glands, genital ducts, and anal glands, which are homologous with them) arise out of paired rudiments. The funnel comes, as has already been mentioned, from one part of a mesoderm sac and only later becomes connected with an ectodermal invagination which yields the terminal vesicle, and, as it appears, the whole nephridial duct also, however long and coiled it may be. The **salivary glands** in the young recently hatched animal still function as nephridia and have funnels opening towards the body cavity, which afterwards close but are still retained in the adult animal as vesicular appendages. Their nephridial ducts grow out far beyond the funnels to form blindly ending tubes posteriorly. Their apertures approach the middle line by the growing up of the oral enclosure and thus reach the floor of the buccal cavity. A new median invagination of the integument then yields their unpaired duct. The genital ducts represent the nephridia of the penultimate limb-bearing segment and develop in a similar manner (Fig. 300). At first their outer apertures lie laterally, and apart. Later they approach the middle line. The uteri in the female and vasa deferentia in the male, which correspond with the nephridial canal of the typical nephridia, are joined by a new median unpaired invagination from without, and from this proceed, in the male the ductus ejaculatorius, and in the female the vagina.

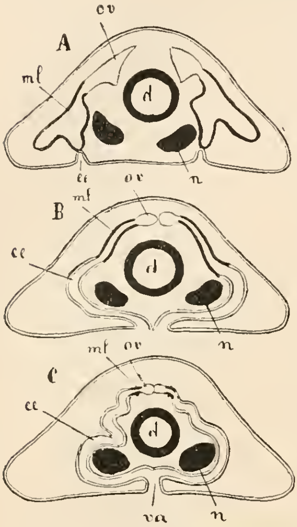

Fig. 300.—*A*, *B*, *C*, **Diagrammatic representation of the development of the female sexual apparatus of Peripatus Edwardsii** in transverse sections (after **v. Kennel**). *ov*, Ovary, proceeding from the median portion of the mesoderm sac; *ml*, that part of the female genital apparatus which corresponds with the nephridial funnel, and from which proceed chiefly the receptaculum ovorum and the piece which connects the uteri with the ovaries; *ee*, paired ectodermal invaginations, which become the uterus. In *B* the two invaginations have approached each other in the middle line, and in *C* at this point a new unpaired ectodermal invagination (*va*) has appeared, the rudiment of the vagina; *d*, intestine; *n*, longitudinal trunks of the nervous system.

The **brain** and **longitudinal nerve trunks** arise as paired thickenings of the ectoderm, which differentiate from before backward and separate from the ectoderm. The rudimentary ganglia of the jaw segment fuse at a later stage with the rudimentary ganglia of the head segment to form the brain.

The Systematic Position of Peripatus.

If we try to estimate what has been said about the organisation and development of this animal from a comparative point of view, we come to the conclusion that *Peripatus* unites typical Annulatan characteristics with typical Arthropodan and especially Tracheatan characteristics. The following are its **Annulatan characteristics**: (1) **segmentally arranged nephridia** of the type of the permanent trunk nephridia of Worms; (2) **segmentally arranged coxal glands**, which are undoubtedly homologous with the **Chætopodan setiparous glands**; (3) a **dermo-muscular tube**, which most nearly approaches that of the *Hirudinea*. The truncated form of the extremities and the structure of the eye are less significant. The following are the Arthropodan and especially **Tracheatan characteristics** of *Peripatus*:—(1) the respiratory organs developed in the form of **tracheæ**; (2) the **dorsal heart lying in a pericardial sinus** and supplied with **many pairs of ostia**, and the **lacunar circulatory system**; (3) the **transformation of extremities into mouth parts** (jaws); (4) the specific form of the **salivary glands.**

The **nervous system** deviates in a characteristic way from the somewhat similar nervous system of the *Annulata* and of the *Arthropoda*, by the lateral position of the ventral longitudinal trunks, the slight development of the ganglia, and the large number of transverse commissures in each segment. The nervous system of *Peripatus* is a ladder nervous system, which shows striking similarity with that of the *Amphineura, Placophora*, and *Zeugobranchia* among the *Mollusca*, and that of certain *Platodes* and *Nemertina*. There is no doubt, however, that the ladder nervous system of *Peripatus* is homologous with the brain and ventral cord of the *Annulata* and *Arthropoda*. Its specifically deviating form may be regarded in two ways: (1) The ladder nervous system of *Peripatus* has arisen out of a typical ventral cord by the moving apart of its symmetrical halves and the increase of the transverse commissures; (2) in contrast with the ventral cord of the *Annulata* it represents a more primitive condition. The latter view seems to us the more plausible, since we adhere to the opinion that the ventral cord of the *Annulata* itself proceeded from a ladder-like nervous system by the moving together of the longitudinal trunks towards the ventral middle line. *Peripatus*, according to this view, would be related only to the typically segmented **racial form** of the *Annulata*. The fact is perhaps not without significance that the *Phyllopoda* also (which are held to stand nearest of all the living *Crustacea* to the racial form) possess a ladder-like nervous system. The large number of transverse commissures in each segment must be a secondary condition. In a few *Annulata* we find more than one transverse commissure, also probably as a secondary condition; the same is also the case in the *Phyllopoda*.

The **tracheæ** of *Peripatus* may perhaps be regarded as **dermal glands** transformed by adaptation to life on land, glands similar to those long mostly unicellular dermal glands which in certain *Hirudinea* and many *Turbellaria* spread far through the body parenchyma.

From the point of view of Comparative Anatomy it is of the greatest importance to have proved that the salivary glands and genital ducts are transformed nephridia, helping us as it does to understand the morphological significance of these organs in the *Tracheata*. No less important is the almost certain proof that **the slime and coxal glands are homologous, and that these dermal glands are homologous with the setiparous glands of the Annulata**, especially with reference to similar glands in the *Tracheata*.

It cannot be certainly proved that the antennæ, jaws, and oral papillæ of *Peripatus* correspond with the antennæ mandibles, and one pair of maxillæ of the *Tracheata*.

Single genus: *Peripatus*. Animals avoiding light, and living on land in damp places, under the bark of old trees, under stones, etc. *P. capensis*: on the wooded slopes of Table Mountain, Cape of Good Hope. *P. Edwardsii*: Venezuela; related species in Trinidad. *P. Novæ Zealandiæ*; *P. Leuckartii*: Australia.

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Class II. **Antennata.**

Systematic Review.

Sub-Class I. **Myriapoda. Millipedes.**

Trunk homonomously segmented, segments usually numerous, of nearly equal size, and, except the last, provided with feet. Without compound eyes. With numerous ocelli.

Order 1. **Symphyla.**

With not more than 12 leg-bearing trunk segments. One pair of branched tracheæ, whose stigmata lie in the head. Unpaired genital aperture in the 4th segment. *Scolopendrella* (Fig. 301, p. 444).

Order 2. **Chilopoda.**

Body more or less flattened dorso-ventrally. Each body ring carries only one pair of limbs and answers to a segment. The two pairs of maxillæ are separate. The first pair of trunk feet moved on to the head as maxillipedes with poison glands emerging on the terminal claw. Unpaired genital aperture on the penultimate segment. Fam. *Scutigeridæ*: with compound eyes. Trunk consists of 15 leg-bearing segments. *Scutigera.* Fam. *Lithobiidæ*: trunk consists of 15 leg-bearing segments. No compound eyes, but ocelli. *Lithobius* (Fig. 323, p. 464), *Henicops.* Fam. *Scolopendridæ*: with 21 or 23 leg-bearing trunk segments (the maxillipedal segment not included). Body elongated. *Scolopendra, Cryptops.* Fam. *Geophilidæ*: body very long, with 31-173 leg-bearing trunk segments. *Geophilus, Himantarium.*

Order 3. **Diplopoda (Chilognatha).**

Body mostly arched. From the 5th segment onwards each ring has 2 pairs of legs and thus corresponds with a double segment. The two pairs of maxillæ are fused to form the so-called gnathochilarium. Without maxillipedes. Paired genital apertures between the 2d and 3d pairs of legs. The legs of the 7th ring in the male are changed into copulatory organs. Fam. *Polyxenidæ*: 15 pairs of feet. Gnathochilarium rudimentary. Copulatory feet wanting. *Polyxenus.* Fam. *Glomeridæ*: 11-14 rings. *Glomeris.* Fam. *Polydesmidæ*: without eyes. 19-20 trunk rings, 29-31 pairs of feet. *Polydesmus, Brachydesmus.* Fam. *Chordeumidæ*: 30 trunk rings, 45-50 pairs of feet. *Atractosoma, Craspedosoma, Chordeuma.* Fam. *Lysiopetalidæ*: number of rings large, indefinite. *Lysiopetalum.* Fam. *Iulidæ*: 30-70 or more rings. *Iulus.* Fam. *Polyzonidæ*: gnathochilarium reduced. Number of the rings inconstant, 30-100 or more. *Polyzonium.*

Order 4. **Pauropoda.**

Feeler with several flagella. Only one pair of weakly developed maxillæ. 10 trunk segments. 9 pairs of legs. Tracheæ as yet not discovered. Genital apertures at the base of the second pair of legs. *Pauropus.*

Sub-Class II. **Hexapoda. Insecta.**

Trunk heteronomously segmented; the almost constant number of segments of unequal size, the body is divided into head, thorax of 3 segments, and hind body of 10 segments. Each of the 3 thoracic segments has a pair of legs. Abdomen limbless. Compound eyes as well as ocelli almost always present. Apertures of the sexual organs always at the end of the hind body.

Legion I. **Apterygota.**

Without wings. With rudiments of abdominal limbs, at least in the *Thysanura*. Without metamorphosis.

Order 1. **Thysanura.**

With 10 abdominal segments and 2-3 jointed bristle-shaped appendages (cerci) on the anal segment. Compound eyes and ocelli may be present or absent. *Machilis*, *Lepisma*, *Nicoletia*, *Campodea* (Fig. 302, p. 444), *Iapyx*.

Order 2. **Collembola.**

With 6 abdominal segments or fewer. Nearly always a springing fork at the end of the hind-body. Without compound eyes. Occasionally with ocelli. *Sminthurus*, *Podura*, *Isotoma*, *Macrotoma*.

Legion II. **Pterygota.**

With a pair of wings on both the 2d and 3d thoracic segments. There are unwinged forms, which, however, are descended from winged ancestors.

Order 1. **Dermaptera (Forficulidæ), Earwigs.**

Insects with gradual metamorphosis, and with biting mouth parts. The last abdominal segment has unjointed appendages (cerci), which form a pincer. Fore-wings short, changed into horny wing covers. Hind-wings large, delicate skinned, fan-shaped, can be folded longitudinally and transversely. Paired genital apertures, of which one may be rudimentary. *Forficula*, *Labidura*.

Order 2. **Orthoptera.**

Insects with gradual metamorphosis, with biting mouth parts; with 2 pairs of membranous or parchment-like wings, sometimes wanting. Fore-wing generally shorter and more chitinous than the hind-wing. Variously shaped cerci on the hind body. Sexual apertures unpaired. *Embidæ*, *Blattidæ* (cockroaches: *Periplaneta*, *Blatta*). *Mantidæ* (Mantis, praying insect). *Phasmidæ* (stick or spectre insects, *Bacillus*, *Phasma*, *Phyllium*). *Saltatoria*, including the 3 families, *Acridiidæ* (grasshoppers: *Acridium*, *Œdipoda*, *Mecostethus*, *Stenobothrus*, *Tettix*, etc.); *Locustidæ* (*Locusta*, *Thamnotrizon*, *Platycleis*, *Decticus*); and *Gryllidæ* (*Gryllus*, *Gryllotalpa*, *Myrmecophila*).

Order 3. **Ephemeridæ.**

Insects with incomplete metamorphosis. Mouth parts somewhat reduced, of the biting type. Hind-wing small or wanting, fore-wing large, wings finely membranous. Hind body with 3 (rarely 2) long cerci. Paired genital ducts, emerging separately. Larvæ apneustic, *Thysanura*-like, with tracheal gills, and with biting mouth parts, live in water. *Ephemera*, *Palingenia*, *Chloë*.

Order 4. **Odonata (Libellulidæ).**

Insects with incomplete metamorphosis, and with biting mouth parts. Hind body with 2 unjointed anal processes. Both pairs of wings are large, and glass-like, with a rich network of veins. Thoracic legs moved forward. Larvæ in water with various sorts of tracheal gills, apneustic. *Libellula*, *Æschna*, *Calopteryx*, *Agrion*. etc.

Order 5. **Plecoptera** (**Perlaria**).

Insects with incomplete or gradual metamorphosis, with biting mouth parts. Hind body generally with 2 long cerci. Both pairs of wings large, veins forming large meshes, the hinder pair often broader than the front pair, and partly foldable. The *Thysanura*-like larvæ live in water, with tracheal gills, apneustic. The tracheal gills often persist in the imago. *Perla* (Fig. 317, p. 456), *Nemura*.

Order 6. **Corrodentia.**

Insects without, or with gradual metamorphosis, with biting mouth parts. Wings often wanting. In the *Termites* they are finely membranous, and in the sexual animals deciduous. They are wanting in the workers. Some *Psocidæ* and the *Mallophaga* are wingless. The compound eyes are wanting in the *Mallophaga*. The wings of the winged *Psocidæ* are glassy, areolate, and like those of the *Hymenoptera*. Young forms *Thysanura*-like. *Termitidæ* (white ants, which form communities, *Termes*, *Calotermes*); *Psocidæ* (*Troctes*, *Psocus*, book lice; *Mallophaga*, parasites feeding on the fur of animals or feathers of birds; *Trichodectes*, *Philopterus*, bird lice; *Liotheum*).

Order 7. **Thysanoptera** sive **Physopoda.**

Insects with gradual metamorphosis, the larval form very like the imaginal. The last larval stage goes without food. Sucking mouth parts. The claws of the short feet with the adhering lobes of the tarsus changed into a protrusible vesicular apparatus. Wings very narrow, with reduced veining, with long fringed edges, often wanting or rudimentary. Only 3 or 4 pairs of stigmata, one or 2 on the thorax, one on the first and one on the eighth ring of the hind body. Nervous system concentrated. *Thrips*.

Order 8. **Rhynchota.**

Insects with gradual metamorphosis (in the males of the *Coccidæ* complete metamorphosis). Mouth parts form a proboscis adapted for piercing and sucking. Compound eyes are wanting in the parasitic Rhynchota.

Sub-Order 1. **Phytophthires.**

With two pairs of membranous wings. Generally wanting in the female. The *Coccidæ* have only fore-wings, the hind-wings being changed into halteres. Fam. *Psyllidæ*: with 2 pairs of wings (fore-wings parchment-like); *Psylla*, *Livia*. Fam. *Aphidæ*: with 2 pairs of membranous wings, generally wanting in the female; *Aphis*, *Chermes*, *Schizoneura*, *Phylloxera*. Fam.: *Coccidæ*, scale insects; *Coccus*, *Lecanium*, *Aspidiotus*.

Sub-Order 2. **Pediculidæ (Aptera), Lice.**

Without facet eyes and without wings. *Pediculus*, *Hæmatopinus*, *Phthirius*.

Sub-Order 3. *Heteroptera* (*Hemiptera*), Bugs.

Four wings (seldom wanting). The anterior horny wing-covers are membranous at their points. Hind-wings membranous. *Geocores* (land bugs: *Hydrometra*, *Halobates*, *Pentatoma*, *Coreus*, *Corizus*, *Alydus*, *Pyrrhocoris*, *Lygaeus*, *Miris*, *Capsus*, *Acanthia* [bed-bugs], *Reduviis*, etc.) *Hydrocores* (water-bugs: *Nepa*, *Ranatra*, *Naucoris*, *Corixa*, *Notonecta*, etc.)

Sub-Order 4. **Homoptera.**

Fore-and hind-wings similar in shape and membranous, but the fore-wings are always somewhat harder. *Cicada*, *Fulgora*, *Pseudophana*, *Centrotus*, *Aphrophora*, *Tettigonia*, *Ledra*, etc.

Order 9. **Neuroptera.**

Insects with complete metamorphosis and biting mouth parts. 2 pairs of membranous glassy wings, closely reticulate. Fam. *Megaloptera*: *Myrmeleon*, *Mantispa*, *Hemerobius*, *Chrysopa*. Fam. *Sialidæ*: larvæ mostly in water, with tracheal gills. *Sialis*, *Corydalis*, *Raphidia*.

Order 10. **Panorpata.**

Insects with complete metamorphosis and biting mouth parts. 2 pairs of narrow membranous wings, widely reticulate. Larvæ catterpillar-like. *Panorpa*, *Bittacus*, *Boreus* (wings rudimentary).

Order 11. **Trichoptera (Phryganidæ)**, Caddis-flies.

Insects with complete metamorphosis. Mandibles rudimentary. Maxillæ form a membranous blunt proboscis. Body mostly hairy, less frequently scaly. Hind-wings generally larger than the fore-wings, folding like a fan. The larvæ, which resemble those of cockchafers, live in tubes or cases chiefly in the water, have tracheal gills, and are apneustic. *Phryganea*, *Limnophilus*, *Halesus*, *Hydropsyche*, *Mystacides*, etc.

Order 12. **Siphonaptera** *sive* **Aphaniptera, Fleas.**

Insects with complete metamorphosis, with piercing and sucking mouth parts. No wings. No facet eyes. Parasites. *Pulex*, *Sarcopsylla*, *Ceratopsyllus*.

Order 13. **Coleoptera, Beetles.**

Insects with complete metamorphosis and biting mouth parts. Fore-wings as horny wing cases (elytra). Hind-wings membranous, can fold transversely and longitudinally, serve exclusively for flight. Larvæ variously shaped, often *Thysanura*-like, occasionally like the cockchafer larvæ, seldom limbless (*Curculionidæ*), with biting mouth parts. Several thousand genera with over 80,000 species.

Sub-Order 1. **Cryptotetramera.**

The tarsi are four-jointed, one joint being rudimentary. Fam. *Coccinellidæ*, *Endomychidæ*.

Sub-Order 2. **Cryptopentamera.**

Tarsi five-jointed, one joint being] reduced and hidden. Fam. *Chrysomelidæ*, *Cerambycidæ*, *Curculionidæ*, *Bostrychidæ*, etc.

Sub-Order 3. **Heteromera.**

Tarsi of the two anterior pairs of legs five-jointed, those of the posterior pairs four-jointed. Fam. *Meloidæ* (*Cantharidæ*), *Rhipiphoridæ*, *Tenebrionidæ*, *Œdemeridæ*, *Cistelidæ*, etc.

Sub-Order. 4. **Pentamera.**

Tarsi as a rule five-jointed in all legs. Fam. *Xylophaga*, *Malacodermata*, *Elateridæ*, *Buprestidæ*, *Lamellicornia*, *Silphidæ*, *Pselaphidæ*, *Staphylinidæ*, *Hydrophilidæ*, *Dytiscidæ*, *Carabidæ*, *Cicindelidæ*, etc.

Order 14. **Lepidoptera.**

Insects with complete metamorphosis and sucking mouth parts, forming a proboscis which can generally be curled up. Body covered with scales. Both pairs of wings similar, membranous, covered with scales, rarely foldable. Hind-wings generally somewhat smaller than fore-wings. The larvæ are caterpillars, with anal feet, with biting mouth parts, rarely (*Micropteryx*) footless.

Sub-Order 1. **Microlepidoptera.**

Fam. *Pterophoridæ*, *Tineidæ*, *Pyralidæ*, *Tortricidæ*.

Sub-Order 2. **Geometrina.**

Fam. *Phytometridæ*, *Dendrometridæ*.

Sub-Order 3. **Noctuina.**

Fam. *Ophiusidæ*, *Plusiadæ*, *Agrotidæ*, *Cucullиadæ*, *Acronyctidæ*, etc.

Sub-Order 4. **Bombycina.**

Fam. *Bombycidæ*, *Saturnidæ*, *Psychidæ*, *Zygænidæ*, *Cossidæ*, *Liparidæ*, *Euprepiadæ*, *Notodontidæ*.

Sub-Order 5. **Sphingina.**

Fam. *Sesiadæ*, *Sphingidæ*.

Sub-Order 6. **Rhopalocera.**

Fam. *Hesperidæ*, *Lycænidæ*, *Satyridæ*, *Nymphalidæ*, *Heliconiidæ*, *Equitidæ*.

Order 15. **Hymenoptera.**

Insects with complete metamorphosis, with mandibles adapted for biting and maxillæ generally adapted for sucking. Usually 4 membranous, transparent, slightly veined wings. Various sorts of caterpillars—those of the *Tenthredinidæ* and *Uroceridæ* are footless, *i.e.* maggot-like.

Sub-Order 1. **Terebrantia.**

Female with ovipositor (borer or tube). Fam. *Tenthredinidæ*, *Uroceridæ*, *Cynipidæ* (gall flies). The larvæ of the *Pteromalidæ*, *Braconidæ*, *Ichneumonidæ*, *Evaniadæ*, are generally parasitic in the larvæ of other insects.

Sub-Order 2. **Aculeata.**

Female with poison sting and poison glands. Fam. *Formicidæ* (ants), *Fossoria* (sand wasps), *Vespidæ* (social wasps), *Apidæ* (bees).

Order 16. **Diptera.**

Insects with complete metamorphosis, with sucking and sometimes also piercing mouth parts. Fore-wings membranous, transparent. Hind-wings transformed into halteres. Larvæ maggot-shaped (without legs), with or without head.

Sub-Order 1. **Pupipara.**

Viviparous. The larvæ are born shortly before entering the pupal state. Parasites. Wings often rudimentary. *Melophagus*, *Braula*, *Nycteribia*.

Sub-Order 2. **Brachycera, Flies.**

Feelers short, generally three-jointed. Many families: *Muscidæ*, *Conopidæ*, *Oestridæ*, *Syrphidæ*, *Empidæ*, *Asilidæ*, *Bombyliidæ*, *Therevidæ*, *Tabanidæ*, *Leptidæ*, *Xylophagidæ*, *Stratiomyidæ*.

Sub-Order 3. **Nemocera (Tipularia), Gnats.**

Feelers long, many-jointed, in the male often plumose. Fam. *Bibionidæ*, *Fungicolæ*, *Noctuiformes*, *Culiciformes*, *Culicidæ*, *Gallicolæ*, *Limnobiidæ*.

Of the above enumerated orders that of the *Dermaptera* is usually placed as a family of the *Orthoptera*. The *Ephemeridæ*, *Odonata*, *Plecoptera*, *Corrodentia*, and *Thysanoptera* are often united into the order of the *Pseudoneuroptera*, and the *Panorpata* incorporated with the *Neuroptera*.

I. Outer Organisation.[1]

A. The Body.

Myriapoda.

The body consists of a head and a large number of uniform trunk segments, the anterior 3 of which correspond with the 3 thoracic segments of the *Hexapoda* (*Insecta*). The head has almost certainly arisen from at least 4 fused segments.

Symphyla (*Scolopendrella*).—The trunk in this division, which probably stands nearest to the common racial form of the *Myriapoda* and *Hexapoda*, consists of 12 distinct leg-bearing segments, and an anal segment with 2 processes which may be described as spinning stylets (Fig. 301). Two feelers, which lie in front of these spinning processes, are perhaps transformed legs, and indicate the existence of a 13th pre-anal segment. If so, the whole number of trunk segments would be 13 or 14, and would then almost exactly correspond with the original number of segments in the Hexapodan trunk, in which the thorax has 3 and the abdomen 10 (perhaps 11) segments. The

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[1] This representation of the outer organisation can only be of the most general character. For details, which are of great zoological importance, we must refer the reader to systematic works on Entomology.

Pauropoda have the smaller number of 10 trunk segments (including the anal segment). In the *Chilopoda* (Fig. 323, p. 464) and *Diplopoda* the number of trunk segments is larger and often very considerable (in *Himantarium* there are as many as 173). It is possible that this large number of segments is not an original peculiarity of the *Chilopoda* and

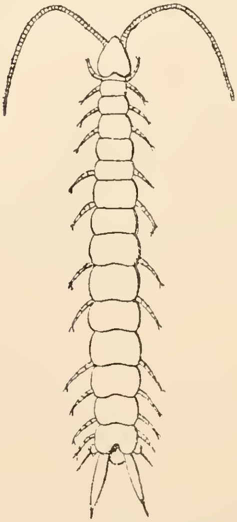


Fig. 301.—**Scolopendrella immaculata** (after **Latzel**).

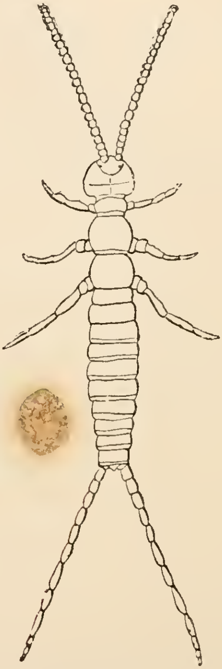


Fig. 302.—**Campodea staphylinus**, without the setæ and hairs (after **Lubbock**).

Diplopoda, but secondarily acquired, as in the serpents. In the *Diplopoda* only the 4 or 5 anterior trunk rings represent single segments, each subsequent ring is a **double segment.**

Hexapoda.

The body of the *Hexapoda* falls typically into 3 parts quite distinct from each other: head, thorax, and hind body (abdomen). The unsegmented **head** probably originally consisted of 4 segments. The **thorax** is composed of 3 segments: **prothorax, mesothorax,** and **metathorax,** answering to the 3 anterior trunk segments of the *Myriapoda.* The typical number of segments of the hind-body is 10 or 11. The thorax and the abdomen together form the trunk, which may be compared with the trunk of the *Symphyla.* Among the

Apterygota the *Thysanura* possess 10 abdominal segments, and the *Collembola* a varying number, but always less than 10. In the *Pterygota* the number of abdominal segments in the adult animals varies, and is generally less than 10. This diminution is caused by the fusing of those segments which are connected with the genital apparatus and lie in front of the last, and secondly by the fusing of the anterior abdominal segments (usually only the first) with the thorax. On the other hand in a few insects (*Macrolepidoptera*, *Diptera*, and *Rhynchota*) the last (3d) thoracic segment is joined with the abdomen.

B. The Limbs.

The limbs of the *Insecta* consist of single rows of joints. We distinguish the limbs of the head from those of the trunk. It is certain that each trunk segment was originally provided with a pair of limbs (as is now the case in *Peripatus* and the *Myriapoda*). In the *Hexapoda*, however, only the limbs of the 3 anterior trunk segments, *i.e.* of the thorax, have been retained.

1. The Limbs of the Head.

There are, typically, 4 pairs of cephalic appendages, which are called, in the order from before backward, the **Antennæ (feelers) Mandibles, anterior** and **posterior Maxillæ.**

Comparing these cephalic limbs with the **analogous** limbs of the *Crustacea*, we see that in the *Myriapoda* and *Insecta* one pair of antennæ is wanting.

The cephalic limbs themselves are divided into 2 groups, the **feelers**, and the **oral limbs** or **mouth parts** (mandibles and maxillæ).

The **feelers (antennæ)** of the *Myriapoda* and *Hexapoda* are always found in one single pair, and are pre-oral, springing from the forehead; they are long and slender, many jointed, very variously formed in details, and very often different in the two sexes. They are organs of touch, and at the same time carry the olfactory organs. They are innervated from the brain.

The **oral limbs (mouth parts)** vary extraordinarily in form, according to the special functions to which they are adapted, these functions being chewing, triturating, biting, sucking, and piercing, etc. The tracing back of all these variously transformed mouth parts of the *Hexapoda* to 3 pairs of oral limbs (mandibles, and anterior and posterior maxillæ) is one of the greatest achievements of comparative anatomy. We can only take into consideration the principal forms of these oral limbs. The mouth parts of the *Orthoptera* form the best starting-point in our review, because in them the composition of the lower lip (labium) of 2 lateral pieces (posterior maxillæ) is most evident. The whole apparatus (Fig. 303) is as follows.

1. The **upper lip** (labrum *lbr*) is an unpaired piece which covers the oral aperture in front and from above, and has **nothing to do with the limbs.**

2. **The Mandibles** (upper jaws, *md*) consist on each side of a powerful but unsegmented masticatory plate with toothed edge.

3. **The anterior maxillæ (lower jaw).** Each of these 2 maxillæ consists of a 2-jointed basal portion (mx_1), which carries first a 5-jointed feeler (*pm*, palpus maxillaris), and second, 2 unjointed

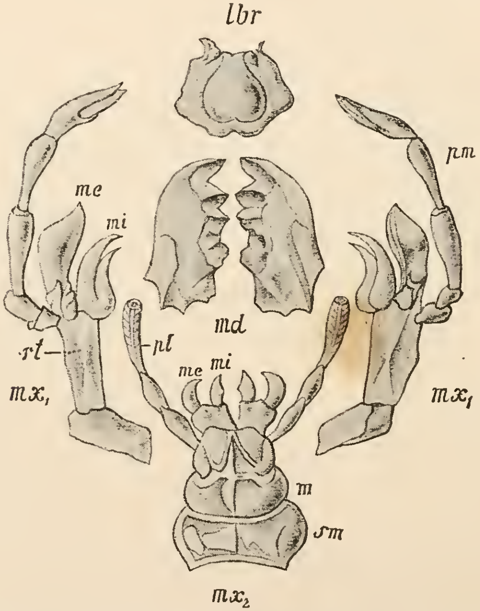


Fig. 303.—**Mouth parts of Blatta (Orthoptera,** after **Savigny).** *lbr*, Labrum (upper lip); *md*, mandible; mx_1, anterior pair of maxillæ; mx_2, posterior pair of maxillæ = lower lip (labium); *st*, stipes (stem); *m*, mentum; *sm*, submentum; *mi* and *me*, mala interna and externa, inner and outer ridges of the 1st and 2d pairs of maxillæ; *pm*, palpus maxillaris, feeler of the anterior maxillæ; *pl*, palpus labialis, feeler of the posterior maxillæ.

masticatory ridges, one outer (*me*, mala externa) and one inner (*mi*, mala interna).

4. The **posterior maxillæ** together form the **lower lip** (labium, mx_2). Each posterior maxilla consists of the same parts as the anterior maxillæ (basal part, 3-jointed feeler *pl*, outer and inner masticatory ridges *me* and *mi*), but the 2 basal parts on each side have grown together behind and below the mouth in the middle line.

These mouth parts are adapted for biting and chewing.

We shall now describe the most important modifications of the above type in systematic order.

Myriapoda.

Symphyla.—Mouth parts for chewing. Upper lip, mandibles, and 1 pair of maxillæ with only 1 masticatory ridge and rudimentary feeler. The *Pauropoda* have similar mouth parts also weakly developed. The mouth parts of both groups require further investigation.

Chilopoda (Fig. 304).—The mouth parts, apart from the upper lip and the hypopharynx which belongs to the lower œsophageal wall, consist of the typical limbs, mandibles, anterior and posterior maxillæ. The anterior pair of maxillæ has well developed masticatory ridges, but has no feeler or only a rudimentary one. The feelers are well developed on the 2d pair of maxillæ, but the masticatory ridges are wanting. The basal portions of these maxillæ are sometimes separate, sometimes fused.

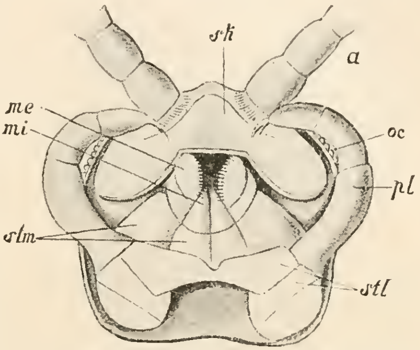


Fig. 304.—**Lithobius validus.** The head from below after removal of the maxillipedes (after **Latzel**). *a*, Antennæ; *sk*, frontal portion of the cephalic shield; *oc*, grouped ocelli; *pl*, feeler of lower lip or of the 2d pair of maxillæ; *stl*, stems of the same fused in the middle line; *stm*, stems of 1st pair of maxillæ; *me*, *mi*, outer and inner ridges of the same.

Diplopoda.—The mouth parts are here complicated and difficult to explain. The powerful upper jaw is followed by the lower lip (gnathochilarium, Fig. 305). This lower lip is said by some observers to consist of only 1 pair of maxillæ. Others explain the pieces represented in the figure in such a way that the paired halves of the middle piece, each of which is provided with a masticatory ridge, correspond with the stem pieces of the posterior maxillæ (lower lip), and the 2 lateral pieces each provided with 2 masticatory ridges with the stem portions of the anterior maxillæ, the palps being absent. Although this last view, which rests upon analogous modification of the 2 pairs of maxillæ in certain beetle larvæ (*Elateridæ*), is preferable from the point of view of comparative anatomy, it is not yet quite certainly established. The developmental history, as far as it is as yet known, seems rather to support the first view, since the mandibles and the gnathochilarium of the *Diplopoda* are said to come from the rudiments of 2 pairs of feet. A comparison of the mouth parts of the *Myriapoda* on a new ontogenetic basis is urgently needed.

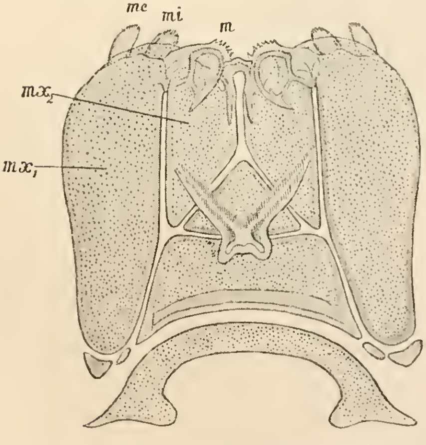


Fig. 305.—**The Gnathochilarium of Lysiopetalum carinatum (Diplopoda, after v. Rath).** mx_1, Stem of the anterior; mx_2, of the posterior maxillæ (?); *me* and *mi*, outer and inner masticatory ridges of the anterior maxillæ; *m*, masticatory ridge of the posterior maxillæ (lower lip).

Hexapoda.

Apterygota.—The mouth parts of the Apterygota are adapted for mastication and agree in all essential points with the Orthopteran type above described. The composition of the lower lip out of 2 maxillæ is especially clearly shown in the *Aptera.* Both pairs of maxillæ possess well developed palps.

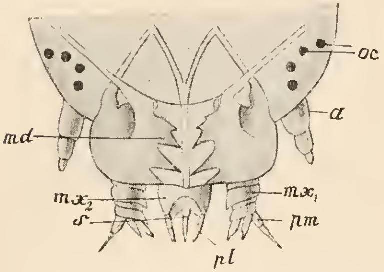


Fig. 306.—**Mouth parts of a Macrolepidoptera larva (Ocneria).** Lettering as in Figs. 303 and 309.

Pterygota.—The mouth parts of the *Orthoptera* were described and illustrated above. As, however, the mouth parts of other orders of the *Insecta* deviate markedly from these, it is necessary to describe the more typical forms or arrangements.

A knowledge of the mouth parts of a small family of the *Microlepidoptera*, the *Micropterygina*, throws light on the mouth parts of the *Lepidoptera.* We here still find the typical parts: (1) **toothed mandibles**, capable of mastication; (2) anterior **maxillæ**, with separate basal portions, with 6-jointed palps and 2 separate masticatory ridges; and (3) a **lower lip** (posterior maxillæ) whose basal portions are fused into one common piece, but carry 3-jointed palps and masticatory ridges still distinctly separate. The 2 inner ridges have grown together and form a short tube. In the other *Microlepidoptera* the mandibles lose their teeth and become rudimentary. On the anterior maxillæ only 1 ridge is found. The ridges

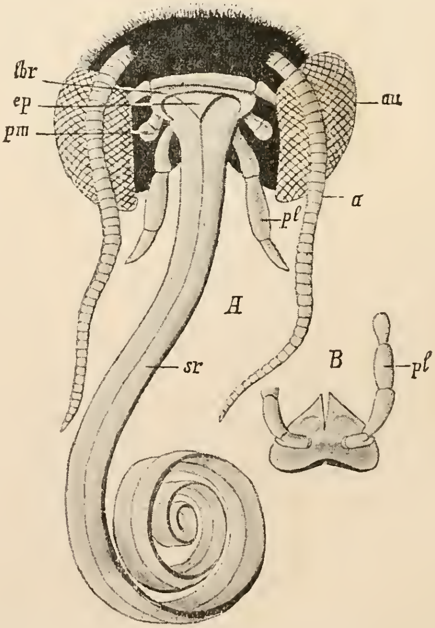


Fig. 307.—*A*, **Mouth parts of the Macrolepidoptera.** *B*, The lower lip (2d pair of maxillæ), isolated. Lettering as before. *sr*, Sucking proboscis, corresponding with the fused ridges of the 1st pair of maxillæ.

of the 2 pairs of maxillæ fit together to form a sucking proboscis which can easily be coiled up. In the *Macrolepidoptera* the mandibles have disappeared, but the sucking proboscis formed by the 2 ridges of the anterior maxillæ is on the contrary very strongly developed and capable of being coiled. The maxillar and labial palps are nearly always retained, the former generally in a very reduced condition (1-jointed in the *Sphingina* and many *Rhopalocera*). In some of the latter the maxillar palp has, however, altogether disappeared.

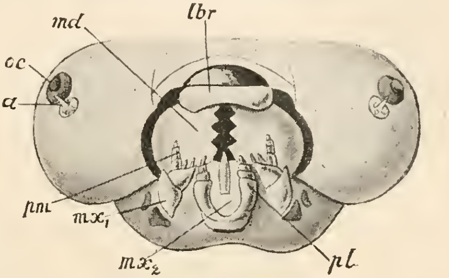


Fig. 308.—**Mouth parts of a Tenthredo larva.** Lettering as before.

A series analogous to that of the Lepidoptera is afforded by the *Hymenoptera*. At the head of the series stands the *Tenthredinidæ*, whose mouth parts show great agreement with those of the *Micropterygina*. Besides the mandibles which, as in the other *Hymenoptera*, are adapted for biting, we find anterior maxillæ, on whose basal portions 6-jointed palps and 2 maxillar ridges are quite distinct. On the posterior maxillæ (lower lip)

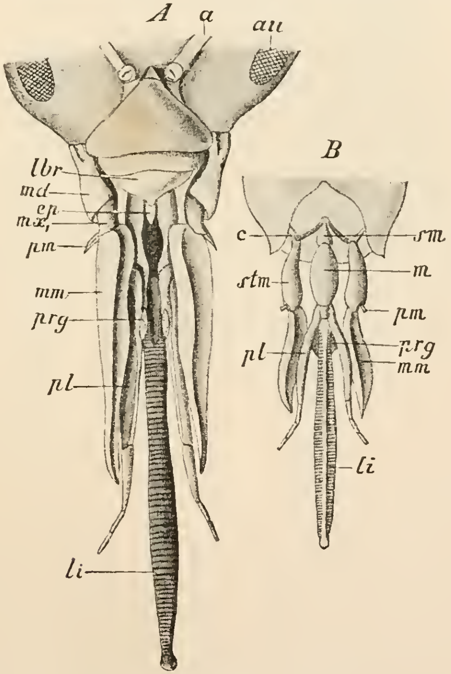


Fig. 309.—*A*, **Mouth parts of the Hymenoptera (Apis melifica).** *B*, The two pairs of maxillæ. *au*, Facet eye; *a*, antenna; *lbr*, upper lip; *md*, mandible; *ep*, epipharynx; mx_1, anterior maxillæ; *pm*, palp of the same; *mm*, the fused ridges of the same; *prg*, paraglossa = outer ridge of the posterior maxillæ (labium or lower lip); *li*, tongue (glossa) = inner ridge of the posterior maxillæ; *c*, cardo; *sm*, submentum; *m*, mentum; *stm*, stem (stipes) of the anterior maxillæ.

the basal portions are fused, the 2 4-jointed palps are well retained, the outer masticatory ridges are separate, but the 2 inner ridges fuse to form a tube. In the other *Hymenoptera* (Fig. 309) the mandibles are always retained in a condition capable of masticating or biting; both the maxillæ go to form sucking or licking mouth parts. The palps on the anterior maxillæ become reduced, the basal portions elongate and the masticatory ridges grow together on each side into a long piece (*mm*). On the under lip also the basal portion elongates, the feeler remains well developed, and slender, 2-4 jointed; the inner ridges together form the long tongue, and the outer ridges small lateral appendages to it, called the accessory tongues **(paraglossa).**

The mouth parts of the *Diptera* (Fig. 310) are adapted for piercing and sucking, and together form a peculiar proboscis. The bristle-shaped mandibles in the male, and occasionally in both sexes, are wanting as separate pieces, and are then no doubt fused with the upper lip. The proboscis is principally formed out of the following parts much elongated: first, the upper lip; second, the basal portion of the lower lip, 2 lips (labella) at the end of this representing the transformed palps; and third, a prolongation of the lower œsophageal wall (hypopharynx), developed into a piercing setæ, at whose point the salivary vessels emerge. The anterior maxillæ form 2 slender setæ, which lie together with the seta-like mandibles in the sucking proboscis. Their 1-5-jointed palps are mostly well developed.

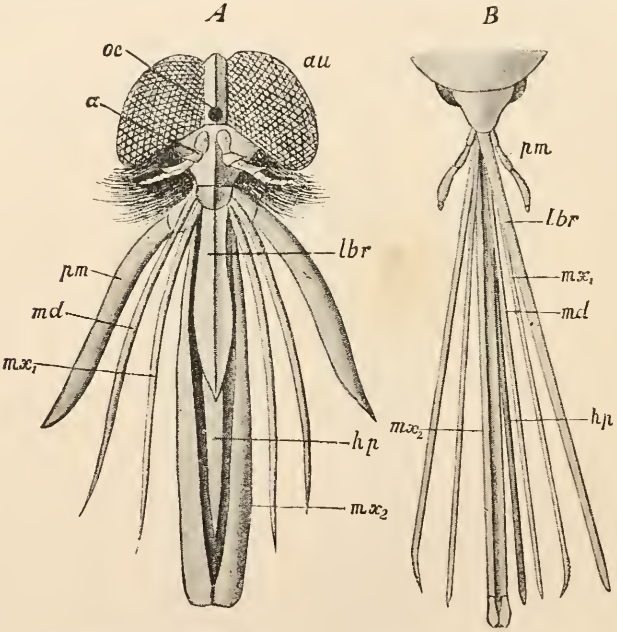


FIG. 310.—**Mouth parts of the Diptera.** *A*, **of Tabanus.** *B*, **of Culex.** Lettering as before. *a*, Antenna, *au*, facet eye; *oc*, simple eye (ocellus).

The mouth parts of the *Rhynchota* (Fig. 311) together form a proboscis adapted for piercing and sucking. The elongated, generally 4-jointed lower lip (posterior maxillæ) forms a channel in which lie the mandibles and interior maxillæ, transformed into setæ covered at their basal part by the upper lip (labrum).

The mechanism for sucking and stinging, which is occasionally very complicated, and to which certain adaptations in the œsophagus (pumps, "fish trap" apparatus, etc.), belong, cannot be here more exactly described.

The mouth parts of the other *Hexapoda* must be referred to one or other of the types depicted.

The mouth parts of the *Coleoptera* are for biting and masticating, similar to those of the *Orthoptera*; the masticatory ridges of the anterior maxillæ are rarely transformed into a sucking tube.

The mouth parts of the *Dermaptera*, *Ephemeridæ*, *Odonata*, *Plecoptera*, *Corrodentia*, *Neuroptera*, and *Panorpata* are also adapted for biting, and belong with various deviations to the type of those of the *Orthoptera* and *Coleoptera*.

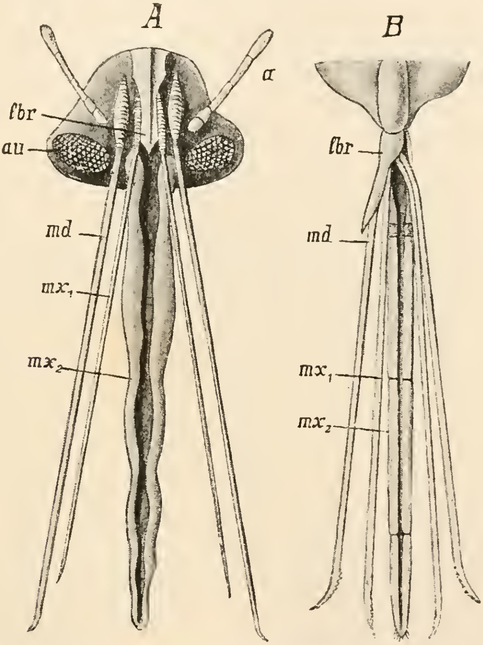


FIG. 311.—**Mouth parts of the Hemiptera.** *A*, of **Pentatoma**. *B*, of **Pyrrhocoris**. Lettering as before.

The mouth parts of the *Thysanoptera* (*Physopoda*) hold a position intermediate between the biting mouth parts of the *Orthoptera* and the sucking mouth parts of the *Rhynchota*. The mandibles are changed into piercing setæ, and come to lie within a short tubular proboscis, which arises by the growing together of the upper lip with the anterior maxillæ and the lower lip (posterior maxillæ). The 2 pairs of maxillæ have distinct palps and otherwise generally show the typical parts variously modified. In the *Trichoptera* the mandibles are rudimentary, the 2 pairs of maxillæ together form a sort of proboscis (for piercing and sucking), the 4 palps remaining separate on it. The palps, however, as well as the proboscis itself, may disappear.

In the *Aphaniptera* (Fleas) the mouth parts are for piercing and sucking. The mandibles are toothed ridges which, together with the upper lip form the sucking tube. The anterior maxillæ are short and ear-shaped with 4-jointed palps. The 2 many-jointed palps of the small lower lip lie on the sucking tube laterally.

The various piercing and sucking mouth parts found among Insects have no doubt developed independently of one another from masticatory mouth parts.

The special morphology of the mouth parts is therefore necessary for a knowledge of the relationships of the members of one and the same order, but not for a knowledge of the phylogeny of the Insect-orders themselves.

It sometimes occurs that the larvæ of certain Insects (*Megaloptera* among the *Neuroptera*) have sucking mouth parts while the adults possess biting mouth parts. This is an interesting fact, which shows how within a small group the larvæ may develop sucking mouth parts in adaptation to special conditions of existence. In those *Lepidoptera*, *Diptera*, *Aphaniptera*, and certain *Hymenoptera* which are provided with sucking mouth parts, those of the larvæ, when not degenerated, are of the biting type.

2. The Limbs of the Trunk.

In the ancestors of the Antennata (*Myriapoda* and *Hexapoda*) in every case each trunk segment was certainly provided with a pair of limbs, as is still the case in *Peripatus* and in the *Myriapoda*.

In the *Hexapoda* only the 3 pairs of limbs of the 3 anterior trunk segments have been retained, these 3 segments together forming the thorax. Rudiments of extremities, however, are not wanting, as we shall presently see, on the segments of the hind-body even in the *Hexapoda*.

The trunk limbs are throughout distinctly jointed and consist of several parts, whose number and constitution is extremely important in classification. The legs may be variously formed according to their special functions. We thus distinguish ambulatory, springing, swimming, seizing legs, etc. Among the *Myriapoda* the 1st pair of trunk feet in the *Chilopoda* moves to the head as a pair of maxillipedes (Fig. 323, p. 464). These are very strong, and shaped like pincers. Their basal segments are fused together into a plate in the middle line. A poison gland lying in the maxillipede itself emerges at its terminal claw.

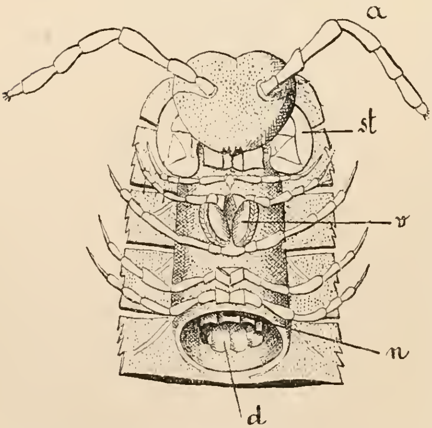


Fig. 312.—**Anterior end of the body of a female Polydesmus complanatus**, from the ventral side (after **Latzel**). *a*, Antennæ; *st*, stems of the mandibles; *v*, vulvæ (apertures of the female sexual organs); *n*, ventral chord; *d*, intestine.

In the *Diplopoda* (Fig. 312) the double segments (*i.e.* the rings following the 4th or 5th trunk rings) have each 2 pairs of legs, while the 4 or 5 anterior rings are only provided with 1 pair each. One of the 4 or 5 anterior rings—in the *Iulidæ* it seems to be the 4th —may be limbless. The extremities of the 7th ring are usually transformed in the male into copulatory organs.

Rudiments of abdominal limbs in the Hexapoda.

In order to prove the existence of such rudiments we must recall the coxal glands emerging on the legs of *Peripatus*. Similar glands emerge in the *Chilopoda* on the coxæ of the 4 or 5 last pairs of legs, on the pleura of the last leg-bearing segment, and on the anal segment. In the *Diplopoda* these glands apparently correspond with the protrusible warts which occur in the *Lysiopetalidæ* on the coxal joints of the 3d-16th pairs of legs, and also with the pores on the coxæ of the *Chordeumidæ*. A knowledge of these organs in the *Symphyla* (*Scolopendrella*), which perhaps of all living Antennata stands nearest the common racial form of the *Myriapoda* and the *Insecta*, is extremely important. On the coxal joints of the legs in *Scolopendrella* protrusible saccules, apparently glandular (Fig. 313, *cd*), can be distinctly made out, especially on the 3d-11th pairs. Laterally from these saccules, which must be homologous with the coxal glands of other *Myriapoda* and of *Peripatus*, there is a stylet-shaped appendage *hs*, which must be considered as a modified process of the coxal joint (coxal spur). In addition to these coxal saccules, *Scolopendrella* possesses 2 spinning glands, which emerge externally (*dg*) at the point of the spinning processes (*sg*), on the terminal segment of the body. These glands also probably belong to the category of coxal glands, and thus the spinning processes probably represent the last pair of limbs considerably transformed. The coxal saccules of *Scolopendrella* and the coxal glands of the *Myriapoda* and *Protracheata* (*Peripatus*) now throw much light on similar arrangements in the lowest *Hexapoda*, the *Apterygota*. In *Campodea* there are in the first abdominal segment two indistinctly jointed appendages which are rudimentary extremities. In the subsequent abdominal segments as far as to the 8th there occurs on each side ventrally a protrusible saccule on whose outer side lies a movable pointed process. These saccules evidently correspond with the coxal glands of *Scolopendrella*, and are to be considered as degenerated coxal glands, while the

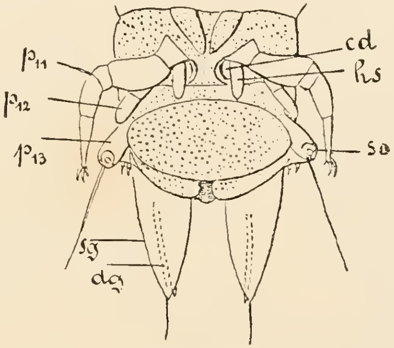
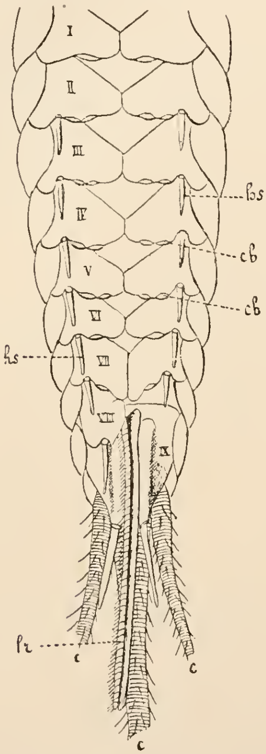


FIG. 313.—**Posterior end of body of Scolopendrella immaculata**, from the ventral side (after **Latzel**). p_{11} 11th, p_{12} 12th undeveloped, pairs of legs, p_{13}, transformed legs (13th pair) carrying organs of touch (*so*) ; *sg*, spinning processes with the duct (*dg*) of the spinning gland ; *cd*, coxal gland : *hs*, coxal spur of the 11th pair of legs.

pointed process answers to the coxal spur of *Scolopendrella*. The coxal saccules and spurs of *Campodea* must therefore be regarded as remains of coxal joints of abdominal limbs, in short, as rudiments of coxæ. Similar organs are also found in other *Aptera* (Figs. 314 and 315), principally in the *Thysanura*. On the other hand, the coxal rudiments may be wanting or be limited sometimes to the saccules and sometimes to the spurs. It is interesting also to relate that the above-mentioned processes on the abdominal segments of the *Thysanura* were by many observers at once assumed to be degenerated abdominal feet.



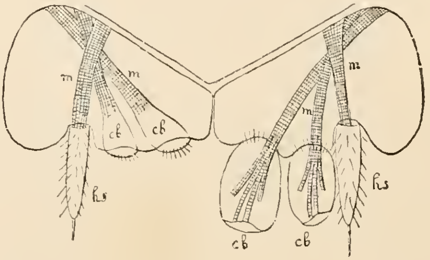


Fig. 315.—**A ventral shield of Machilis maritima,** with two protrusible saccules (*cb*) on each side. On the left the saccules are withdrawn, on the right protruded. *hs*, movable appendages (coxal spurs), muscles of the same and of the protrusible saccules (after **Oudemans**).

Fig. 314.—**Ventral side of the hind-body of a female Machilis maritima** (after **Oudemans**). The left half of the 8th ventral shield is removed. *I-IX*, segments of the abdomen; *c*, bristle-like jointed appendages (cerci) of the 10th abdominal segment; *cb*, protrusible saccules = coxal glands in the act of degenerating; *hs*, movable appendages = coxal spurs, conjectural rudiments of abdominal feet; *lr*, ovipositors.

In the **winged Hexapoda** (*Pterygota*) rudiments of abdominal feet have also been observed. They appear at certain embryonic stages exactly like the rudiments of the thoracic feet, *i.e.* as prominences or stumps on the most anterior, or on several anterior, or on all the abdominal segments, sooner or later again to disappear. They have been observed in *Coleoptera* (*Hydrophilus*, Fig. 316, *A* and *B*, *Melolontha*), *Orthoptera* (*Gryllotalpa*, *Mantis*, *Periplaneta*, *Œcanthus*, *Blatta*), and *Trichoptera* (*Neophalax concinnus*). In a few forms (*Gryllotalpa*, *Œcanthus*, *Periplaneta*, *Blatta*, *Melolontha*) the rudiments of the 1st pair of abdominal feet, before the hatching of the embryo, become short stalked vesicles of considerable size, which may be compared with the protruded coxal sacs of the *Thysanura*. A respiratory function has without sufficient foundation been ascribed to both these structures.

Considering the widespread occurrence of rudimentary abdominal feet in the **Embryos** of winged Insects we are justified in asking the question, whether the truncated feet (anal feet) of the larvæ of butterflies and wasps are not rather the remains of real limbs than new formations.

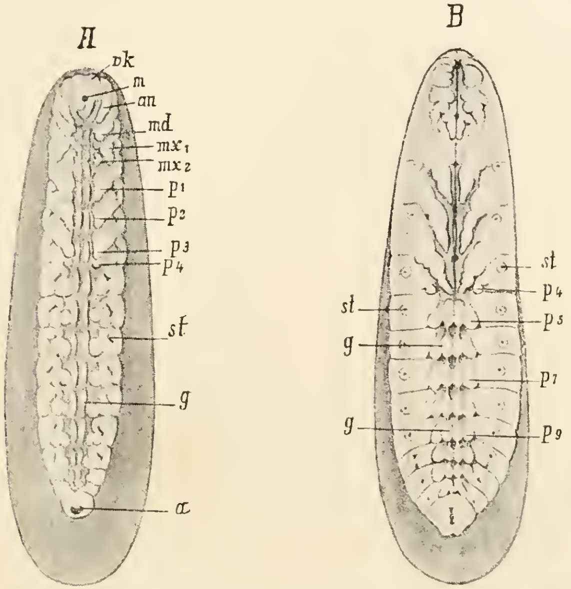


Fig. 316.—*A* and *B* **Hydrophilus embryos with the rudiments of extremities** (after **Heider**). In the somewhat older embryo, *B*, the rudiments of abdominal feet, which disappear later, can be very distinctly seen; *a*, anal aperture; *an*, antenna; *g*, rudiment of the ventral ganglionic chain; *m*, oral aperture. *md*, Mandible; mx_1, 1st maxillæ; mx_2, 2d maxillæ (rudiment of the lower lip); p_1, p_2, p_3, thoracic pairs of legs; p_4, p_5, p_7, p_9, rudiments of extremities of the 1st, 2d, 4th, and 6th abdominal segments; *st*, stigmata; *vk*, procephalon.

C. The Wings.

Wings are altogether wanting in the *Myriapoda*. Among the *Hexapoda* the *Apterygota*, as their name implies, are entirely wingless. Since neither the adult *Apterygota* nor the embryos at any stage of their development have wings or organs belonging to wings, we are justified in assuming that their ancestors also were wingless, in short that the wingless state is as much the original condition here as in the *Myriapoda* and *Protracheata*. This assumption is not without support from other points in their constitution. All other *Hexapoda*, however, are typically provided with wings, and originally indeed with 2 pairs, and although within the different orders of the *Pterygota* the wings may be reduced to 1 pair, or may be entirely wanting (in both sexes or only in the female), we here have to do with a derived condition and with animals which have lost the wings once possessed by their ancestors. In such insects the rudiments of wings or of organs belonging to wings can often still be pointed out.

The wings are thin lamellate unjointed folds of the body wall, specially of the integument. The 2 lamellæ of a wing fold lie close to each other. The wings are veined like the leaf of a plant. The veins for the most part are thickenings of the chitinous cuticle. Within the narrow interior space of the wing, nerves and especially **tracheæ** enter, branching like the veins. Blood-vessels also accompany the veins. The arrangement of the veins is very important for classification. The exact investigation of the courses of the veins and their development, and especially the observation of rudimentary veins or veins in the act of disappearing, have led to the result that the wings of the various *Hexapodan* orders must be traced back not from one to the other, but to a common form of wing. Thus the examination of wings confirms the assumption that all orders of winged insects are derived from a common winged racial group.

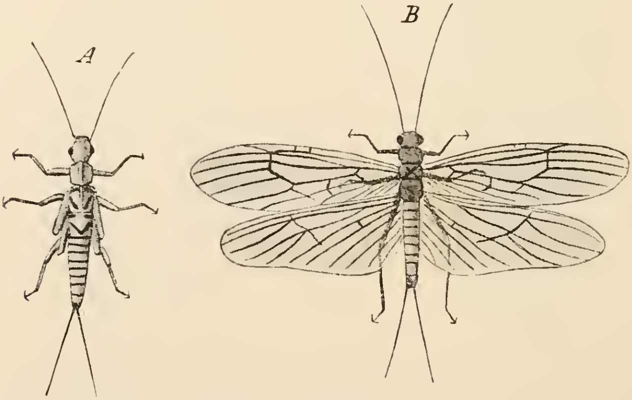


Fig. 317.—*A*, **Larva.** *B*, **female imago of Capnia nigra** (Perlid) (after **Pictet**).

The 2 pairs of wings are appendages of the meso- and meta-thorax of the Insects. There are never more than 2 pairs. Their narrowed basal portions are articulated with the dorso-lateral parts of the meso- and meta-thorax. Strongly developed wing muscles serve to move them (see section on musculature).

The problem of the **phylogenetic origin of the wings of insects** is extremely difficult, and as yet by no means solved. The rise of such organs is not explained by saying that they are integumental folds, which gradually increased in size, stood out from and eventually articulated with the body. The wings must in all stages of their phylogenetic development have performed definite functions. It is impossible that they were originally organs of flight. What function it was they performed before they became exclusively organs of flight is, however, entirely a matter of conjecture. The following view is at present the most acceptable. (1) The ancestors of the *Hexapoda* were, like the now living *Apterygota*, wingless land animals breathing through tracheæ. (2) The *Apterygota*-like ancestors of the *Pterygotan* racial group became adapted to living in water. Dorsal integumental folds served for breathing in the water. The rise of such respiratory folds offers no difficulty, since every increase of surface, small or large, is of service. (3) The respiratory appendages (into which tracheæ were continued) became movable and may perhaps have assisted in locomotion (swimming). This assumption also offers no difficulty, since the gills of many aquatic animals are movable, and their power of moving is an advantage on account of the exchange of water thus caused. (4) In a new gradual change to land life the respiratory function became less important and the locomotory function came to the front. Here, however, lies the greatest difficulty. It may, however, be assumed, that the animals while still living in water were capable of gliding over the surface of the water by the swinging of their branchial leaves, just as flying fish do by means of their thoracic fins.

The limitation of the wings to the 2 pairs of the meso- and metathorax must be explained mechanically, as more suited for the propulsion of the body in flight. We still see among living insects an undoubted tendency to the stronger development of one of the pairs of wings.

The so called **tracheal gills** of the larvæ of the *Phryganidæ*, *Sialidæ*, and *Ephemeridæ* may serve as an example for this conjectural formation of integumental folds serving for breathing in water. The *Phryganid* larvæ live in the water in tubes of their own construction, and possess on their soft-skinned abdomens thread-like appendages into which tracheal branches enter. Such appendages are called **tracheal gills.** Similar appendages are found on the abdomens of the Sialid larvæ. In the *Ephemerid* larvæ, which live free in water, there are found, on the segments of the hind-body, 6 or 7 pairs of lateral, movable, tracheal gills (Figs. 318, 342, 343), which are sometimes tufted, sometimes leaf-shaped, sometimes thread-like. An anterior pair may even be developed as a sort of branchial cover for the posterior pairs. All these tracheal gills are evidently integumental folds and respiratory organs which have arisen as adaptations to aquatic life. When they are leaf-shaped, the tracheæ which enter them branch more or less richly. They begin to form in a manner altogether similar to ordinary wings, and persist in the later larval stages together with the wing rudiments (Fig. 318).

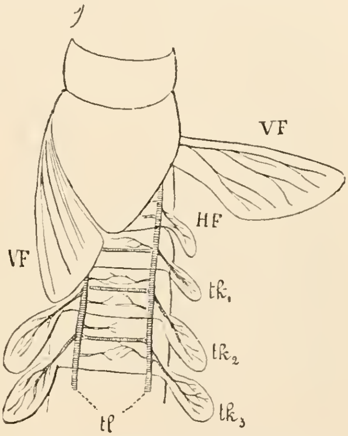


FIG. 318.—**Thorax and anterior abdominal Segments of the Larva of Cloeon dimidiatum** (*Ephemerid*), with tracheal gills (tk_1, tk_2, tk_3) and the rudiments of the fore-wings (*VF*) and hind-wing (*HF*). *tl*, Tracheal longitudinal trunks (after **v. Graber**).

Unsuccessful attempts have been made to trace back the wings of Insects to other organs in other more or less remote animals, *e.g.* to the dorsal gills of the *Chætopoda* or to the dorsal folds of the Crustacea. If there is any such connection the rudiments of the wings as primitive organs ought to appear in Insect embryos; this, however, is not the case.

Some information has already been given in the Systematic Review about the special form and arrangement of the wings in the various orders of the *Insecta*.

II. The Integument and Glands.

The integument is of the same type as that of the *Crustacea* and all other *Arthropoda*, the body being covered by a chitinous cuticle forming an **exoskeleton**. This cuticle is of varying flexibility and thickness, and shows many and great modifications, not only in the various parts of the body and limbs of the same animal, but among the different members of the class. A knowledge of the constitution of the exoskeleton in the various parts of the body is of great importance in classification, as is also a knowledge of the setæ, hairs, scales, etc., which belong to the category of cuticular formations. The epithelium which secretes the chitinous cuticle is here also called the hypodermis.

During **ecdysis**, which accompanies the metamorphoses of the *Antennata* and the growth of the larvæ, the whole exoskeleton is thrown off, together with the chitinous intima of that part of the intestine thus lined, the chitinous intima of the tracheæ, and the ducts of the glands. The chitinous integuments thrown off are known as **exuvia.**

Dermal glands are widely spread in the *Antennata*; they appear in a great number of modified forms, emerge at the most various points of the body, and form secretions differing greatly in constitution. A comparative study of these on a wide basis is urgently needed. Investigation is especially needed as to which glands in the Antennata correspond with the coxal and spinning glands of *Peripatus*, and which glands, if any, are to be considered as transformed nephridia. At present the observations in comparative anatomy and ontogeny necessary to enable us to give a definite answer to these questions are wanting.

Among the glands emerging on the outer integument we may first mention the **salivary glands,** which open in the immediate neighbourhood of the mouth. They are everywhere found in the Antennata, generally lying at the side of the fore-gut, in the head or thorax, and occur in 1-3 pairs. They are either simple or much lobed acinose glands, or else fall on each side into 2 or more glandular sacs. The ducts of the glands of each side, however, nearly always unite in a common duct, which finally unites with the duct from the other side to form an unpaired canal, which usually emerges externally on the lower lip or the hypopharynx, but in any case in the immediate neighbourhood of the mouth. Not infrequently a vesicular appendage (saliva reservoir) is found on each side of the canal. It sometimes happens that there are two separate apertures for a single pair of salivary glands, the unpaired terminal portion being absent. Where there are several pairs of glands, their ducts may also emerge separately; usually, however, the ducts from each pair unite to form a common terminal portion.

The salivary glands are, as far as their development is known, invaginations of the oral edge of the stomodæum. According to some observations, it appears that the unpaired duct forms secondarily, the 2 salivary glands proceeding from paired rudiments.

Spinning glands (sericteries) occur in many Insect larvæ, and are specially strongly developed in those which pass through a pupa stage (*e.g.* caterpillars of *Lepidoptera* and larvæ of *Tenthredinidæ*). The thread-like secretion of these glands, which hardens when exposed to the air, forms the web of which the pupal envelope consists, but it may also serve for other purposes. The sericteries are glandular tubes which are paired, elongated, and coiled, often running through the whole length of the body; the glandular cells of their epithelium often attain to an enormous size, and have cell nuclei in the form of branched networks. The 2 ducts unite, like those of the salivary glands, to form an unpaired terminal duct, whose aperture also lies near the mouth. Accessory glands may also open into the ducts of the sericteries. The ducts of these and other dermal glands have a chitinous intima, which, like the tracheal intima, may become thickened in a close spiral line.

The spinning glands of *Scolopendrella* have already been mentioned when describing the rudimentary abdominal limbs. The glands there mentioned as emerging through pores at the points of stylets on the anal segment, and through the pleural pores of the last leg-bearing segment, are also said to be spinning glands.

Recalling the *Protracheata*, we are led to suppose that the salivary glands of the Antennata are transformed nephridia, and that the spinning glands belong to the same category as the coxal glands of *Peripatus* and the parapodial setiparous glands of the *Chaetopoda*. Compare also on this subject the section on the rudiments of abdominal limbs in the *Hexapoda*.

The morphological worth of the other numerous dermal glands which have been observed in the Antennata cannot at present be rightly estimated. We can only name a few of them.

The *Myriapoda* (*Diplopoda*) have **stink glands** for protection, which emerge through the "foramina repugnatoria" on the dorsal side of a varying number of trunk segments. These foramina are either paired, in which case they lie laterally, or unpaired in the middle line. In *Paradesmus gracilis* the secretion of the protective glands contains prussic acid. These protective glands, of which only 1 pair occurs in a double segment, have been regarded as modified nephridia.

The glands of the *Geophilidæ* among the *Chilopoda*, which emerge through unpaired median ventral pores, may perhaps belong to the category of protective glands.

Stink glands, which yield a strongly smelling secretion evidently serving as a protection to the animal, are also found in many Insects (especially *Heteroptera*, *Coleoptera*, and *Orthoptera*). They are sometimes paired, sometimes unpaired, and emerge at different points of the body. In many *Coleoptera* these organs are appendages of the rectum. An enumeration of the recorded observations, however, could at present yield nothing of special interest to the comparative anatomist.

Poison glands.—The maxillipedes of the *Chilopoda* contain poison glands whose outer aperture lies in the terminal claws. In the female of many *Hymenoptera* a poison gland occurs, which pours its secretion into a stinging apparatus of complicated structure placed at the posterior end of the body. The poison gland itself consists of 2 simple or branched glandular tubes, which enter a poison vesicle or reservoir by means of a common unpaired terminal piece (*cf.* Fig. 347, A, p. 487).

Leg glands are found in many Insects on the terminal joints of the thoracic legs.

Wax glands occur in many *Rhynchota* (*Aphides*, *Coccidæ*). They lie either on the back in cross rows, or near the anus, and secrete filaments, plates, etc., of wax; these are used either for forming a dorsal shield or a down which covers the body, or for enveloping the excrement.

Rectal glands are papillæ or thickenings with glandular epithelium, very commonly found in the rectum of Insects.

In *Mantis* glands enter the coxæ of the 1st pair of legs (coxal glands?).

III. The Musculature.

The arrangement of the muscles in the body and their relation to the exoskeleton is the same in the Antennata as in the *Crustacea* (*cf. Crustacea*, p. 331). The musculature seems to be broken up into a very great number of single muscles, which are arranged in a definite manner suitable for moving the segments, the regions of the body, the limbs and their separate joints, the mouth parts, the ovipositors, stings, etc. The greater part of the muscles of the body can be traced back to a paired system of dorsal and ventral intersegmental longitudinal muscles. While in the *Myriapoda*, in accordance with the homonomous segmentation of the body, the musculature is repeated in all the trunk segments, in the *Hexapoda* the musculature is very differently developed in the head, thorax, and abdomen. The musculature of the thorax is very strong, as might be expected from the fact that its 3 segments carry the limbs and wings. The **wing muscles** generally take a dorso-ventral course in the lateral portions of the thorax. The most important parts among them are played by the elevators and depressors.

The musculature is transversely striated.

IV. The Enteric Canal.

The **mouth** lies in the head between the mouth parts; the **anus** always in the terminal segment of the abdomen. The enteric canal, in most *Myriapoda* and in the *Apterygota*, runs straight through the body and thus is not longer than the body. In the Pterygota, on the contrary, it generally forms more or less marked loops which are wanting or not so strongly developed in the larva. It everywhere falls into the 3 already known divisions: the **fore-gut**, which comes from the ectodermal stomodæum; the endodermal **mid-gut** and the **hind-gut**, coming from the ectodermal proctodæum. These 3 divisions are generally distinct. Each of them can be further subdivided, especially in the *Hexapoda*, where special organs in the form of diverticula are always to be found. Tubular and pouch-like diverticula of the hind-gut (wanting only in a few *Apterygota*) are especially characteristic of the Antennata. They appear in varying numbers, function as excretory organs, and have received the name of the **Malpighian vessels.** The salivary glands and the spinning glands of the larvæ, both of which emerge at or near the mouth, have already been described.

Myriapoda.—The enteric canal runs straight through the body; only in the *Glomeridæ* is it coiled in its posterior part. The mid-gut has numerous short hepatic tubes. At the beginning of the hind-gut 1 or 2 pairs of long Malpighian vessels enter; these run along the gut, frequently winding round it.

Hexapoda.—Each of the 3 principal divisions of the enteric canal may present various modifications, except in the *Apterygota* and the larvæ of those *Insecta* whose straight enteric canals present no complications. The canal is most specialised in carnivorous *Insecta*, while in those *Insecta* that feed on plants it is generally uniform, but much coiled.

The fore-gut often has 3 divisions: (1) a **pharynx** or **oral cavity**, (2) a narrow **œsophagus** passing through the œsophageal ring, and (3) a variously shaped **fore-stomach** widened out like a sac. The latter may be wanting as a separate division. If the fore-stomach is provided with a strong muscular wall it is called a **crop** (ingluvies). In the honey bee it is called the **honey stomach**. In *Insects* with sucking mouth parts, and especially in the *Lepidoptera* (Fig. 348, p. 488) and *Diptera*, it is constricted off in the form of a stalked sac, which opens into the posterior part of the fore-gut and is unsuitably called **sucking stomach**; it is more correctly a receptacle for food. Between the crop and the mid-gut in many carnivorous *Insecta* (many *Coleoptera*, *Neuroptera*, and *Orthoptera*) a muscular **masticatory stomach** is interposed; the chitinous intima of this stomach is much thickened, and in the form of spikes, spines, ridges, teeth, etc. projects into the lumen; these processes in transverse section form most beautiful and ornamental patterns. A peculiar **pumping apparatus** is in a few *Rhynchota* connected with the pharynx. The fore-gut is internally provided with a chitinous intima, the continuation of the chitinous exoskeleton.

The mid-gut, which lies in the abdomen, is the most important division of the enteric canal for the assimilation of food; its epithelium consists of glandular cells and often projects into the lumen in the form of folds or villi. It is a somewhat wide tube frequently forming loops, and in it we can often distinguish an anterior wider portion, the **chyle stomach**, and a longer thinner posterior portion (**small intestine**). The chyle stomach in the carnivorous *Coleoptera* is beset with short diverticula, as if with villi; in the *Orthoptera* longer diverticula enter its anterior portion.

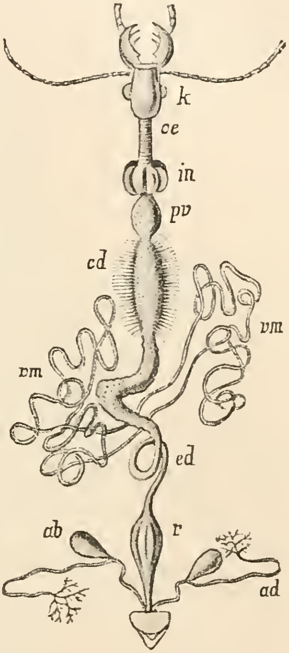


FIG. 319.—**Digestive apparatus of Carabus auratus** (after **Dufour**). *k*, Head with mouth parts; *oc*, œsophagus; *in*, crop (ingluvies); *pv*, masticatory stomach; *cd*, chyle stomach covered with villi; *vm*, Malpighian vessels; *ed*, hind-gut with rectum (*r*); *ad*, anal glands with muscular vesicular appendages *ab*.

The **hind-gut** is lined with a delicate chitinous intima and has a muscular wall which, at the terminal portion ending in the anus, is of considerable thickness. Its length varies, it is often very long and coiled.

The limit between the mid- and hind-guts is often difficult to define, since the mid-gut also may have an intima, and its ontogenetic development is not sufficiently worked out. It is assumed, somewhat arbitrarily, that the hind-gut begins at the point where the Malpighian vessels enter. Although these are undoubtedly formations of the hind-gut, they do not necessarily always appear at its anterior end. The hind-gut is often further subdivided. Its last division sometimes carries an unpaired cæcum. Paired anal glands (stink glands) may also enter it. The anal papillæ, etc. classed as glands have already been mentioned. The intestine of certain *Rhynchota*, *Psyllidæ*, and *Cicadæ* is peculiarly constituted. The mid-gut and part of the hind-gut form a loop (Fig. 322). The 2 limbs of the loop grow together for a certain distance, and wind round each other at this part.

In the larvæ of some *Hymenoptera*, *Neuroptera*, *Myrmeleon*, and *Diptera* (*Pupipara*) the mid-gut ends blindly and is not yet connected with the hind-gut, the latter performing exclusively excretory functions (Fig. 321).

The Malpighian Vessels.—These are long, generally filamentous appendages, which begin to form as invaginations of the proctodæum. Their large epithelial cells (with nuclei often branched) contain coloured concretions in which uric acid is found. The Malpighian vessels occasionally have no distinct lumen ; they then consist of a few rows of cells. The number of the Malpighian vessels is as varied as their manner of entering the hind-gut.

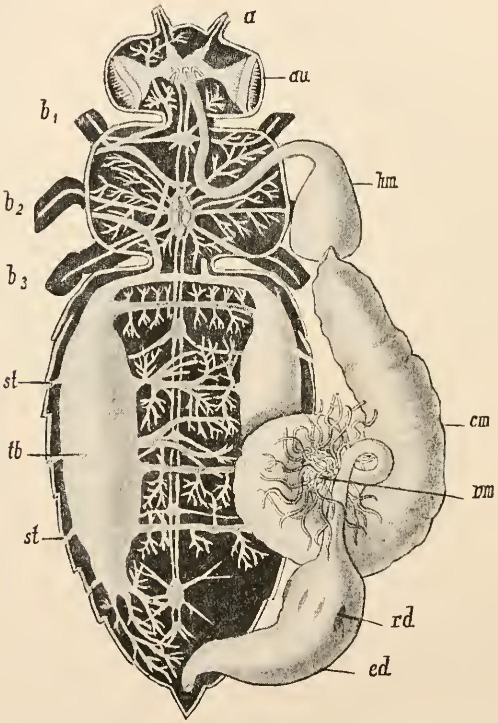


Fig. 320.—**Nervous, tracheal, and digestive systems of the Honey bee** (after **Leuckart**). The fine branchings of the tracheal system are not represented, the tracheal system on the right side of the figure is only partly drawn. *au*, Facet eye ; *a*, antenna ; b_1, b_2, b_3, the 3 pairs of legs ; *tb*, part of the tracheal longitudinal trunks swollen into a large vesicle ; *st*, stigmata ; *hm*, honey stomach ; *cm*, chyle stomach ; *vm*, Malpighian vessels ; *rd*, rectal glands ; *ed*, hind-gut.

Apterygota.—Malpighian vessels are wanting in *Iapyx* and the *Collembola*. In *Campodea* there are ca. 16, and they are here short ; in the other *Thysanura* they are long and 4-8 in number. The tubules always unite in pairs before entering the hind-gut.

Pterygota.—The Malpighian vessels are either very numerous and relatively short or less numerous (2-8) and long. They are more numerous in the *Dermaptera* (ca.

30), *Ephemeridae* (ca. 40), *Odonata* (50-60), *Plecoptera* (40-50), *Orthoptera* (30-50 or more), and *Hymenoptera* (very numerous, often over 100, seldom below 12). On the other hand few (*i.e.* 2-8) are found in the *Corrodentia* (4-6), *Thysanoptera* (4), *Rhynchota* (2-4), *Neuroptera* (4-6), *Panorpata* (6), *Trichoptera* (6), *Lepidoptera* (6, seldom 2 or 4), *Diptera* (4 or 5), *Siphonaptera* (4), and *Coleoptera* (4-6). They generally enter the hind-gut separately, but occasionally the vessels of each side unite into a common duct, and sometimes the ducts from the two sides also have a common unpaired terminal piece. Here and there the vessels open into a paired or unpaired urinary bladder attached to the hind-gut. In the *Aphides* there are on each side 2 vessels which unite together before entering a common duct. In *Aletia*, *Danais* (*Lepidoptera*), there are on each side 3 vessels with short common terminal pieces (Fig. 348, p. 488). In *Galleria* (*Lepidoptera*) there is an unpaired terminal piece into which 5 or 6 branched vessels enter. In *Ephippigera* and the *Gryllidæ* (*Orthoptera*) there are numerous vessels which, uniting into a tuft, enter the hind-gut through a long common ductus excretorius. In *Orthezia* (*Coccidæ*) there are on each side 2 vessels which unite. The 2 terminal ducts themselves enter an unpaired terminal piece. The pupæ of the *Noctuina* have 3 pairs of vessels, united in pairs, entering an unpaired urinary bladder. *Lygaeus* (*Hemiptera*) has on each side 2 vessels entering a urinary bladder.

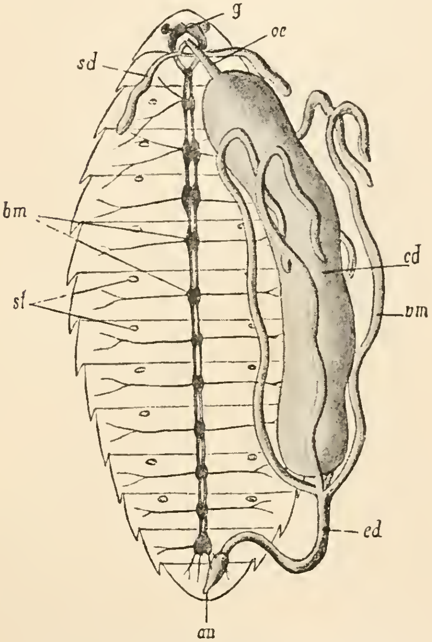


FIG. 321.—**Larva (maggot) of honey bee, anatomy of the digestive and nervous systems** (after **R. Leuckart**). *g*, Brain; *bm*, ventral chord; *oe*, œsophagus; *sd*, spinning glands; *cd*, mid-gut, or chyle stomach; *ed*, hind-gut, not yet connected with the mid-gut; *vm*, Malpighian vessels; *an*, anus; *st*, stigmata.

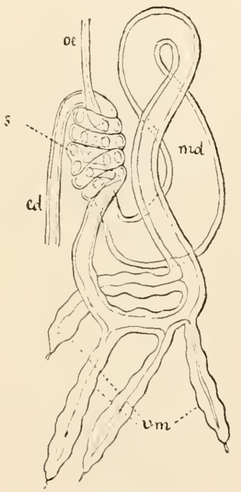


FIG. 322. — **Enteric canal of Psyllopsis fraxinicola** (after **Witlaczil**). *oe*, Œsophagus; *md*, mid-gut; *ed*, hind-gut; *vm*, Malpighian vessels; *s*, the coil formed by the hind-gut and the most anterior part of the mid-gut.

The number of Malpighian vessels is occasionally smaller in the larva than in the adult. Thus the larva of the *Honey bee* (Fig. 321) has only 4 vessels. In the *Blattidæ* and *Gryllidæ* the number increases during the gradual development. In the Lepidoptera the larva usually possesses the same number as the adult. Among the Termites only do the young forms possess more numerous Malpighian vessels than the adults.

V. The Nervous System.

This appears in the form which is characteristic of the *Arthropoda* and consists of the brain (supra-œsophageal ganglion), the œsophageal commissures, and the ventral chord. The **brain**, which lies in the head above the œsophagus, often attains to a high degree of development (especially in the highly developed *Hymenoptera*), and is distinguished by the formation of lobes (ganglion opticum, olfactory lobes, etc.) From it arise the nerves for the sensory organs which lie in the head, for the eyes, the antennæ, and the olfactory organs on the antennæ. We can always distinguish in the ventral chord a cephalic and a trunk portion. The former consists of the infra-œsophageal ganglion, composed of the fused ganglia of the oral limbs, which in the embryo are often separate. The trunk portion of the ventral chord must originally have consisted of as many double ganglia united by longitudinal commissures, as there are trunk segments, but the ganglia of some of the last trunk segments are always fused to form a terminal ganglion, generally somewhat larger in size than the rest. The ventral chord is found in this unconcentrated form in the *Myriapoda*, *Apterygota*, and many *Pterygota*, and especially in the larvæ of the *Hexapoda*. We find, however, within various orders of the *Hexapoda* more or less pronounced concentration of the ventral chord in a way similar to that described in connection with the *Crustacea*. This concentration takes place by the fusing of pairs of ganglia; it may appear in the abdomen as well as in the thorax and

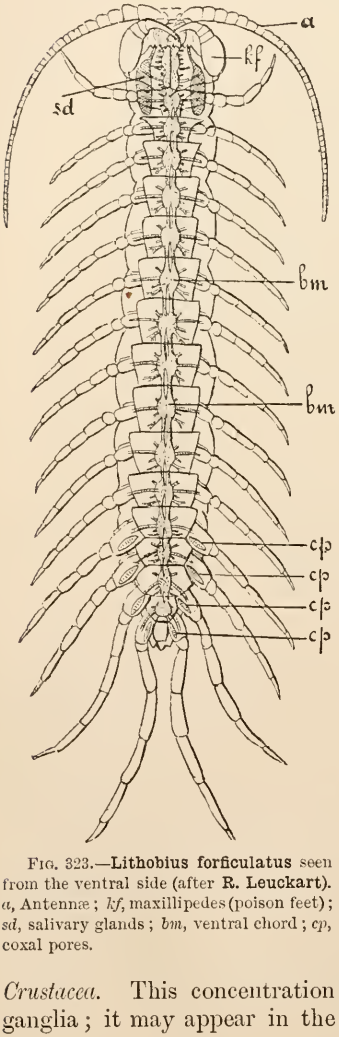


Fig. 323.—**Lithobius forficulatus** seen from the ventral side (after **R. Leuckart**). *a*, Antennæ; *kf*, maxillipedes (poison feet); *sd*, salivary glands; *bm*, ventral chord; *cp*, coxal pores.

generally, not always, proceeds in both from behind forward. A junction of the fused ganglia of thorax and abdomen to form a large thoracic ganglionic mass may even take place (as in the *Brachyura* and many *Copepoda*); such cases occur in the *Diptera* and *Rhynchota*. Although the larvæ generally possess a less concentrated nervous system than the imagines, so that the progressive concentration can often be followed ontogenetically in the same species, this is not always the case, in fact the very reverse occasionally occurs. The interesting relation between the nervous system of the larva and that of the imago will be again referred to.

From the ganglia of the ventral chord of the trunk (thorax and abdomen) arise the nerves for its integument, musculature, glands, and limbs. The 2 ganglia of a double ganglion are always closely contiguous, and appear as one mass consisting of two halves; the longitudinal commissures, however, which unite the consecutive ganglia very often remain separate. A **sympathetic nervous system** seems present in all Antennata.

Myriapoda (Fig. 323).

One ganglion is found in each trunk segment. The ganglia are mostly united by distinctly separate longitudinal commissures. In the *Pauropoda* and *Symphyla*, however, the ventral chord is a median strand with consecutive swellings, corresponding with the ganglia, and in this strand the longitudinal commissures are not separate.

The 2 anterior trunk ganglia (or in Symphyla only the first) generally form with the sub-œsophageal ganglion a single mass, in which, however, the original composition can easily be made out. The limbless anal segment has no separate ganglion, and the ganglia of the 2 or 3 preceding segments are fused together.

The double segments of the *Diplopoda* each have 2 ganglia.

Hexapoda.

Apterygota. — In this division we have very good illustrations of the concentrated and non-concentrated nervous systems. The *Thysanura* have a non-concentrated

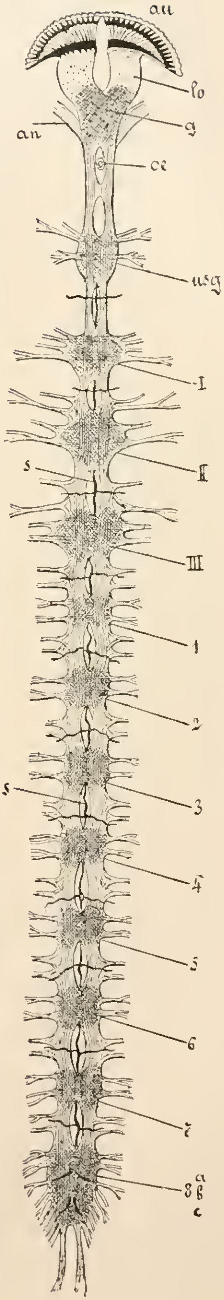


Fig. 324.—**Central nervous system of Machilis maritima** (after **Oudemans**). *au*, Eye; *lo*, lobus opticus; *g*, brain; *an*, antennal nerve; *oe*, œsophagus passing between the œsophageal commissures; *usg*, infra-œsophageal ganglion; *I-III*, thoracic ganglia; *1-8*, abdominal ganglia, the last (8 *a b c*) consisting of three fused ganglia; *s*, sympathetic nervous system of the ventral chord.

nervous system, consisting of the brain, œsophageal commissures, infra-œsophageal ganglion, 3 ganglia of the 3 thoracic segments and 8 (in *Campodea* 7) ganglia of the abdomen (Fig. 324). The finer structure of the last and largest abdominal ganglion and the number of nerves proceeding from it show that it consists of 3 fused ganglia. The number of abdominal ganglia would according to this be 10, corresponding with the number of segments. In the *Collembola* the number of abdominal segments is reduced, and in accordance with this reduction of the body there is, as it appears, only 1 abdominal ganglion. *Sminthurus* is said to have only 1 thoracic ganglion. The 2 longitudinal commissures remain distinctly separate in the *Thysanura*. From each ganglion 2 nerves are given off on each side, and the same number proceed from the œsophageal commissures. In front of the infra-œsophageal ganglion and behind the œsophagus a transverse commissure connects the œsophageal commissures.

Pterygota.—The nervous system of the winged *Insecta* shows very great variety in its arrangement: it is impossible here to go into details—the *Diptera*

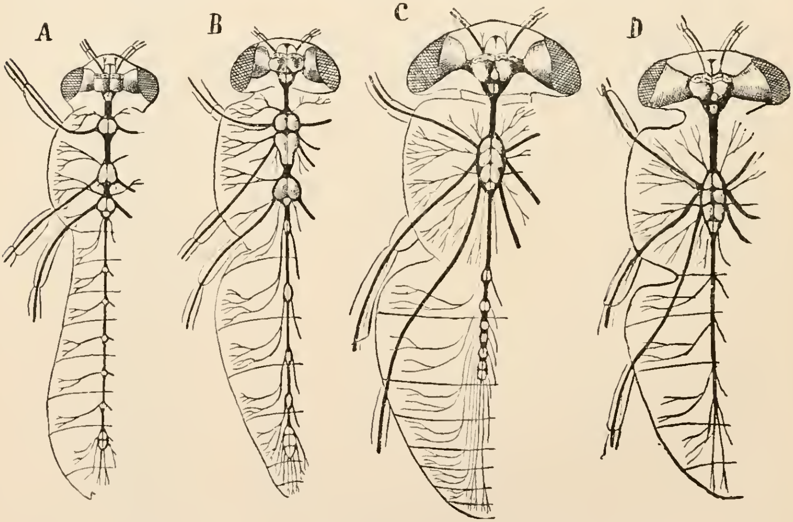


FIG. 325.—*A-B*, **The nervous systems of 4 species of Diptera**, to demonstrate their various degrees of concentration. *A*, Non-concentrated nervous system of **Chrionomus plumosus**, with 3 thoracic and 6 abdominal ganglionic masses. *B*, Nervous system of **Empis stercorea**, with 2 thoracic and 5 abdominal ganglionic masses. *C*, Nervous system of **Tabanus bovinus**, with one thoracic ganglionic mass and the abdominal ganglia moved towards each other. *D*, Nervous system of **Sarcophaga carnaria**. All the ganglia of the ventral chord except the infra-œsophageal ganglion, which always remains separate, are here united into one single thoracic ganglion mass (after **E. Brand**).

(Fig. 325, *A-D*) are particularly instructive. In no other natural order of insects are the extremes so great, and yet connected by such numerous intermediate stages. The series begins with the suborder of the *Nemocera*, the *Culicidæ*, *Culiciformes*, *Tipulidæ*, *Fungicolæ* (*e.g.* *Chironomus*, *A*), which have very slightly concentrated nervous systems. The ventral chord here consists of an infra-œsophageal ganglion, 3 thoracic ganglia, and 5-6 abdominal ganglia. The last thoracic ganglion is not simple, but at least 1 of the anterior abdominal ganglia is fused with it. The last and largest abdominal ganglion is also not simple; it consists of several (in *Chironomus* probably 2) fused ganglia. The concentration of the nervous system among the

Diptera begins in the families of the *Empidæ, Asilidæ, Therevidæ, Xylophagidæ, Bibionidæ* (*e.g. Empis, B*), where the 2 anterior thoracic ganglia become fused, so that there are only two thoracic ganglia. In this respect the *Diptera* form a contrast to other insects with only 2 thoracic ganglia, *e.g.* many *Coleoptera, Lepidoptera,* and *Hymenoptera,* in these cases it is the posterior thoracic ganglion which consists of the 2 fused posterior ganglia. *Tabanus* (Fig. 325, *C*) exhibits a nervous system in which all the 3 thoracic ganglia are fused into 1 thoracic ganglionic mass. This is the case in the families of the *Syrphidæ, Stratyomidæ,* and *Tabanidæ.* The abdominal ganglia show a tendency to approach each other and to fuse. Finally the highest degree of concentration among the *Diptera* is shown by the *Muscidæ, Œstridæ,* and *Pupiparæ,* where all the ganglia of the ventral chord, except the infra-œsophageal ganglion, are fused into 1 large thoracic ganglionic mass (Fig. 325, *D. Sarcophaga*). From this mass a median nerve then runs towards the end of the abdomen, giving off nerves to the abdominal segments at regular intervals.

A series similar to the above occurs in the *Coleoptera,* but the concentration here rarely goes so far as in the *Diptera,* since, though the abdominal ganglia may be wanting (in the *Lamellicornia*), the 2 thoracic ganglionic masses always remain separate. Wherever among insects separate abdominal ganglia are wanting these are fused with the most posterior thoracic ganglion, from which the abdominal nerves then often radiate backward, like the cauda equina in vertebrates. These abdominal nerves, however, may be united on each side into an abdominal longitudinal bundle, or these 2 longitudinal bundles may be fused to form 1 median abdominal strand. The *Rhynchota,* the *Mallophaga* (*Corrodentia*), and the *Thysanoptera* possess a much concentrated nervous system. In many *Rhynchota* all the thoracic ganglia, not excluding the infra-œsophageal ganglion, may fuse into 1 ganglionic mass, as is the case in the *Coccidæ* and also to a lesser degree in the *Aphides.*

All other insects have a non-concentrated or else slightly concentrated nervous system, with separate infra-œsophageal ganglion, at least 2 thoracic and several abdominal ganglionic masses, at the most 8 and rarely only 1.

The full number of abdominal ganglia is not found in any insect larva or imago. In **insect-embryos,** however, the **rudiments** of all the 10 abdominal ganglia have been observed.

It is clear from the above that the arrangement of the nervous system can be as little used as a criterion for the natural division of insects as the structure of any other organic system by itself. It can at the most be used for limiting the subdivisions within the orders.

The relation of the larval Nervous System to that of the Imago.—(1) Where the nervous system of the imago is not concentrated, it is generally not concentrated in the larva ; this is evidently the original condition.

(2) Where single ganglia are fused in the imago, they are often separate in the larva. The honey bee affords an illustration of this ; the bee larva (Fig. 321, p. 463) possesses the fully segmented nervous system : brain, infra-œsophageal ganglion, 3 thoracic and 8 abdominal ganglia. The last abdominal ganglion comes from three rudimentary ganglia, which are separate in the embryo. The adult bee (Fig. 320, p. 462) possesses a brain, infra-œsophageal ganglion, 2 thoracic and 4 abdominal ganglia. The posterior and larger thoracic ganglion consists of the 2d and 3d thoracic ganglia fused together ; the composition of the last abdominal ganglion out of 3 ganglia can still be clearly made out.

(3) Where the nervous system in the imago is much concentrated, it is very often (*e.g. Muscidæ*) much concentrated in the larva also, and at the same time slightly differentiated. We have here a case of the imaginal characteristics being shifted back on to the larval stage.

(4) The nervous system in the larva is seldom much concentrated when not con-

centrated in the imago. *Myrmeleon* is, however, a case of adaptation of the nervous system to the short compressed form of body of the larva.

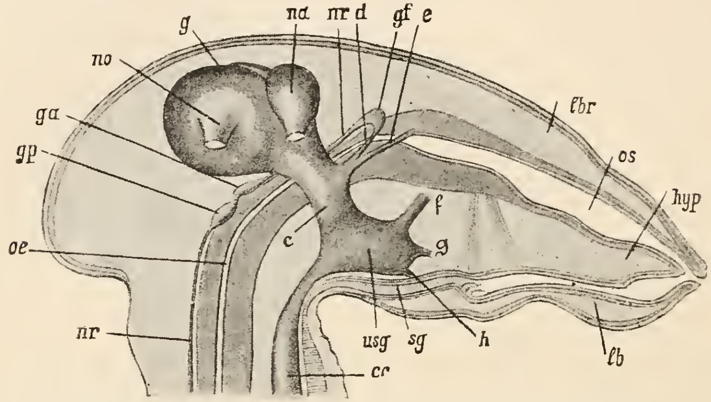


FIG. 326.—**Median longitudinal section through the head of Blatta orientalis.** The nervous system of the head is drawn entire. *hyp*, Hypopharynx; *os*, oral cavity; *lbr*, upper lip; *gf*, ganglion frontale; *g*, brain; *na*, root of the antennal nerve; *no*, root of the optic nerve; *ga*, anterior; *gp*, posterior ganglion of the paired visceral nervous system; *oe*, œsophagus; *c*, œsophageal commissure; *usg*, infra-œsophageal ganglion; *cc*, longitudinal commissure between this and the first thoracic ganglion; *sg*, common duct of the salivary glands; *lb*, lower lip = 2d pair of maxillæ; *nr*, nervus recurrens; *d*, nerve uniting the frontal ganglion with the œsophageal commissure; *e*, nerve from this commissure to the upper lip; *f*, nerve from the infra-œsophageal ganglion to the mandible; *g*, to the anterior maxillæ; *h*, to the lower lip (after **Bruno Hofer**).

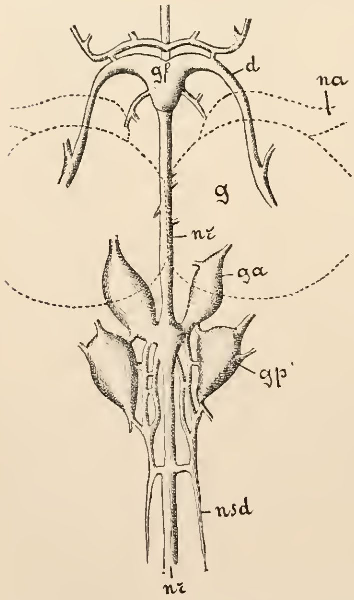


FIG. 327.—**Anterior portion of the paired and unpaired visceral nervous system of Blatta orientalis,** seen from above. The outlines of the brain (*g*) and the roots of the antennal nerve (*na*), which cover a portion of the sympathetic nervous system, are given by dotted lines. Lettering as in Fig. 326. *nsd*, Nerve to salivary-gland. The nervus recurrens (*nr*) enters an unpaired stomach ganglion further back (after **Bruno Hofer**).

(5) In many cases where in the larva there is an apparently concentrated ventral chord, its ganglia are quite distinct although lying very close together. In the imago they separate and the longitudinal commissures become distinct, so that a non-concentrated or less concentrated imaginal nervous system is developed.

The sympathetic nervous system seems to be present in all Antennata. It consists of an unpaired and a paired system. In *Blatta*, whose visceral nervous system (Figs. 326 and 327) has been the most investigated, the unpaired portion shows the following arrangement. In front of the brain on the œsophagus there lies an unpaired **ganglion frontale** *gf*, which gives off nerves to the upper lip and the œsophagus. It is connected by a nerve on each side with the œsophageal commissure, from which another nerve as well goes off to the œsophagus and the upper lip. From the ganglion frontale an unpaired median nerve, the **nervus recurrens** *nr*, runs back under the brain along the dorsal wall of the œsophagus, and enters an unpaired stomach ganglion in front of the masticatory stomach. A lateral pair of nerves arises from this, 2 small ganglia occurring in their course.

The **paired** visceral nervous system consists of two pairs of ganglia *ga* and *gp*, which lie on the œsophagus, the anterior pair being covered by the brain. These nerves are connected with each other, with the nervus recurrens, and with the brain by anastomoses. The nervus recurrens and the paired ganglia give off nerve branches to the œsophagus and to the salivary glands.

Besides the above nerves insects may have sympathetic thoracic and abdominal ganglia either paired or unpaired. The paired portion of the visceral system may also be wanting.

In the *Lepidoptera*, close above the abdominal portion of the ventral chord, is found a longitudinal strand of connective tissue, which seems to be a formation of the Neurilemma of the ventral chord. Muscles are attached to this which run to the neighbouring ventral exoskeleton. This strand, whose significance is not yet sufficiently explained, has been called the **chorda supra spinale.** It has nothing to do with the vertebrate chorda.

VI. Sensory Organs.

A. Eyes.

We can distinguish single-lensed eyes or **ocelli** from **compound eyes** (facet eyes). The *Myriapoda* have ocelli generally in large numbers grouped closely together on each side dorsally. Only *Scutigera* has a compound eye on each side: this eye, however, differs in structure in many respects from the compound eye of the *Insecta.*

Most adult *Hexapoda* have ocelli as well as facet eyes. The small ocelli then generally lie in threes on the frontal region between the two large facet eyes. The larvæ have ocelli only, these often occurring in great numbers. Ocelli are seldom found alone (*i.e.* without facet eyes) in adult *Hexapoda*, but this is the case in the *Collembola* among the *Apterygota*, and in lice (*Pediculidæ*) and fleas (*Aphaniptera*). Ocelli are wanting in adult *Dermaptera*, and among the *Orthoptera* in the *Locustidæ*, among the *Rhynchota* in the *Hydrocora*, among the *Lepidoptera* in the *Geometrina* and *Rhopalocera*, which thus as adults possess only facet eyes.

Structure of the Ocelli.—The simply constructed ocellus of the *Dytiscus* larva is very instructive (Fig. 328). Above the ocellus the chitin thickens into a lens. Below it the hypodermis is depressed in the form of a pit. The hypodermis cells standing at the base of this depression form the retina of the eye. Each retinal cell is connected with a nerve fibre, contains pigment, and produced outward towards the lens in the form of a rod. The cells at the edge of the depression are free from pigment at their outer ends, and push their way in between the retina and the lens, filling it up and forming a sort of vitreous body. The ocelli of other *Insecta* and *Myriapoda* are similarly constructed, with this distinction, that they are in most cases completely demarcated vesicles, over which and below the lens the hypodermis functions as a vitreous body.

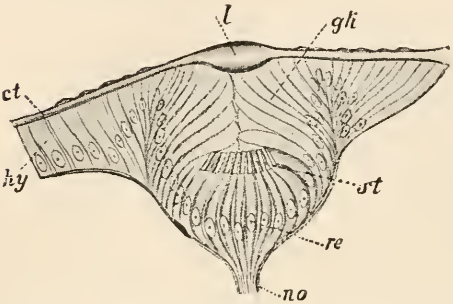


Fig. 328.—**Section through the ocellus of a young Dytiscus larva** (after **Grenacher**). *ct*, Chitinous cuticle; *l*, cuticular lens; *gk*, cells of the vitreous body; *hy*, hypodermis; *st*, rods; *re*, retinal cells; *no*, optic nerve.

The structure of the compound eyes agrees in general with that of the compound Crustacean eye (*cf.* p. 353). There is always a bi-convex corneal lens for each single eye. **Eucone** and **Acone eyes** are distinguished, according to whether crystal cones are formed (as in the Crustacea) or not. Acone eyes are found in the *Coleoptera* (excluding the *Pentamera*), in the *Heteroptera*, the *Tipularidæ* among the *Diptera*, and the *Dermaptera*. In the acone type (*e.g. Tipula*) each corneal lens is separated from its neighbour by a strongly pigmented zone. Under each lens lies a conical group of 4 crystal cells, whose proximal end is imbedded between two pigment cells. The retinula, consisting of 7 cells (6 marginal cells and 1 axial cell), joins the above. Each of the retinular cells contains in its proximal portion a nucleus, and in its distal portion a rod (rhabdomere). The single eyes are separated from each other by pigment cells.

The elements of the optic ganglia (ganglion opticum and retinal ganglion) are arranged in a very complicated manner in the *Insecta*.

The Ocellus and the Facet Eye.—Attempts have been made to connect these two forms of eyes. According to the view most widely approved, the two eyes are to be derived from a primitive eye resembling the single eye (ommatidium) of the acone eye of *Tipula*. **An increase of the elements of this primitive eye led to the formation of the ocellus; an increase in number of the primitive eyes and their approximation led to the formation of the compound facet eye.** For confirmation of this view we are referred to the groups of closely contiguous single eyes of the *Myriapoda*, considered in connection with the compound eye of *Scutigera*. But it is difficult to reconcile with this view several facts in the ontogeny of the eye, and especially the structure of the middle eye of the *Scorpion*. Such a scorpion eye on the one hand contains only a single lens, while on the other the retinal elements are grouped into retinulæ.

The last word is certainly not yet spoken with regard to the finer structure and the morphological significance of the Arthropodan eye, and we must here briefly allude to an entirely new view. According to this view the compound eye consists of two layers: (1) of a hypodermis layer which yields the single corneal lenses, and (2) of a subjacent layer of single eyes. The latter is said to be a single layer, the elements of the single eye known as crystal cells, retinular cells, and pigment cells running with their processes through its whole thickness (Fig. 329, *A*). The rhabdomes and the rhabdomeres forming them are not secreted products of the retinula, but belong, like the crystalline cone, to the crystalline cone cells, which are called retinophoræ. The crystalline cones are the elements actually sensitive to light. The retinophoræ are surrounded by pigment cells. A proximal (inner) ring of these cells corresponds with the so-called retinulæ, but these cells are also continued in the form of fine processes as far as the hypodermis. Fig. 329, *A*, illustrates this view. The layer of single eyes is said to answer to the posterior wall of a vesicular eye, which first forms as an ectodermal depression and later becomes constricted off. The whole compound eye would according to this be a modified and differentiated ocellus, in which the epithelial cells of the posterior proximal wall of the eye-pit differentiate into retinophoræ and pigment cells, grouped together as ommatidia (as in the middle eye of the *Scorpion*). The hypodermis, further, which spreads over the vesicular eye, instead of forming **one** cuticular lens, forms many such lenses, which as corneal facets correspond in number and position with the ommatidia. The ocelli themselves may also be compared with the similarly constructed visual organs in the *Annelida* and *Mollusca* which arise as ectodermal invaginations.

If this new view of the facet eye is established, *i.e.* if the so-called crystalline cones are not simply refractive bodies, but the actual terminal apparatus of the optic nerve, sensitive to light, it would lead to considerable modification of the theory of sight by means of the compound eye.

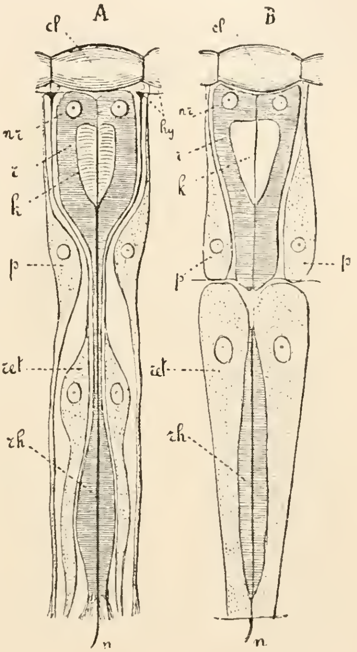


FIG. 329.—**The structure of an ommatidium (single eye)** of the facet eye. *A*, According to **Patten's** view. *B*, according to **Grenacher's** view. *cl*, Cuticular corneal lens; *hy*, hypodermis cells of the corneal lenses; *r*, retinophoræ = crystal cells; *nr*, nuclei of the same; *k*, crystalline cone; *p*, pigment cells; *ret*, retinulæ; *rh*, rhabdome; *n*, nerve. According to **Patten** (*A*) the ommatidium is, apart from the corneal hypodermis, of one layer, all its elements passing by means of thin processes through its whole thickness from the base to the corneal lens; according to **Grenacher** the ommatidium apart from the corneal lens consists of two layers.

B. Auditory Organs.

In the most various parts of the bodies of the *Insecta* peculiar nerve endings occur which are evidently sensory; their structure is as follows: A peripheral nerve fibre enters a ganglionic cell, which is in its turn connected with the integument by means of a long slender stretched tube. An axial thread from the ganglionic cell enters the tube, and there ends in a **terminal rod.** The tube which conceals this rod is called the **scolopophore,** and that part of it which becomes attached to the integument is the **terminal tube.** Scolopophores with their ganglia are rarely found singly, they are usually united in groups of varying size (Figs. 330, 331, and 332). If the number of scolopophores is small their terminal tubes are gathered into a bundle, but if great, the terminal tubes are generally isolated, running either irregularly or radially, or in the shape of a fan, etc., to the integument. These peculiar sensory organs are called **chordotonal organs**, and are considered to be auditory. A chordotonal organ may be either simply connected with the integument by a prolongation of its nerve, or bent at right angles to its nerve and run parallel to the integument (Fig. 330). The latter is the case when the terminal tubes of the chordotonal organ unite into one tube, and then the bent portion is connected with the integument by a second tube, the **chordotonal ligament.** The chordotonal organ, together with the chordotonal ligament, then form a chord stretched between two parts of one and the same segment.

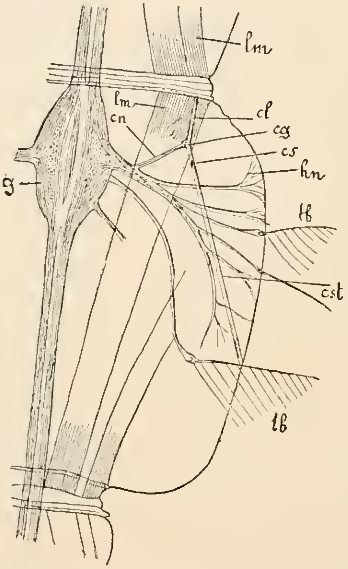


FIG. 330.—**Right half of the 8th trunk segment of an older larva of Corethra plumicornis**; nervous system and sensory organs (after **v. Graber**). *g*, Ganglion of the ventral chord; *lm*, longitudinal muscles; *cn*, chordotonal nerve; *cl*, chordotonal ligament; *cg*, chordotonal ganglion; *cs*, rod of the chordotonal organ; *cst*, terminal strand; *tb*, tactile setæ; *hn*, outgoing fibres of the integumental nerves.

The nerve forms a terminal ganglion cell at the point where it joins the chord.

If the exoskeleton is affected by vibrations of sound, this apparatus with its terminal rods is set in vibration, and a sensation of sound may thus be produced.

Chordotonal organs, which offer great varieties of structure, occur in all orders of the *Pterygota*, and are found in the most various parts of the body, in the trunk, in the legs, the wings, the mouth parts, and the antennæ. They may appear in different forms in various parts of the body of the same animal.

In the wings, but especially in the halteres or balancers of the *Diptera*, which are minute transformed hind wings, they are connected with areas of the exoskeleton provided with peculiar pores or papillæ. They always lie superficially. A chordotonal organ is, further, never stretched between points of the integument of two consecutive segments of the body, or limbs, movable on one another, but always runs within one of the same joint or segment, and is thus not affected by the movements of the animal. The chordotonal nerves always arise out of the ganglion belonging to their own segment. Chordotonal sensory organs have till now been chiefly observed in the larvæ of the Insecta.

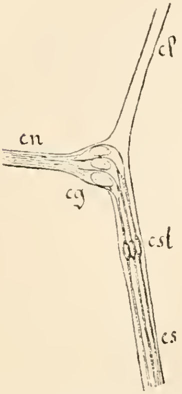


FIG. 331.—**The Chordotonal organ** of Fig. 330, strongly magnified. *cl*, Chordotonal ligament; *cn*, chordotonal nerve; *cg*, chordotonal ganglion; *cst*, chordotonal rod; *es*, terminal tube.

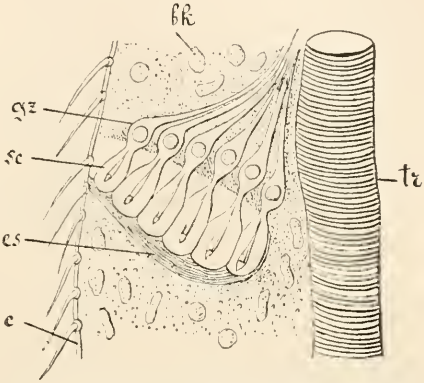


FIG. 332.—**So-called sub-genual chordotonal organ in the tibia of the middle leg of Isopteryx apicalis** (*Perlid*) (after **v. Graber**). *tr*, Trachea; *bk*, blood corpuscles; *gz*, nerve cells; *sc*, scolopophores with their rods; *es*, terminal fibrous strands, attached to the integument (*c*).

The **tympanal organs** of the *Saltatoria*, which have been long known, agree in the finer structure of their nerve endings with the chordotonal organs. It was this agreement which led to the assumption that the so-called chordotonal organs were also auditory organs, for the tympanal organs of the *Saltatoria* have long been universally regarded as auditory organs, although the animals continue to hear after their removal. This last fact favoured the view of the acoustic properties of the chordotonal organs, since the latter occur together with the tympanal organs.

Scolopophores are very numerous in the *Saltatoria* (over 100). In the *Acridiidæ* their terminal tubes are attached to points of the inner surfaces of the hypodermis of special parts of the exoskeleton, which, as compared with the surrounding exoskeleton, are thinned away like a membrane and are called **tympana** (Figs. 333 and 334). Such a tympanum may be stretched between thickened portions of the skeleton, which form a frame for it; and, as in an outer ear, the integument may grow round it as a covering fold for its protection. A tracheal trunk widens to form a cavity under the tympanum, which may be compared with the hollow of a drum. Between the cavity

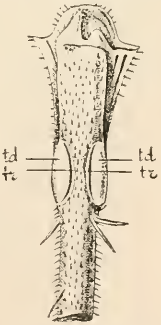


FIG. 333.—**Tibia of the fore leg of Locusta viridissima.** *td*, Cover of the drum; *tr*, fissure between the drum and its cover (after **v. Graber**).

and the tympanum lies the terminal nerve apparatus, the so-called "Müller's" ganglion with the scolopophores, whose terminal tubes attach themselves by peculiar inner processes to the middle of the tympanum. The tympanum can be stretched by special muscles. In the *Gryllidæ* and *Locustidæ* the terminal tubes of the scolopophores are not attached to the tympanum itself, but above it to the integument. The *Locustidæ* possess, besides the Müller's ganglion with its scolopophores, another series of somewhat different scolopophores, lying on a hollow formed by the trachea, which acts as a resonator.

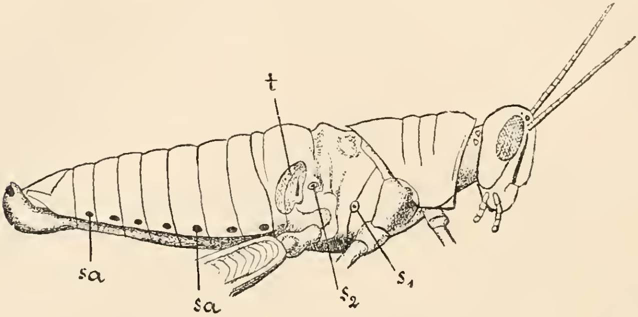


FIG. 334.—**Side view of Acridium tartaricum.** s_1, Stigma of the mesothorax; s_2, stigma of the metathorax; *sa*, stigmata of the abdomen; *t*, drum of the tympanal auditory organ (after **Fischer**).

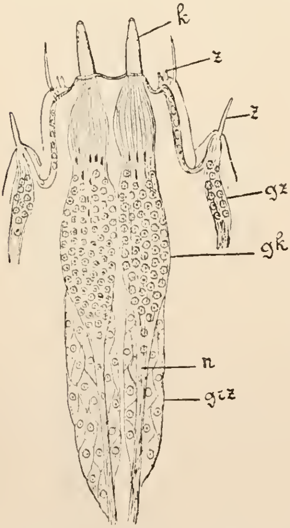


FIG. 335.—**Sensory organs considered to be olfactory at the end of the Antennæ of Iulus Sabulosus,** longitudinal section through the antenna. *k*, Sensory cones; *z*, sensory points; *gk*, ganglia of the sensory cones; *gz*, ganglia of the sensory points; *n*, nerve; *grz*, large cells in the ganglia of the sensory cone (after v. **Rath**).

The tympanal auditory organs of the *Saltatoria* lie either (*Acridiidæ*, Fig. 334) in a single pair at the sides of the first abdominal segment, or (*Gryllidæ*, *Locustidæ*, Fig. 333) on the tibiæ of the fore-legs. In the last case there are generally on each tibia 2 tympana lying opposite one another.

Between the basal portions of the maxillæ of *Scutigera* there lies on each side a pouch, from the base of which small closely-packed plates and hairs rise into the cavity. These plates and hairs stand on equally closely arranged folds of the cuticle. It has been conjectured that these formations, which need further examination, may prove to be auditory organs.

C. Olfactory Organs—Gustatory Organs.

The seat of the sense of smell is, as in the *Crustacea*, to be sought in the antennæ (and perhaps in the maxillar palps as well). The antennæ are in the *Insecta* very often more strongly developed in the males than in the females. The olfactory organs are short processes in the shape of knobs or cones, and generally open at the point; they are found either free or at the base of pits in the antennæ.

Beneath each olfactory process there is a pore in the cuticle, through which the fibrillæ of a hypodermal ganglion pass (Fig. 335). Similar terminal apparati, which have been observed at the base and at the point of the tongue, and on the lower side of the maxillæ of *Hymenoptera*, on the inner surface of the labellum of the proboscis in the fly, and in the gnathochilarium of the *Diplopoda*, may perhaps be considered as **gustatory organs.**

Specific organs of touch are found in the long, simple, or feathered setæ (Fig. 330, p. 472) which occur all over the body surface, and especially on the feelers and maxillar palps of the Antennata, on the labellum of the proboscis of the fly, etc. An axial thread enters the sensitive hair from a hypodermal ganglion cell, and runs through it.

VII. The Circulatory System.

This is very simple in the Antennata. The colourless or light-yellow or light-green blood, containing amœboid blood corpuscles, flows in definite directions in a lacunar system (body cavity). The circulation of the blood is maintained by the contractions of a **dorsal vessel (dorsal heart)**, which in the extremely reduced condition of the arterial vascular system is almost the only part which has walls of its own. The dorsal vessel is a delicate tube running longitudinally above the intestine, and covered externally and lined internally by membranes probably elastic. Between the two membranes there runs a system of delicate muscle fibres, which generally have a circular course and sometimes cross each other. The dorsal vessel falls into successive segmental chambers, separated by valvular arrangements, which prevent the streaming back of the blood from the anterior into the posterior chambers during the progressive contraction of the vessel from behind forward. The dorsal vessel is provided with paired lateral ostia, which, as it appears, are mostly placed intersegmentally, and maintain an open communication between the surrounding parts of the body cavity and the interior of the heart. The heart may be connected in various ways by muscular fibres with neighbouring parts of the body, *i.e.* with the intestine, with the dorsal integument, etc. Paired so-called **alary muscles** are particularly constant in their occurrence; they are almost triangular, and become attached by their narrowed ends to the latero-dorsal body wall, while their broad ends are fastened to the chambers of the heart. These alary muscles together form an incomplete horizontal partition wall above the intestine, marking off a dorsal sinus in which the heart lies. This sinus may be called the **pericardial sinus.** This partition wall is arched upwards, and if the alary muscles which form it contract, it straightens out and becomes flat; the pericardium thus becomes more spacious, and the blood streams into it from the rest of the body cavity. It was formerly thought that the alary muscles served to expand the heart.

This expansion, however, seems to be merely a result of the elasticity of its own walls. The whole mechanism, however, requires fresh investigation.

The heart ends blindly behind, but is continued anteriorly into an **aorta**, which empties the blood into the lacunar system of the body. We can occasionally distinguish with special clearness a ventral sinus surrounding the ventral chord (in *Myriapoda*, *Orthoptera*, and perhaps also in certain *Apterygota*); in this sinus the blood flows from before backward. A nerve supplying the heart like that in *Peripatus* has here and there been observed.

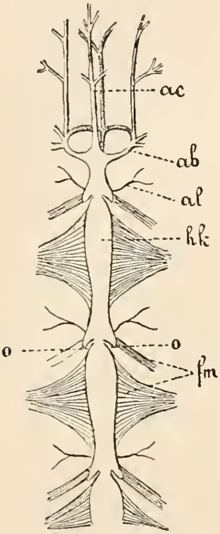


Fig. 336.—**Anterior end of the heart of Scolopendra** (after **Newport**). *ac*, Arteria cephalica; *ab*, arterial rings; *al*, lateral arteries; *hk*, cardial chamber; *o*, ostia of the heart; *fm*, alary muscles of the same.

Myriapoda (Fig. 336).—The heart runs through the whole body, and has as many chambers and pairs of alary muscles as there are trunk segments. From the most anterior chamber an aorta arises, which divides into three branches in the head. In the *Iulidæ* and *Scolopendridæ* lateral arteries are said to diverge in the neighbourhood of the ostia.

Hexapoda, Apterygota.—The heart of the *Thysanura* consists of 9 chambers, and has 9 pairs of ostia and 9 pairs of weakly developed alary muscles; this is the highest number reached among the *Hexapoda*. It runs forward as far as the last thoracic segment, or even to the second; this is an important fact, as in all *Pterygota*, with the exception of a few *Orthoptera* (*Blatta*), the heart is exclusively confined to the abdomen. The aorta is short in the *Thysanura*, as the heart extends so far forward. The number of cardial chambers and pairs of ostia is reduced in the *Collembola* (5 in *Macrotoma*).

Pterygota.—With the exception of a few *Orthoptera*, the heart is restricted to the abdomen, and has 8 pairs of ostia at the most. The number of pairs of ostia, of alary muscles, and of cardial chambers may be reduced like the number of the ganglia of the ventral chord. The aorta runs through the thorax and may be traced as far as into the head.

In the *Lepidoptera* the aorta bends up dorsally in the thorax, widens considerably and forms a loop (Fig. 348, *ac*, p. 488). In a few cases the aorta has been found branched in the head. In the larva of the *Ephemeridæ*, blood vessels with walls of their own pass from the last cardial chamber into the three caudal setæ. The valves between the last cardial chamber and the one before it are here placed in such a way that they prevent the passage of the blood from the former into the latter. When the last chamber contracts, therefore, the blood is driven into the three arteries of the caudal setæ.

The want of a developed arterial vascular system is compensated for as well as conditioned by the extremely profuse branching of the respiratory organs (tracheæ), the oxygen being thus conveyed to the blood in all parts of the body. Thus, whilst, as a rule in the higher animals, the blood in its closed channels generally seeks out the localised seat of the respiratory processes, here, on the contrary, the respiratory organs seek out the blood and the blood tissue in the most remote parts of the body.

VIII. Fat Bodies—Luminous Bodies.

In the body cavity lies a mass of large cells filled with small drops of fat, and forming together the so-called **fat body.** This is variously shaped, and covers inner organs which appear enveloped in it; it also forms a layer under the integument, etc. It is specially strongly developed in the larvæ, and forms a reserve of nutrition, which is drawn upon during metamorphosis, during the formation and ripening of the sexual products, etc. The metabolism which goes on in the fat body is very active, as is proved by the fact that its cells often contain concretions of uric acid. In some cases it has been proved that the fat body in the larva is rich in fat and poor in concretions of uric acid, while in the imago it is poor in fat and rich in concretions of uric acid.

There are *Coleoptera* which possess either on the abdomen (*Lampyridæ*) or on the thorax (a few *Elateridæ*, *Pyrophorus*) intensely luminous areas. The seat of light is a **luminous organ** which, morphologically, must be considered as a specially differentiated portion of the fat body. The cells of this luminous organ secrete, under the control of the nervous system, a substance which is burnt during the appearance of the light; this combustion takes place by means of the oxygen conveyed to the cells of the luminous body by the tracheæ, which branch profusely in it and break up into capillaries. A weakly luminous dorsal layer of the luminous organ, which lies ventrally in the penultimate and antepenultimate abdominal segments of the *Lampyridæ*, contains very numerous concretions of uric acid.

Other cell elements occurring in the body cavity (*e.g.* the pericardial cells lying on the alary muscles of the heart, and occasionally containing fat) cannot here be more closely considered. They form, together with the blood corpuscles and the fat body, the so-called **blood tissue.**

IX. The Respiratory Organs.

A. The Tracheal System.

The respiratory organs of the Antennata are **air-conducting canals (tracheæ)** which, on the one hand, communicate with the outer world by means of paired, strictly segmentally arranged outer apertures (stigmata), and on the other spread all over the body, penetrating between the various organs and even the component parts of organs, breaking up into the finest capillaries. The essential structure of the tracheæ is everywhere the same, whether we examine a principal trunk or a fine terminal branch. The tracheal tube (Fig. 337) is lined internally with a chitinous intima, which is a continuation of the chitinous cuticle of the body, and, like the latter, is shed during ecdysis. The intima is crenulated spirally. This chitinous spiral chiefly serves for holding the tracheæ open. The intima is clothed with an outer layer of cells, the boundaries of which are often difficult to distinguish. This layer represents the epithelium which secretes the intima, and is a continuation of the outer hypodermis. The outer apertures of the tracheal system, the so-called **stigmata**, are wonderfully varied in their arrangement. They sometimes lie openly on the surface, sometimes are partly concealed by cuticular folds, or again are covered by the elytra (*Coleoptera*). Setæ often project over the aperture from its edges, and these may be elegantly branched or feathered, so as to represent a kind of fish-trap apparatus, which prevents the entrance of foreign bodies, dust, etc., with the air. The outer aperture is often long and slit-like; in other cases, on the contrary, it is large and has a sieve-like membrane stretched over it. Beneath each stigma, at the beginning of each principal tracheal trunk, there is a closing apparatus which we cannot here more minutely describe; by means of this apparatus, into which nerves enter, the trachea can be completely closed towards the exterior. The air in the tracheæ is chiefly renewed by the respiratory movements of the abdomen (in the *Hexapoda*); these movements are caused by the contractions of the muscular fibres which run dorso-ventrally. By the contraction of the abdomen (exspiration) the tracheæ are compressed and the air driven out through the stigmata, or, if the stigmata are closed, forced into the tracheal system of the thorax, head, and extremities. By the expansion of the abdomen (inspiration) new air from without again enters the tracheæ, the elastic spiral of the tracheal tube playing an important part in its expansion.

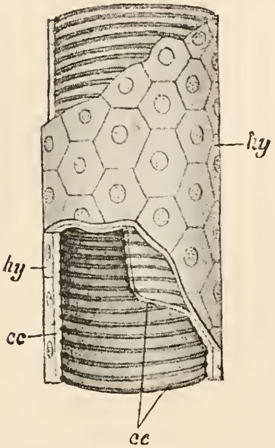


Fig. 337.—**Structure of a trachea.** Diagrammatic; portions of the epithelium and chitinous intima removed in order to show the structure. *hy*, Tracheal epithelium = tracheal hypodermis = matrix of the chitinous intima (*cc*), in which can be seen the spiral thickening (spiral thread).

We are justified in assuming, that the tracheal system of the Antennata originally consisted of as many pairs of isolated tracheal bundles and stigmata as there were body segments (excluding the anal segment). Reduction, however, has everywhere taken place, first of all at the anterier and posterior ends of the body, so that in some cases only a single pair of stigmata is left; the tracheal system undergoes corresponding modifications, the most important of which is the connecting together of the originally separate bundles of tracheæ by means of transverse and longitudinal anastomoses.

With reference to the scattered and irregular apertures of the tracheæ in the *Protracheata*, we must point out that the arrangement of the tracheal system in all Antennata indicates a strictly segmental order of tracheal apertures in the racial form. There is never more than one pair of tracheæ in one segment in the Antennata.

Myriapoda.

The most primitive arrangement is found in the *Diplopoda*, where one pair of stigmata and one pair of tracheal bundles occurs in each trunk segment. Each double segment also has 2 pairs of stigmata and 2 pairs of tracheal bundles. The separate tracheal bundles are not connected by anastomoses. Each stigma leads into a tracheal sac, whose base is produced in the form of pointed horns, into which the numerous but unbranched tracheæ enter. Branched tracheæ seem to occur only in the *Glomeridæ*.

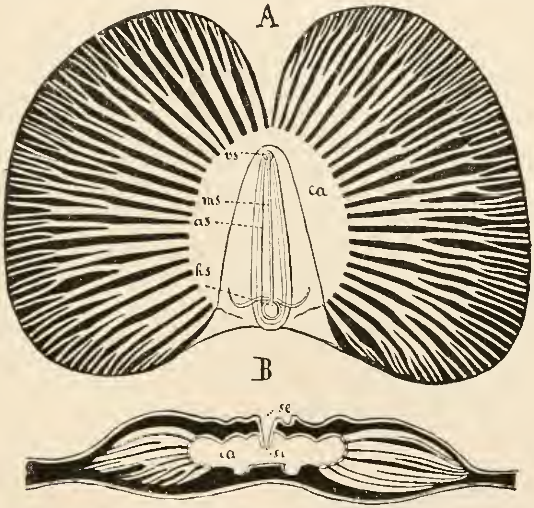


Fig. 338.—**Tracheal mass of a dorsal plate of Scutigera coleoptera.** *A*, from above; *B*, in transverse section through the inter-segmental fold of the dorsal plate; diagrammatic (after **Haase**). The tracheæ, which enter the air cavity (*ca*) from both sides, are marked white. *vs*, Anterior; *hs*, posterior stomatic aperture; *as* (*A*) and *se* (*B*), outer; *ms* (*A*) and *si* (*B*), inner stomatic slit.

The tracheal system of the *Chilopoda* is seen to be a secondary development from the fact that the tracheæ branch profusely, and that the tracheæ belonging to each stigma anastomose with one another transversely and longitudinally. Only in the *Geophilidæ* and *Plutonium* one pair of stigmata is retained on each leg-bearing segment, except the first and last. In the species *Lithobius* and in the *Scolopendridæ* (except *Plutonium*), beginning with the third trunk segment, a pair of stigmata is found with considerable regularity on every second segment. The last leg-bearing segment is here also without stigmata. In *Scutigera* and *Henicops* the stigmata belong to the trunk segments 1, 3, 5, 8, 10, 12 (and 14 when there are 15 trunk segments in all).

The *tracheal system of Scutigera* (Fig. 338) is distinguished by many peculiarities. The stigmata here are unpaired and lie in the dorsal middle line. Each stigma leads into an air sac, into which on each side about 300 closely packed, radially placed, branched tracheal tubes enter. This form of trachea is specially interesting, as perhaps helping to explain the origin of the so-called book-leaf tracheæ of the *Arachnoidea*, which will be described later.

The respiratory system of the *Symphyla*, which in other respects may be reckoned as very primitive Myriapodan forms, is much reduced. There are only 2 stigmata, and these are on the under side of the head under the feelers. This is the only case in the whole division of the Antennata in which a pair of stigmata has been retained in the head. The branched tracheæ do not extend either into the legs and feelers, or into the posterior region of the body at all.

In the *Pauropoda* the tracheal system seems to be entirely degenerated.

Hexapoda.

Apterygota.—The tracheal system in a few *Thysanura* exhibits the original condition in so far that the longitudinal and transverse anastomoses are wanting (in a few species of *Machilis*, and in the *Campodea*, Fig. 339). In other *Thysanura*, however, they are present (*Iapyx*, *Nicoletia*, *Lepisma*, and a few species of *Machilis*). The most frequent number of pairs of stigmata seems to be 10 (*Nicoletia*, *Lepisma*, *Lepismina*) ; in this case two occur on the thorax and 8 on the abdomen. *Machilis maritima* has only 9 pairs of stigmata, 2 thoracic, and 7 abdominal. *Iapyx* is said to possess 11 pairs, viz. 7 on the abdomen, and—an arrangement standing quite alone among the Antennata—4 on the thorax. In *Campodea* the number is reduced to 3 pairs belonging to the thorax (the last pair possibly belonging to the first abdominal segment).

Pterygota (Fig. 340).—Transverse and longitudinal anastomoses appear to be everywhere present. Among the longitudinal anastomoses on each side one develops more than the rest, and at first sight it appears as if these tracheal trunks formed the central portion of the tracheal system, from which, besides numerous lateral branches penetrating the body, branches run to the stigmata, and there open outwardly. In the *Diptera*, *Hymenoptera*, and among the *Coleoptera* in the *Hydrophilidæ* and *Lamellicornea*, the tracheæ may widen out in some places into large tracheal sacs without spiral crenulations, known as air sacs (Fig. 320, p. 462). The number and arrangement of the stigmata vary within wide limits. In the same insect, at the same time, there are never more than 10 pairs of stigmata. Of these 10 pairs there is one pair on the mesothorax, one on the metathorax, and one on each of the first 8 abdominal segments.

The imagines of by far the greater number of insects are **holopneustic**, *i.e.* they possess many pairs of open stigmata, though the number of stigmata may be reduced, especially in the abdomen. The *Aphaniptera* alone have more than 2 pairs of stigmata in the thorax ; in them there is one prothoracic pair, not met with in other adult *Insecta*. The tracheal system of the larvæ of insects exhibits interesting peculiarities, which are of great morphological importance.

1. The most primitive condition is found in those insects which undergo gradual metamorphosis, and whose larvæ live during all stages, like the imagines, on land (*Orthoptera*). These larvæ are holopneustic, and their tracheal system simply passes into that of the imago. Holopneustic larvæ may also occur in insects with complete metamorphosis, as in many *Coleoptera* (*Malacodermata*), which thus appear to be a primitive group.

2. In many Insects with incomplete metamorphosis the holopneustic condition of the tracheal system is much altered in the larvæ by the adaptation to aquatic life. In the aquatic larvæ of the *Ephemeridæ, Odonata, Plecoptera,* for instance, there are no open stigmata, the tracheal system is **completely closed,** *i.e.* it is **apneustic.** The rudiments of the tracheal branches running from the stigmata to the longitudinal trunks are, however, present, but they are empty of air, and appear in the form of strands (Fig. 343, *vf*); these play an important part in the shedding of the larval tracheæ, and then for a time open outwardly. When the last larval stage passes into the imaginal stage these strands become hollow, and the tracheal system becomes **holopneustic.** All such larvæ breathe by means of tracheal gills.

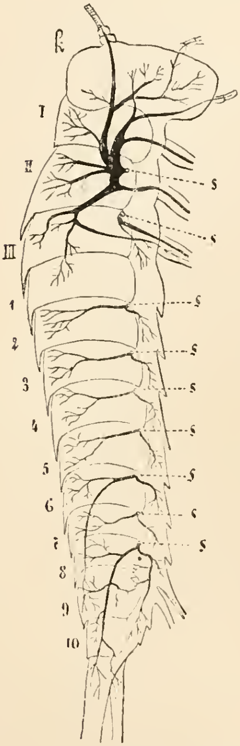


Fig. 339.—**Machilis maritima,** representing the tracheal system of the right side (after **Oudemans**). *k*, Head; *I, II, III,* thoracic segments; 1-10, abdominal segments; *s*, stigmata.

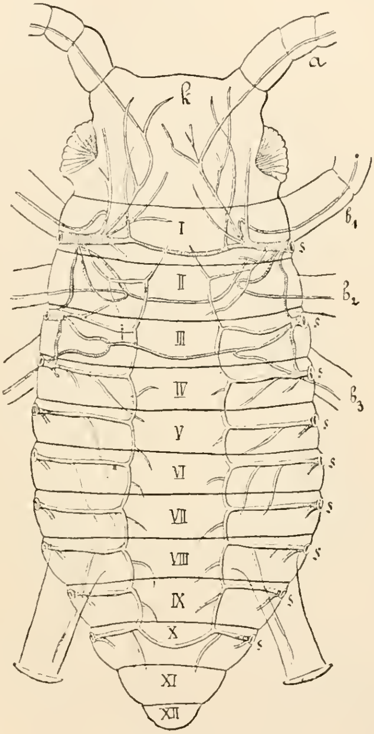


Fig. 340.—**Half-developed larva of an agamous unwinged female of Aphis Pelargonii. The tracheal system** seen from above (after **Witlaczil**). *k*, Head; *a*, antenna; *I, II, III,* segments of the thorax; *IV-XII*, segments of the abdomen; b_1, b_2, b_3, the 3 pairs of legs; *s*, the stigmata of the tracheal system.

3. In the majority of the larvæ of insects which undergo complete metamorphosis, the stigmata of those segments which in the imago carry wings (meso- and metathorax) are closed, but on the other hand one pair of prothoracic stigmata wanting in the imago is usually found. We evidently have here a delayed differentiation of the tracheæ which supply the wings and their musculature, referable to the absence

of wings in the larvæ. The **stigmatic strands** belonging to these parts are present as rudiments. The tracheal system of these larvæ is **peripneustic.**

4. The tracheal system of peripneustic larvæ may be modified in various ways by adaptation to different modes of life: (*a*) it may become apneustic in larvæ inhabiting water, as in the larvæ of the *Phryganidæ* and *Sialidæ*, which breathe through tracheal gills. (*b*) By adaptation to life in water or parasitic life all the stigmata may remain closed in the larvæ except the last pair. The tracheal system is then called **metapneustic.** The larvæ then obtain air at the surface of the water or of the host, by means of this posteriorly placed pair of stigmata, which is often elongated like a siphon, or provided with other suitable structural adaptations. The larvæ of the water beetle and of many *Diptera*, which are aquatic or parasitic, are metapneustic. (*c*) There is occasionally besides the posterior an anterior prothoracic open pair of stigmata (Fig. 341). This **amphipneustic** tracheal system is found in many parasitic or half-parasitic *Diptera* larvæ (*Oestridæ*, *Asilidæ*), which stretch only their anterior and posterior ends beyond the medium which surrounds the rest of the body. The larval stigmata of the meta- and amphipneustic fly larvæ disappear during metamorphosis.

In all cases where the larva is not holopneustic, the stigmatic branches of the tracheal system are present as rudiments. We must distinguish between such first rudiments remaining latent during the larval period, and those rudiments of stigmatic branches which are found in the imagines of the various *Insecta.* The latter are the remains of stigmata which have disappeared. Several pairs of such stigmata are often found in the abdomen.

The peculiar arrangements of the tracheal system in insect larvæ show very clearly to what an extent special conditions of existence may influence the organisation of free-living larvæ.

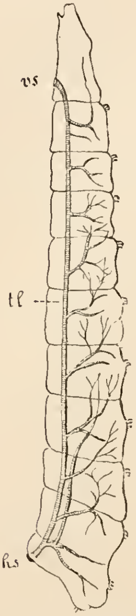


FIG. 341.—**Right side of the tracheal system of a fly maggot,** seen from the side. *vs*, Anterior stigma; *hs*, posterior stigma; *tl*, longitudinal tracheal trunks.

B. The Tracheal Gills (Figs. 342 and 343).

Something has already been said about these respiratory organs of aquatic insect larvæ in the section on "wings." Tracheal gills, *i.e.* delicate membranous processes of the body into which tracheæ extend, are found not only in the larvæ of the *Ephemeridæ*, *Trichoptera*, and *Sialidæ* there mentioned, but also in the larvæ of the *Plecoptera* (*Perlidæ*), *Odonata*, and the aquatic larvæ of a few species of *Diptera*, *Hymenoptera*, *Lepidoptera*, and *Coleoptera.* The tracheal gills of the *Odonata* are either external (*Agrion*) in the form of 3 branchial leaves on the last abdominal ring, or they are internal (*Libellula*, *Æschna*) in the form of folds in the rectum. In the latter case water is alternately drawn in and expelled through the anus. The tracheal gills of the larvæ of the *Perlidæ* are very variously formed; they are pouch-shaped or tufted, etc., and occur at very different parts of the body. The same is the case with the tracheal gills which occur singly in the larvæ of *Diptera*, *Hymenoptera*, *Lepidoptera*, and *Coleoptera.* Larvæ which are provided with tracheal gills are apneustic. The tracheal gills, according to all observers, are respiratory organs, which have arisen independently of each other in various insect orders as adaptations to aquatic life. They are thrown off during the transition to the imaginal form in the *Ephemeridæ*, *Agrionidæ*, and *Diptera*, but are retained in the imagines of the *Perlidæ*, *Æschnidæ*, *Sialidæ*, *Lepidoptera*, and *Coleoptera*.

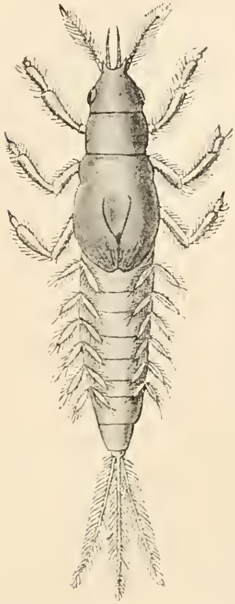


Fig. 342.—**Ephemerid larva with two tracheal gills on each side of each abdominal segment, and with 3 caudal processes (cerci)** (after **R. Leuckart**).

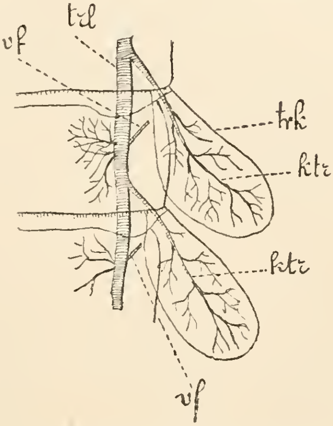


Fig. 343.—**Right half of the middle abdominal segment of the larva of Baetis (Chloë) binoculatus with tracheal gills** (after **Palmen**). *trl*, Longitudinal tracheal trunks; *vf*, strand like threads of attachment of the longitudinal trunks to the integument (stigmatic strands); *ktr*, gill tracheæ; *trk*, tracheal gills.

X. Sound-Producing Apparatus.

It is well known that many insects can produce sounds. These sounds, which play many different parts in insect life, are principally produced—

1. By rapid vibrations of the wings (*Hymenoptera*, *Diptera*), and by the vibration of the halteres against the alulæ (*Diptera*).

2. By the vibration of leaf-like appendages in the tracheæ. These often lie in great numbers near the stigmata, and are made to vibrate during the respiratory movements of the animal by the inward and outward streaming of the air (*Hymenoptera*, *Diptera*).

3. By the rubbing together of rough uneven portions of the integument. The *Acrididæ* stridulate by scraping their posterior femur

like the bow of a fiddle over the projecting ribs of the upper wing. In the *Locustidæ* and *Gryllidæ* only the males stridulate, by rubbing the rough basal portions of their wing cases against each other. In other insects sounds are produced by the rubbing together of other parts of the body.

4. In the singing *Cicada* also only the male can produce the well-known shrill sounds. The sound apparatus is here somewhat complicated. It consists of a pair of drum-skins (thin elastic extensions of the cuticular skeleton) on the first abdominal segment, and of strong muscles moving these skins. The abdomen filled with air acts as a resounding apparatus. As a protection to the delicate drum-skins folds of the thoracic and abdominal cuticular skeleton arch over them from before and behind.

The sounds produced by male insects are calls for attracting the females.

XI. Sexual Organs.

The sexes are separate in all Antennata. A comparative study of the sexual organs justifies us in giving the following general plan of the sexual apparatus. It consists of a **pair of germ glands** (ovaries in the female, testes in the male) **which pass into paired ducts, the latter opening separately.** The sexual glands and ducts appear, as far as their ontogeny is known, to proceed from a paired mesodermal genital rudiment. Ectodermal invaginations of the cuticle are often connected with the ends of the ducts.

Since the ducts of the sexual organs in the *Protracheata* are transformed nephridia, we may perhaps infer the same for those of the Antennata. There is, however, a considerable difference in the two cases, as the greater part of the ducts in *Peripatus* arise out of the ectoderm, while in the Antennata, on the contrary, they come from the mesoderm. But it must not be forgotten that in the *Annulata* the greater part of the nephridium (nephridial duct) is of mesodermal origin

Sexual organs, which are paired throughout (as in the plan above sketched), are only found in reality in the *Ephemeridæ* (Fig. 344, *A*). In all other Antennata there are unpaired portions of the sexual apparatus arising in various ways.

1. The two germ glands may fuse to form 1 unpaired germ gland, while the ducts remain separate either throughout their whole length or at any rate towards their ends, and always open externally through separate paired apertures. Such cases are found in the *Diplopoda* among the *Myriapoda*.

2. The germ glands remain paired. The ducts remain paired for the greater part of their course, only uniting to form a common terminal portion. This is the case in all Antennata except the *Ephemeridæ* and the *Diplopoda*.

In rare cases (*Scolopendra*) we find an unpaired germ gland and an unpaired duct, into whose end, however, paired accessory organs (glands, receptacula seminis, vesiculæ seminales) enter.

The unpaired portion may arise in very various ways.

A. In the male of certain *Forficulidæ* (*Dermaptera*) the ducts unite at one part of their course to form an unpaired sperm vesicle, from which the two ducts again as vasa deferentia separately run towards the two male genital apertures. One of these ducts, however, becomes reduced (Fig. 344, *B*), while the other, as an unpaired ductus ejaculatorius, runs from the sperm vesicle to the outer aperture.

B. An unpaired invagination of the integument grows from without to meet the two ducts, so that these open externally as through an unpaired terminal portion lined with a chitinous cuticle (Fig. 344, *C-F*). The 2 ducts may open into the unpaired terminal section either by two separate apertures or by a single aperture. This arrangement is found in the *Apterygota*, also in the *Libellulidæ*, *Plecoptera*, *Orthoptera*, *Rhynchota*, and perhaps in other orders as well. Paired or unpaired accessory structures may appear in the terminal portion through secondary invaginations.

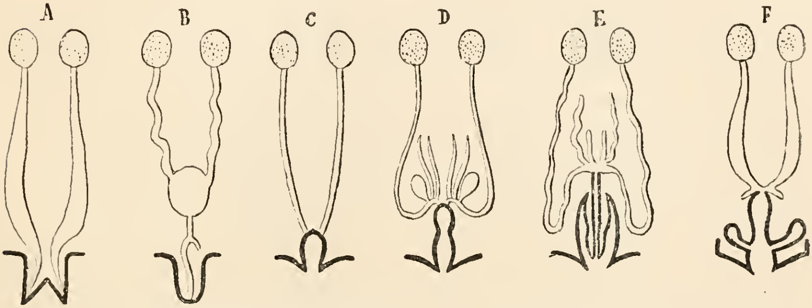


FIG. 344.—*A-F*, **Diagrammatic representation of the sexual apparatus of various Insects.** *A-E*, Male organs. *F*, Female apparatus. The parts proceeding from invagination of the outer integument are indicated by thick black lines. *A*, **Ephemerid.** *B*, **Forficula auricularia.** *C*, **Larva of Orthoptera.** *D*, **Œdipoda** (belonging to the *Acridiidæ*). *E*, **Cetonia aurata** (*Coleoptera*). *F*, **Æschna** (*Libellulid*) (after **Palmen**).

C. A second unpaired section is sometimes added to the unpaired terminal portion described under *B*; this section arises by the fusing of the two sperm ducts or oviducts throughout tracts of varying length to form one unpaired duct (ductus ejaculatorius, uterus, vagina, etc.), this unpaired duct enters the ectodermal invagination. This is probably the case in all the so-called higher insects (insects with complete metamorphosis).

The **position of the outer genital apertures** is very various.

In the *Chilopoda* among the *Myriapoda* the unpaired genital aperture lies in the penultimate body segment, *i.e.* in the genital segment, whose limbs may be transformed into genital appendages.

In the *Diplopoda* and *Pauropoda* the two genital apertures lie behind the 2d pair of legs, generally at the boundary between the 2d and 3d trunk segments.

In the *Symphyla* (*Scolopendrella*) the unpaired genital aperture lies on the 4th trunk segment between the legs of this segment.

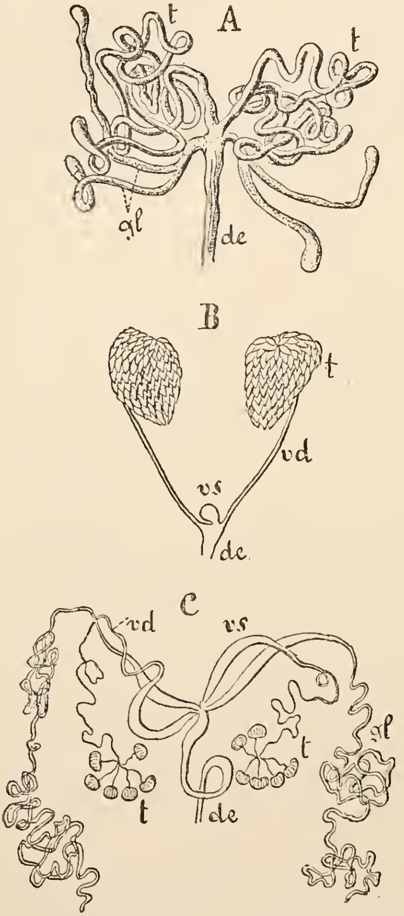


Fig. 345.—**Inner male sexual organs.** *A*, **Of Melophagus ovinus.** *B*, **Of Acheta campestris.** *C*, **Of Melolontha vulgaris** (after **Carus** and **Gegenbaur**). *t*, Testes ; *vd*, vas deferens ; *vs*, seminal vesicle ; *de*, ductus ejaculatorius ; *gl*, accessory glands.

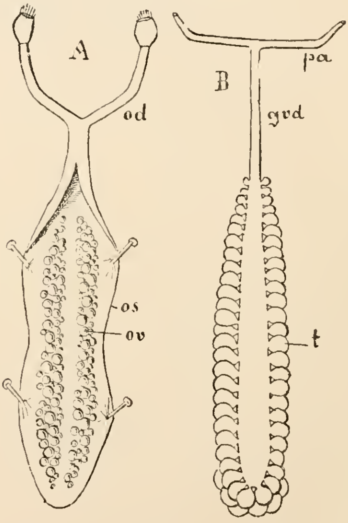


Fig. 346.—*A*, **Female.** *B*, **Male sexual organs of Glomeris marginata** (after **Fabre**). *os*, Opened ovarial sac, in which the two ovaries (*ov*) are seen ; *od*, oviduct ; *t*, testes ; *gvd*, common vas deferens ; *pa*, paired ducts.

In all *Hexapoda* the genital apertures lie at the end of the abdomen, in the male almost always behind the 9th, in the female behind the 8th (in the *Ephemeridæ* 7th) abdominal segment.

Accessory organs are almost always found connected with the ducts of the male and female sexual apparatus of all Antennata ; the special arrangement of these is very varied. Single or paired **sperm vesicles (vesiculæ seminalis)**, serving as sperm reservoirs, are often found in the male sex, either as invaginations of the ductus ejaculatorius or of the vas deferens. **Accessory glands** enter either the ductus or further back enter the vas deferens and mix a secretion with the sperm. Such glands occasionally yield a hardening secretion which encloses small masses of sperm in the form of capsules (spermatophores). The terminal section of the male sexual apparatus is often protrusible as a **penis.**

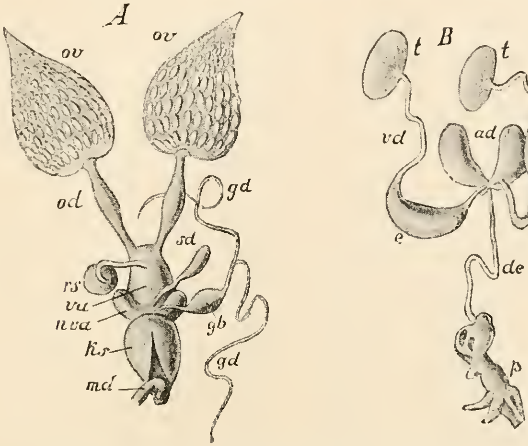


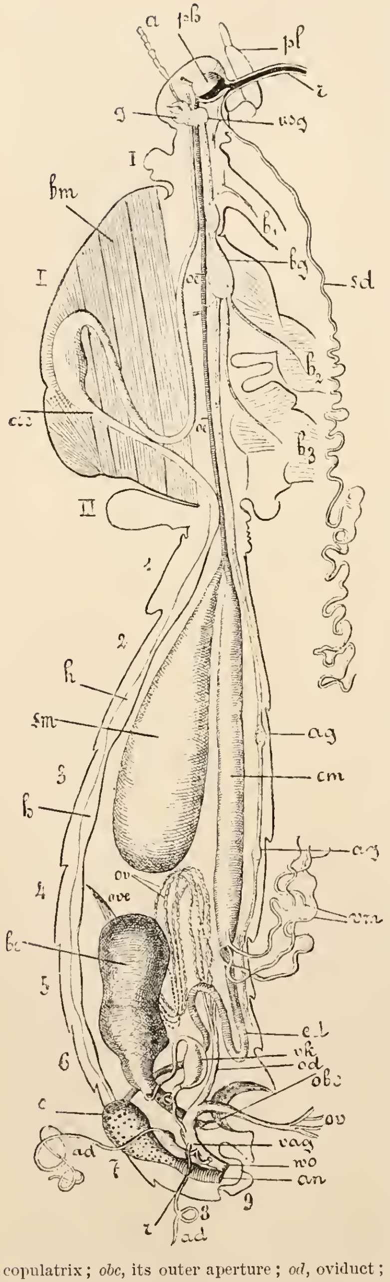
Fig. 347.—*A*, **Female.** *B*, **Male sexual apparatus of the Honey-bee** (queen and drone) (after **R. Leuckart**). *ov*, Ovaries, consisting of numerous chambered ovarian tubes; *vd*, oviducts; *rs*, receptaculum seminis; *va*, vagina; *nva*, accessory sac of the same; *ks*, bulb of the stinging apparatus; *md*, rectum twisted back and cut off; *sd*, colleterial gland; *gd*, poison glands; *gb*, poison vesicle; *t*, testes; *vd*, vas deferens; *e*, wider portion of the same; *de*, common ductus ejaculatorius; *ad*, accessory glands; *p*, penis.

Special invaginations from the vagina serve as **bursæ copulatrices** for the reception of the penis during copulation, and as **receptacula seminis** for the reception and the preservation of the semen. In the *Lepidoptera* (Fig. 348) the bursa copulatrix opens outward separately from the vagina, but is connected with the receptaculum seminis by a duct. The sexual apparatus often enters, close to the anus, the base of a common depression (cloaca). As in the male, so in the female, outer organs are formed by the integument of the last abdominal segments, and are brought into the service of the sexual apparatus as ovipositors, etc.

Colleterial or cement glands for attaching the eggs to foreign objects enter the vagina.

In most *Diplopoda* among the *Myriapoda* the legs of the 7th trunk ring are transformed into copulatory appendages.

The **germ glands of the Hexapoda** have still to be specially considered. The testes are, as has been already mentioned, almost always paired; in the *Lepidoptera*



alone they may fuse to form an apparently unpaired organ. Each testis consists of a smaller or greater number of **blind tubes** or **testicle follicles**; these, which are sometimes short, sometimes long and coiled, usually lie embedded in a common envelope. It may be accepted as a general rule, that where the testicle tubes are very long, they are few in number, and *vice versâ*. The *Diptera* and *Orthoptera* may serve as examples of the two extremes. In the former (Fig. 345, *A*) there is on each side only one very long coiled testicle tube, in the latter there are often many hundred short tubes or follicles united into one mass (*b*). The testis on each side also may fall into separate tubes or into separate groups of tubes (*c*). Only one **vas deferens** is, however, found on each side, into this enter the testicle tubes united into one testis, or the separate testicle tubes, or the ducts of several groups of such tubes. Just as the testes consist of a varying number of long or short testicle tubes, so each of the **ovaries** consists of a varying number of **ovarian tubes**, which together enter an oviduct. In each of these ovarian tubes (Fig. 349) we can distinguish three parts: (1) the terminal filament, (2) the terminal chamber, and (3) the actual ovarian tube, divided into chambers, this last is the largest.

FIG. 348.—**Danais archippus (Lepidoptera) Female.** Showing the **anatomy** after removal of the right half of the body. **Lettering of the head:** *a*, Antenna; *ph*, pharynx; *pl*, labial palps; *r*, proboscis; *g*, brain; *usg*, infra œsophageal ganglion. **Lettering of the thorax:** *I*, *II*, *III*, thoracic segments; b_1, b_2, b_3, the coxal joints of the 3 pairs of legs; *bm*, musculature; *ac*, aorta cephalica with its swelling; *oe*, œsophagus; *bg*, thoracic ganglia of the ventral chord; *sd*, salivary glands of one side, those of the other side cut off near their entrance into the common salivary duct. **Lettering of the abdomen:** *1-9*, abdominal segments; *h*, heart; *sm*, so-called sucking stomach (food reservoir); *cm*, chilific stomach (mid-gut); *ag*, abdominal ganglia; *ed*, hind-gut with colon (*c*) and rectum (*r*); *vm*, Malpighian vessels; *ov*, ovarial tubes, those of the right side cut off; *ove*, terminal filaments of the ovaries; *bc*, bursa copulatrix; *obc*, its outer aperture; *od*, oviduct; *vag*, vagina; *wo*, its outer aperture; *ad*, glandular appendages of the vagina partly cut away; *vk*, connective canal between vagina and bursa copulatrix with swelling (receptaculum seminis); *an*, anus (after **Burges**).

The thin **terminal filaments** of the egg tubes are generally attached to or near to the dorsal vessel, and thus form a sort of suspender. The elements of these are the same as those of the **terminal chamber.** The latter contains undifferentiated cell elements as remains of the ovarial rudiments, from which proceed (either in the embryo or the larva), on the one hand, the follicle epithelium of the ovarian tubes, and on the other, the ripening eggs and nutritive cells contained in these tubes. In the terminal chamber these cell elements remain undifferentiated, excepting when required for the renewal of the follicle epithelium, eggs, and nutritive cells in the adult insect. The **third section** which leads into the oviduct has usually the form of a string of beads. It contains the ripening eggs. The youngest and smallest lie nearest to the terminal chamber, the oldest and largest near the entrance into the oviduct. Two sorts of egg tubes have been distinguished: those without nutritive cells and those with nutritive cells. The most simple are the ovarian tubes **without nutritive cells** (Fig. 349, *A*), which are found *e.g.* in the *Orthoptera* and *Apterygota* (excluding *Campodea*). Here in each tube there is a simple row of eggs from the terminal chamber to the oviduct. Between these consecutive eggs the tube appears constricted, and this causes the beaded appearance. Those parts of the egg tube which lie between two constrictions, each of which contains one egg, are called **ovarian chambers.** In the **ovarian tube with nutritive cells** we must again distinguish two different types. In the **one type** (Fig. 349, *B*) **there is a regular alternation of egg chambers and nutritive chambers,** each of the latter containing one or more nutritive cells, which serve for the nourishment of the ripening egg contained in the neighbouring chamber. The ovarian and nutritive chambers may be distinctly separated externally by constrictions (*Hymenoptera* and many *Coleoptera*), or one nutritive and one egg chamber may lie in **each** section of the ovarian tube, which is externally visible as a swelling (*Lepidoptera*, *Diptera*). In the **second type** with nutritive cells, the actual tube consists (Fig. 349, *C*) of ovarian chambers only, the nutritive cells here remain massed together in the large terminal chamber. The single eggs in the tube are united with the terminal chamber by connective strands, which convey the nutritive material to the eggs.

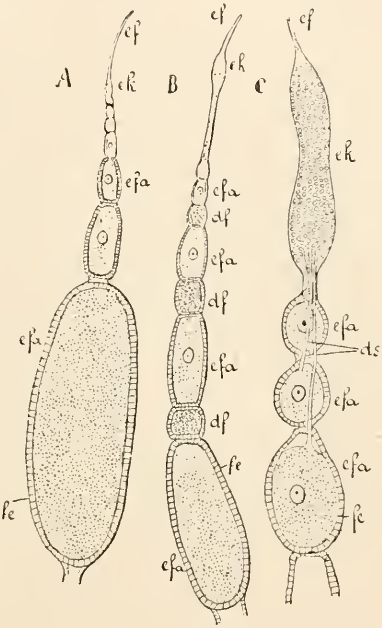


FIG. 349.—**Various types of ovarian tubes,** diagrammatic. *A*, Ovarian tube without nutritive cells. *B*, Egg tube with alternating nutritive and egg compartments. *C*, Ovarian tubes in which the terminal chamber (*ek*) is developed into a nutritive chamber, with which the developing eggs remain connected by means of strands (*ds*); *cf*, terminal filament; *ek*, terminal chamber; *efa*, egg compartments or chambers; *fe*, follicle epithelium; *df*, yolk chambers.

Egg cells, nutritive cells, and the cells of the follicle epithelium (epithelium of the chambers of the ovarian tubes) are, according to their origin, similar elements, like the egg and yolk cells of the Platodes; division of labour leads to their later differentiation. Only a few of the numerous egg germs develop into eggs, the rest serving as envelopes and food for these few.

In a few *Thysanura* (*Machilis*, *Lepisma*, and especially *Iapyx*) the ovarial tubes (5-7 on each side) are placed in the abdomen in more or less strict segmental arrangement. Each independently enters one of the two oviducts, which run through the abdomen as straight canals. The two oviducts open externally by a short unpaired terminal piece ; this common piece is said to be wanting in *Machilis*, only the outer aperture of the two oviducts being in this case common to both. In *Campodea* and the *Collembola* the ovaries and testes on each side are simple tubes.

XII. Dimorphism—Polymorphism.

In all insects the males and females differ, not only in the arrangement of their sexual organs, but also in various details of their outer organisation. This sexual dimorphism is in some cases very remarkable, and is generally connected with the absence of wings in the female, *e.g.* in the scale insects (*Coccidæ*), in the luminous *Coleoptera* (*Lampyridæ*), and in a few *Bombycina* (*Psyche*, *Orgyia*). In the parasitic *Strepsiptera* the females are legless, wingless, eyeless, and feelerless, and are thus like maggots. They are viviparous, and remain, as long as they live, enclosed in their pupal envelopes, inside the host, *i.e.* in the abdomen of various *Hymenoptera*.

In colonial insects polymorphism arises in consequence of division of labour between the individuals of the colony. In many colonial *Hymenoptera* (bees and ants) only a few of the females (queens) are sexually mature and capable of reproduction. The great majority of the other females (workers) have reduced sexual organs, and, among the ants, are wingless. Among the ants different forms of workers may appear (soldiers and workers proper). In the colonial *Termites*, and also among the *Corrodentia*, there are, besides the winged reproductive males and females, unwinged males and females with rudimentary sexual organs ; these are again divided into castes (workers, fighters), and vary in form accordingly.

XIII. Development and Life-History.

A. The Metamorphoses of Insects.

The greater part of the developmental processes, by means of which the adult insect is produced from the fertilised egg, take place within the egg-envelope. The time passed within the egg is the **period of embryonic development**. The organism which escapes from the egg-envelope, or in other words, is hatched from the egg, is always already very highly developed, and, apart from the fact that it has no wings, no mature sexual organs, and no compound eyes, is provided with all the typical insect organs in functional condition. It possesses a completely segmented body, antennæ, mouth parts, thoracic limbs, developed nervous, digestive, and tracheal systems, the dorsal vessel, the body musculature, etc. It moves and feeds itself independently. It is called a **larva**. The larvæ of the insects are thus, when hatched, far more highly developed than the larvæ of most other Invertebrata.

The changes which an insect undergoes before it becomes an adult sexually mature animal (**imago**) are extraordinarily various, and are conditioned by a whole series of co-operating factors, among which the most important are : (1) the degree of deviation of the imaginal form from the racial form ; (2) the different modes of life and of places of habitation of the larvæ and imagines.

I. The *Apterygota* (*Thysanura* and *Collembola*) are considered to have retained their original wingless condition, and in other ways also appear to stand nearest to the common racial form of the *Insecta*. The distinction between larva and imago is here wanting. The young animal hatched from the egg resembles in all points the sexually mature form, which it reaches by simple growth accompanied by ecdyses and by complete development of the sexual organs. Both young and adult animals live on land and lead the same sort of life. **Development without metamorphosis** (**Ametabole**).

II. The adult insect is, apart from the complete development of the sexual organs, principally distinguished by the possession of wings. In the simplest cases, in the *Orthoptera*, *Corrodentia*, *Thysanoptera*, and most *Rhynchota*, the larvæ lead the same kind of life as the imagines. They change gradually into the imaginal form, growing slowly through numerous ecdyses, while the wings arise and become more strongly developed each time the integument is shed. **Gradual metamorphosis.**

III. In the *Cicada* the modes of life of the imagines and the larvæ differ. The former live on trees and shrubs, the latter underground on roots, and for this purpose possess strong fore-feet adapted for digging. The transition from the last larval stage to the imago must here be accompanied by a transformation of the fore-legs. Since an intermediate life between that on trees and on the earth is not easily conceivable, and since, consequently, any intermediate form between ordinary feet and digging feet would be purposeless, the transition from the larva to the imago has become direct. The last larval stage is then what is called **quiescent**, *i.e.* the organisation of the imago develops within the chrysalis at the expense of the accumulated reserve material. **Gradual metamorphosis with pupal stage.**

IV. The modes of life of the larvæ and imagines of the *Ephemeridæ*, *Odonata*, and *Plecoptera* are very different. The imagines live on land, the larvæ have become adapted to aquatic life. In the transition to the imaginal form the tracheal gills are generally thrown off (*Ephemeridæ* and many *Libellulidæ*), the stigmata break through, and the tracheal system becomes holopneustic. In other forms the metamorphosis and the growth of the larvæ occur gradually (in *Chloë* by means of more than 20 ecdyses). **Incomplete metamorphosis** (**Hemimetabole**).

In cases II. III. and IV. the transformation of the larva into the imago is, as a rule, accomplished very gradually. The still wingless larva hatched from the egg shows an external organisation like that which the *Apterygota* possess throughout life, even in their sexually mature condition.

V. Some *Rhynchota* are wingless (the *Pediculidæ*, many bugs and the females of the plant-lice), and so are some *Corrodentia* (the *Mallophaga*), *Orthoptera* (various genera and species of *Blattidæ* and *Phasmidæ*), and *Dermaptera*. The wingless condition in these forms is derived, as opposed to that of the *Apterygota*; they are descended from wing-bearing *Rhynchota*, *Corrodentia*, *Orthoptera*, and *Dermaptera*, but their wings have been reduced in consequence of parasitism or of other habits of life. The larva hatched from the egg has not, therefore, to develop wings. This process is suppressed, and with it the metamorphosis. The young form becomes, by simple growth, the sexually mature imago. In contrast to the original ametabole of the *Apterygota* we have here an **acquired ametabole**.

VI. In contradistinction to the insects as yet mentioned, all others, *i.e.* the *Neuroptera*, *Panorpata*, *Trichoptera*, *Lepidoptera*, *Diptera*, *Siphonaptera*, *Coleoptera*, and *Hymenoptera*, are distinguished by so-called **complete metamorphosis** (**holometabole**). A wingless larva is hatched from the egg, which indeed grows and moults, but, nevertheless, always retains the same organisation and undergoes no transformation during the larval stage. At the end of larval life, however, when the fat body has become strongly developed by rich nourishment, the larva moults and passes over into the differently formed **pupal stage**. The pupæ are very variously shaped, often distinctly segmented with rudimentary extremities and wings, often with concealed extremities. They are generally quiescent, immovable, and not capable of taking food, and are often surrounded by special protective envelopes—**cocoons**. The best known cocoons are those of the Lepidoptera, which are spun by the caterpillars from the secretion of their spinning glands. At the end of pupal life the envelope is opened and the imaginal insect (beetle, butterfly, fly, etc.) issues from it.

This complete metamorphosis evidently proceeds from an incomplete or gradual metamorphosis. The wingless larva adapts itself to various conditions of existence, or is provided by its parents with excessive nourishment. It accumulates so much reserve material in its fat body that the further larval stages do not need to feed independently. By the suppression of numerous ecdyses these successive larval stages are abbreviated into one stage,—the stage of the outwardly quiescent pupa, within which the imago attains development at the expense of the reserve nourishment.

The larvæ of insects with complete metamorphosis vary much in their organisation, each being adapted to its own special surroundings. Two principal groups can, however, be distinguished: (1) **with feet**, *e.g.* the larvæ of the *Neuroptera*, the "caterpillars" of the *Lepidoptera*, the larvæ of the *Coleoptera* and *Trichoptera*; (2) **without feet**, maggot-like larvæ of the *Diptera*, larvæ of most *Hymenoptera* and *Siphonaptera*. The former by possessing legs are the least removed from the Thysanura-like larval form of other winged insects; they move freely, and with few exceptions feed independently. Many are carnivorous, living either on land or in water; many feed on plants, on the leaves (caterpillars) or roots (cockchafer grubs). Among the *Hymenoptera* the larvæ of the *Tenthredinidæ* are vermiform, and like the butterfly caterpillars possess parapodia-like appendages on several abdominal segments in addition to the thoracic feet.

The modes of life of the footless larvæ of the *Diptera* and most *Hymenoptera* are very varied. They sometimes live free and are carnivorous, generally living then in water; sometimes they are parasitic in the bodies of other animals or in plant tissue; sometimes in putrefying matter, dung, etc.; sometimes inside cases or cells which are filled with nutritive material; sometime they are fed by the adults, etc. etc. Headless maggots without feelers or ocelli and with reduced mouth parts are distinguished from larvæ which have heads with these organs.

The larvæ of insects with complete metamorphosis are all originally peripneustic. By adaptation to aquatic or parasitic life they may become amphipneustic, metapneustic, or even apneustic, and in the last case may develop trachæal gills. The mouth parts of the larva may differ greatly from those of the imago. This difference is best known and most striking in the *Lepidoptera*, whose larvæ have masticating mouth parts, while their imagines have sucking mouth parts.

The more specialised the larva on the one hand and the imago on the other, and the greater the difference in organisation between them, the more far-reaching naturally are the transformations by means of which during the pupal period the larval organisation becomes that of the imago. For instance, in the bee, the larva does not pass direct into the pupal stage, but first into the pre-pupal stage.

In certain *Coleoptera* several larval stages differing very much from one another are met with. The Coleopteran genus *Sitaris* (Fam. *Meloidea*) lives parasitically on a bee (*Anthophora*). The larvæ of this beetle, which are hatched from the egg, are active little animals with thoracic legs. They lurk in flowers in order to spring upon the bees coming to gather honey. They are thus carried to the hive, where they seize upon the eggs of the bee as soon as these are laid in the honey of the cells, and devour them. They afterwards moult and appear, after ecdysis, as metapneustic maggot-like larvæ with reduced feet, floating on the surface of the honey, the mouth placed below, and the posterior end on the surface. When the honey is exhausted they pass into a pupa-like stage, out of which, however, not the imago, but a new larva emerges. Still further pupa-like stages of development then follow, till at last the final real pupa stage occurs. Here we can very clearly recognise, especially in the first two larval stages, the influence of various modes of life on the larvæ of one and the same animal.

Many *Pteromalidæ* (*Hymenoptera*) pass through a series of peculiarly shaped larval stages, which are as yet by no means explained. The larvæ live parasitically in the eggs, larvæ, and pupæ of other insects, in which the *Pteromalidæ* lay their eggs by means of an ovipositor. It is remarkable that the youngest larvæ possess far less highly developed inner organs than are usually found in the larvæ of other insects.

The above is naturally but a very incomplete description of this most interesting subject.

B. The Embryonic Development of Insects.

Hydrophilus, the water beetle, affords us a good illustration of this development.

The egg is a long oval, with pointed anterior and blunt posterior pole. The segmentation is that typical of the centrolecithal eggs, and leads to the formation of a blastosphere. In this blastosphere we can distinguish a single superficial layer of small cells, the **blastoderm**, and, enveloped by it, the **nutritive yolk** with scattered nuclei.

The formation of the embryo proceeds from one side of the blastosphere only, *i.e.* from the future ventral side, on which the blastoderm cells are higher than elsewhere. We may call this portion of the blastoderm the embryonic rudiment. At an early stage we can distinguish the boundaries of the segments, appearing externally as transverse streaks or lines. Anteriorly and posteriorly two longitudinal furrows appear, grow towards each other and unite, so as to mark off on the embryonic rudiment a peripheral portion, the **lateral plates,** from a central portion, the **middle plate.** The middle plate sinks below the surface, and so forms the floor of a channel-like medio-ventral invagination, whose edges grow towards each other on each side. This invagination is represented in transverse section in Fig. 350, *A*. Its edge is to be considered as the edge of the blastopore. How the lateral edges of this blastopore approach each other in the middle line and finally fuse with each other is illustrated by Fig. 352, *A*, *B*, *C*. After the closing of the blastopore the invagination becomes a medio-ventral longitudinal tube, over which the blastoderm of the former lateral plates spreads. From this invaginated tube proceed the mesoderm and perhaps also the endoderm (epithelium of the mid-gut).

Even before the closing of the blastopore the rudiments of the embryonic envelopes so common among insects, viz. the **amnion** and the **serous envelope**, appear. They first appear as a fold of the blastoderm at the edge of the embryonic rudiment. This fold grows more and more from all sides over the embryonic rudiment, finally covering it. The embryonic rudiment thus comes to lie in the base of a cavity whose mouth, wide open at first, grows smaller and smaller by the growing and final closing together of the amnion folds; the final closing takes place over the anterior end of the embryonic rudiment. The tranverse section *B*, Fig. 350, shows the rising amnion folds, the transverse section *C* shows them grown over the embryonic rudiment so as to form a continuous cover. In the surface views of Fig. 352 the folds are denoted by *af′* and *af″*.

The cavity which is formed by the amnion is called the **amnion cavity.** Its roof, in correspondence with its origin, consists of 2 epithelial lamellæ, an inner one, which at the edge of the embryonic rudiment is continued into its blastoderm and represents the actual **amnion,** and an outer one, which at the edge of the embryonic rudiment is continued into the blastoderm of the whole remaining surface of the egg, and

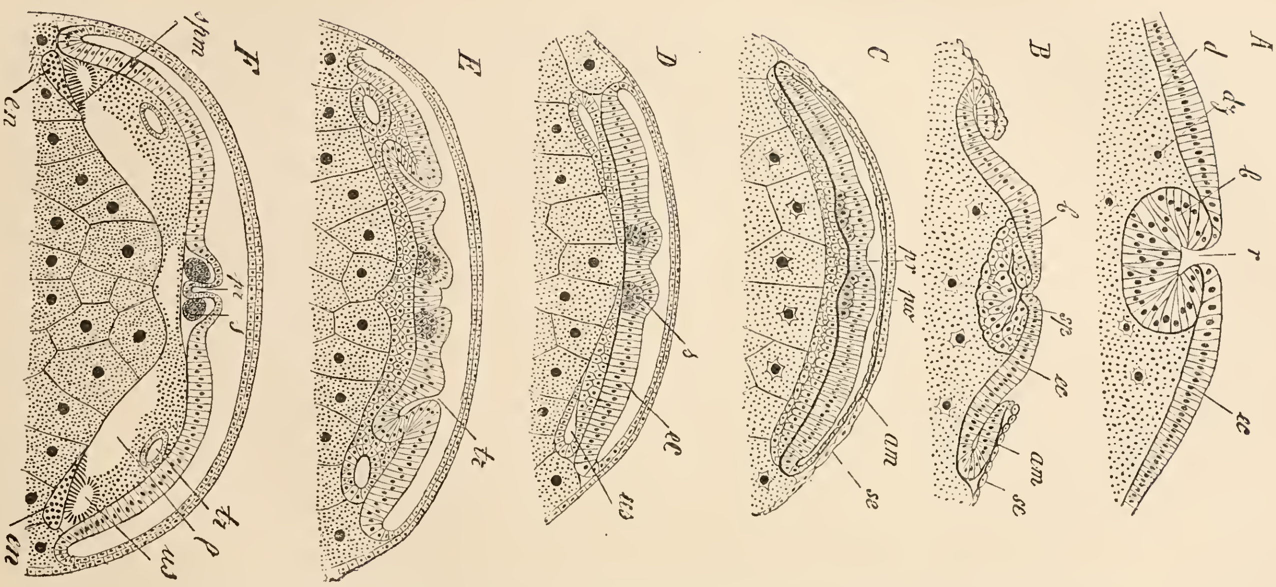


Fig 350.—**Transverse section through the embryonic rudiment at 6 consecutive stages of the development of Hydrophilus** (after **Heider**). *A* corresponds with the stage depicted in Fig. 352, *A*, at the point *a*, where the edges of the invagination have most nearly approached each other. *B* is a transverse section through the stage Fig. 352, *D*, at the point where the amnion folds have not yet completely overgrown the germ streak at the anterior end of the body. *C* is a transverse section through a trunk segment of the stage depicted in Fig. 352, *E*. *D*, *E*, *F* are transverse sections of older stages; *am*, amnion; *b*, median invagination of the blastoderm, the greater part of which becomes the mesoderm; *d*, nutritive yolk; *dz*, yolk cells; *ec*, ectoderm; *pr*, primitive groove; *pw*, rudiment of the central nervous system; *r*, blastopore; *sp*, slit in the mesoderm (remains of the lumen of the invagination); *se*, serous envelope; *l*, definitive cœlome; *en*, endoderm; *s*, lateral strands of the ventral ganglionic chain; *spm*, visceral layer of the mesoderm; *tr*, tracheal rudiment (in *E* as an invagination of the ectoderm, in *F* in transverse section); *us*, primitive segment (mesoderm cavity).

together with this represents an unbroken epithelial membrane, the **serous envelope**; this latter surrounds the whole egg with its embryonic rudiment and the amnion on all sides.

The amnion and the serous envelope have no share in the building up of the embryo. The latter develops exclusively out of the blastoderm of the embryonic rudiment and the invaginated tube, which we will call the germ streak. The blastoderm of the embryonic rudiment grows further and further dorsally at its peripheral edges, so that at last it envelops the embryo on all sides as **ectoderm.** Though somewhat out of its strict order, for the sake of clearness, this process as well as the fate of the **amnion** and **serosa** may be here illustrated by means of the following diagramatic transverse sections. Fig. 351, *A*, represents the same stage as Fig. 350, *F*, but the position of the embryonic rudiment is reversed. In Fig. 351, *B*, we see the amnion and the serous envelope torn in the ventral middle line, after they had previously grown together. The amnion and the serous envelope thus form on each side a fold projecting ventrally. In *C* the serosa has contracted and has become the so-called dorsal plate, which now consists of high cylindrical epithelium. At the same time the ectoderm of the embryonic rudiments on both sides has extended

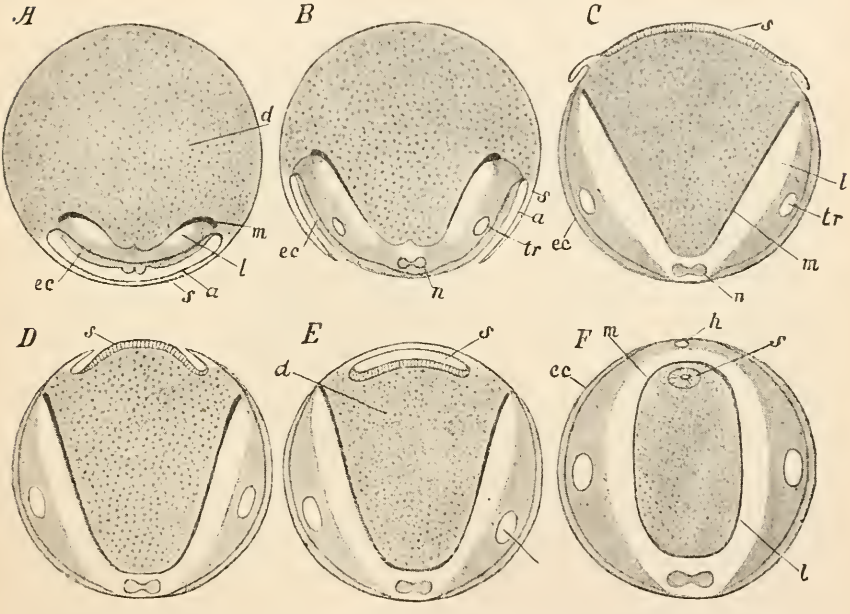


Fig. 351.—**Formation of the dorsal tube (process of involution of the embryonic integuments) in Hydrophilus (after Graber and Kowalevsky).** *A*, Transverse section through an egg, whose embryonic rudiment is still covered by the amnion (*a*) and serosa (*s*). *B*, Amnion and serosa having grown together in the middle line have now torn open, drawing back on each side to form a fold. *C*, The fold, by the contraction of the serosa becomes more dorsal. *D*, The contracted serosa (dorsal plate) is being grown over by the fold. *E*, The dorsal tube has become closed by the growing together of the folds. *F*, The mid-gut is closed dorsally and has enclosed the dorsal tube (*s*). *a*, Amnion; *d*, nutritive yolk; *h*, heart; *l*, cœlome; *m*, rudiments of mid-gut; *n*, nervous system; *s*, serosa and the structures developed out of it, *i.e.* the dorsal plate and dorsal tube; *tr*, principal tracheal trunk; *ec*, ectoderm.

further dorsally. In *D* the fold (which proceeded from the amnion and a part of the serous envelope) has bent back and the dorsal plate has contracted still more. In *E* the folds have overgrown the dorsal plate and their edges have grown together in the middle line. By this process the so-called **dorsal tube** comes into existence, and then sinks into the yolk. The ectoderm then joins over the dorsal side of the embryo. The tube of the mid-gut enclosing the yolk, together with the dorsal tube, is formed by the complete surrounding of the yolk by the endoderm. The dorsal tube is then broken up with the yolk and reabsorbed within the mid-gut.

In other insects these processes take the same course. The most important difference is caused by the fact that from the first the yolk penetrates between the amnion and the serosa, so that the embryo with the amnion seems to be imbedded deep in the yolk. The amnion remains connected with the serosa at one place only. At the place where the two membranes adhere a rent arises later, through which the embryo together with the amnion are everted. In the *Lepidoptera* no dorsal tube is formed. The embryonic integuments are here simply constricted off from the embryo and serve as the first food of the young grub. This is perhaps also the case in the *Diptera* and *Hymenoptera*.

To return now to the **developmental processes in the embryonic rudiment itself,** we must go back to Fig. 350, *B*. The blastopore here appears closed. The invaginated tube (germ streak) is compressed dorso-ventrally and has a slit-like lumen. The transverse section *C* of a still later stage shows us the germ-streak spread out flat under the ectoderm. On each side of the middle line the latter is thickened and bilaminar. The thickened parts are transverse sections of **longitudinal thickenings** (primitive thickenings), between which there is a shallow median longitudinal groove (primitive groove). The deeper cells of the longitudinal thickenings form the two **lateral strands**, from which come the paired portions of the ventral chord. The so-called **yolk furrowing** has taken place at this stage, the yolk belonging to each nucleus being marked off, so that the whole is divided into irregular masses.

In the transverse section *D* we see the germ streak divided into two lateral halves, a cavity appearing in each half; these cavities become those of the primitive segments. These appear more clearly demarcated in the transverse section *E* of an older stage. They are the **mesoderm cavities**, which are repeated segmentally on each side. The remaining mesoderm of the germ streak has again united in the middle line. On each side near the primitive thickenings the ectoderm becomes invaginated to form a trachea. These **tracheal rudiments** appear segmentally in pairs, as is shown in the ventral surface view, Fig. 353, where their outer apertures (stigmata) are seen.

In the transverse section *F* of a later stage the germ streak has drawn back somewhat from the surface of the yolk, and so gives rise to a cavity, which becomes the definitive cœlome and later joins the segmental cavities. The longitudinal trunks of the tracheæ are already formed, as shown in transverse section. The lateral strands of the nervous system have separated from the ectoderm (hypodermis), and the primitive groove between them has deepened. The fusing of its base with the lateral strands yields the **transverse commissures of the ventral chord.** We find in each side between the yolk and the segmental cavities a newly formed layer of cells. This cell layer represents the **endoderm.** Gradually extending all over the surface of the yolk, it becomes the **epithelium of the mid-gut which encloses the yolk.** The yolk is gradually absorbed later. The wall of the mesoderm cavities which is in contact with the endoderm follows the latter, as it grows over the yolk and yields, as the **visceral layer** of the mesoderm, the muscular wall of the mid-gut.

Long before all these processes have taken place the **stomodæum** has formed at the anterior (head) end of the embryonic rudiment and at the posterior end (in the terminal segment) the **proctodæum,** both being ectodermal invaginations which become connected with the mid-gut at a later stage. The **Malpighian vessels** arise as invaginations from the ectodermal proctodæum.

The **limbs** (Fig. 353) appear as paired bud-like outgrowths of the ectoderm and the subjacent mesoderm; they appear between the primitive thickenings of the nerve chord and the stigmata.

It is an important fact that besides the rudiments of the head and thoracic limbs, which alone are present in the adult animals, there occur at a certain stage distinct rudiments of abdominal limbs as well, those of the first abdominal segment being particularly clear (cp. especially Fig. 353, *B*). These rudiments degenerate later.

The origin of the two endodermal cell layers, which we saw appear in the transverse section (Fig. 350, *F*), is difficult to explain. At the stage at which this section is taken, the whole endodermal rudiment consists of two lateral cell streaks between the yolk and the two rows of mesoderm cavities. Anteriorly at the stomodæum and posteriorly at the proctodæum the two streaks pass into one another. At earlier stages the endoderm consists of an anterior and a posterior U-shaped double streak. The limbs of the U, which are very short to begin with, are at first directed backward in the anterior double streak, and forward in the posterior streak; they gradually elongate till at last the two anterior limbs meet the two posterior, and thus give rise to the two above-mentioned endodermal streaks. The first origin of the two U-shaped double streaks must probably be sought in the anterior and posterior ends of the median invagination of the blastoderm of the embryonic rudiments, which elsewhere forms only mesoderm. The whole invagination would thus be the rudiment of the mesoderm plus the endoderm, and might be regarded as the gastrula invagination. In a transverse section of the still open anterior part of the invagination its base would represent the formative zone of the U-shaped endodermal streaks, while the lateral somewhat bulged-out walls yield mesoderm. The mesodermal germ streak would thus be continued anteriorly in two lateral bulgings of a gastrula invagination, and we are therefore inclined to regard the mesodermal formation of insects as a modification of that manner of forming the mesoderm in which it proceeds from paired invaginations of the archenteron.

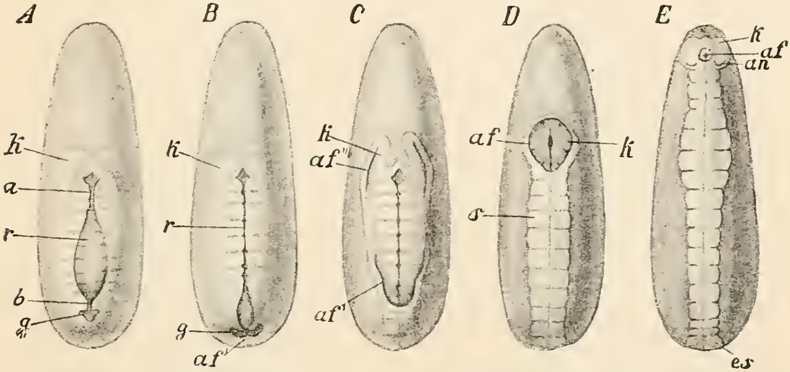


Fig. 352.—*A-E*, **Ventral view of 5 stages in the development of Hydrophilus** (after **Heider**). The anterior end is directed upward. *a* and *b*, Points at which the blastopore first closes; *af*, edge of the amnion fold; *af'*, caudal fold; *af''*, paired cephalic fold; *an*, antenna; *es*, terminal segment; *g*, pit-like invagination (rudiment of the amnion cavity); *k*, procephalic lobes; *r*, groove-like medio-ventral invagination; *s*, germ-streak covered by the amnion.

According to another view, the yolk with its nuclei represents the endoderm, and yields the epithelium of the mid-gut in a way which has not been more closely observed. Other observers, again, maintain that the whole enteric epithelium is formed from the proctodæum and the stomodæum.

It would perhaps be worth while to investigate whether the endoderm does not arise from the yolk cells by a kind of micromere formation, in a way similar to that in which the ectoderm is produced in many animals whose eggs contain much nutritive yolk (cp. p. 124, etc.)

The **heart** arises out of two lateral originally widely separated rows of mesoderm cells. Each row, by sending out muscular processes, forms the side of a groove. The two sides move towards each other, uniting later in the middle line to form the cardial tube.

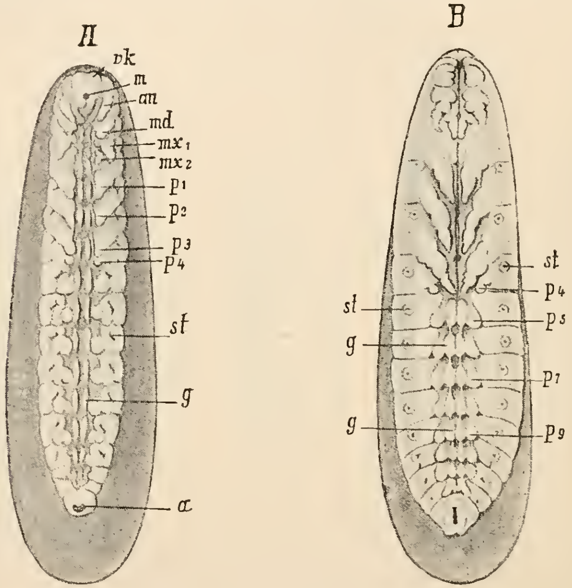


Fig. 353.—*A* and *B*, **Hydrophilus embryos with the rudiments of the extremities** (after **Heider**). In the somewhat older embryo, *B*, the rudiments of abdominal feet, which disappear later, are distinctly seen. *a*, Anal aperture; *an*, antenna; *g*, rudiment of the ventral ganglionic chain; *m*, oral aperture; *md*, mandible; mx_1, first maxilla; mx_2, second maxilla (rudiment of the lower lip); p_1, p_2, p_3, thoracic legs; p_4, p_5, p_7, p_9, rudiments of the extremities of the first, second, fourth, and sixth abdominal segments; *st*, stigmata; *vk*, procephalon.

The **brain** arises, like the ventral chord, as two lateral ectodermal thickenings (neural plates), which remain separate from each other for a considerable time, but from their first appearance are continuous with the lateral strands of the ventral chord. Besides this a second ectodermal invagination on each side takes part in its formation.

Opinions as to the development of the **eyes** in insects still differ very much. According to recent observations it appears probable that both the compound and the simple eyes proceed from invaginations of the ectoderm, which become constricted off as vesicles, and only secondarily become connected with the optic portion of the brain (ganglion opticum).

The first appearance of the **sexual organs** is not yet sufficiently investigated.

C. The Inner Processes in the Metamorphoses of Insects.

In insects without metamorphosis or with gradual or incomplete metamorphosis the organs of the larva simply pass into those of the imago. There is no breaking up and disappearance of the larval organs, and no new formation of the imaginal organs, if we leave out of account the throwing off of tracheal gills and the formation of wings, compound eyes, and so on.

In insects with complete metamorphosis the case is different. The larval organisation has here been adapted, independently of the imago, to special conditions of existence. A gradual continuous transformation of the larval organs into the often quite differently constructed organs of the imago, during which the different stages would feed independently, is inconceivable, since organs undergoing such complete transformations could hardly be capable of functioning. There are, further, numerous phenomena in the most various divisions of the animal kingdom which prove that organs which have functioned actively during larval life are only slightly capable of development and metamorphosis. They are more often reabsorbed or thrown off in the further course of development. We thus see why in insects with complete metamorphosis the transition from the larva to the imago almost necessarily takes place during a pupal stage, the pupa changing into the imago partly at the expense of the reserve nourishment accumulated by the larva, it being unable to acquire food for itself.

So as to understand the inner processes in the metamorphosis of the holometabolistic insect, we will take as an example the larva of *Corethra plumicornis* (*Diptera, Tipularia*). Most of the larval organs here simply pass during metamorphosis into those of the pupa and of the imago. The larva, however, is footless and wingless. The rudiments of feet and wings form shortly before the pupal stage. Three pairs of ventral and 3 pairs of dorsal invaginations of the hypodermis appear and are called imaginal discs. In the bases of these invaginations outgrowths appear and grow continuously longer, while the invagination in which they lie deepens (Fig. 354). The outgrowths in the 6 ventral invaginations are the rudiments of the thoracic limbs, the outgrowths of the 2 posterior dorsal pairs of imaginal discs are the rudiments of the wings and halteres which thus lie hidden within the body, till they are protruded and attain development. The muscles of the wings are already rudimentarily present in the embryo as cell strands, but they only begin to differentiate at the end of larval life.

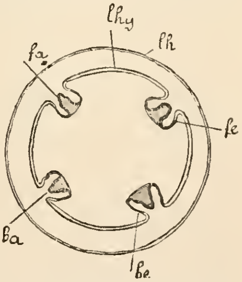


Fig. 354.—**Rudiments of the imaginal discs in the larva of Corethra,** diagrammatic. Invaginations (*fe* and *be*) of the larval hypodermis (*lhy*), in whose bases the rudiments of wings (*fa*) and legs (*ba*) arise; *lh*, chitinous integument of the larva.

The complete metamorphosis of some insects, especially of the *Muscidæ* (*e.g. Musca vomitoria*), is accompanied by far more thorough transformations.

It must, first of all, be pointed out that the distinction between larval, pupal, and imaginal stages rests upon external phenomena. In the inner organisation the series of alterations is continuous; the larva on the one hand already possesses the rudiments of the imaginal organs, and in the pupa on the other, the larval organs only gradually disappear. Speaking generally the inner metamorphosis is such that the imaginal organs proceed out of parts of corresponding larval organs, which remain during larval life in an undifferentiated embryonic condition (formative centres); the portions which function during larval life gradually disappear during metamorphosis in proportion as the imaginal parts attain development. The amœboid blood corpuscles play an important part in the breaking up and disappearance of the larval organs; since they, as **phagocytes (leucocytes)** seize upon the elements of the larval organs, and like amœbæ take them into their protoplasm. The phagocytes thus laden with the wrecks of the larval organs and floating in the body cavity are themselves later turned into food for the developing imaginal portions, especially for the epithelia, into which they immigrate and break up.

At the end of larval life there are found in the **thorax** imaginal discs similar to those in the *Corethra* larva. They here lie, however (Fig. 355), much deeper in the body, and are connected with the hypodermis by means of long cell strands which are hollow only in the neighbourhood of the imaginal discs. The thoracic limbs and wings begin

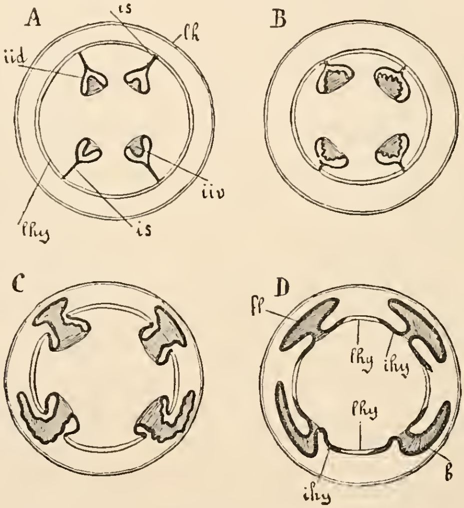


FIG. 355.—*A*, *B*, *C*, *D*, Diagrammatic representation of the **development of the wings, legs, and the imaginal hypodermis of the Muscidæ from the imaginal discs of the larva during metamorphosis,** diagrammatic transverse sections. *lh*, Chitinous integument of the larva, from which the subjacent hypodermis (*lhy*) has withdrawn; *iid*, imaginal discs of the wings; *iiv*, of the thoracic legs; *is*, the strands connecting them with the hypodermis; *fl*, wing rudiments; *b*, leg rudiments; *ihy*, imaginal hypodermis, spreading out in *D* from the imaginal discs. The imaginal rudiments of the hypodermis are indicated by thick black outlines, the larval hypodermis by two thin parallel lines.

to form in just the same way as in *Corethra* as outgrowths within the imaginal sacs. At a later stage the processes of the imaginal discs which are connected with the hypodermis shorten and become hollow. The larval hypodermis then opens over the imaginal discs, which have moved outwards, and the feet and wings come freely to the surface. A new hypodermis layer spreads out from the imaginal discs over the thorax: this is the rudiment of the imaginal hypodermis, while in proportion as the imaginal hypodermis spreads, the larval falls to pieces and disappears, in such a way that the larval and imaginal hypodermis taken together at all stages of the metamorphosis form a continuous cover round the body. While in the thorax the formation of the imaginal hypodermis proceeds from the imaginal discs, in the **abdomen** it proceeds (later than in the thorax) from the formative centres, the so-called islands, in the hypodermis. In each abdominal segment there are four larger and two smaller islands (Fig. 356).

In trying to understand these metamorphosic processes we must always keep in view that ecdysis only affects the chitinous cuticle of the body, from which the subjacent hypodermis withdraws, secreting a new chitinous integument under the old one.

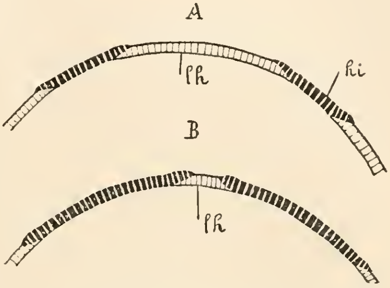


Fig. 356.—*A* and *B*, Diagrammatic representation of the **formation of the imaginal hypodermis in the abdomen of the Muscidæ**, proceeding from the centres of the imaginal hypodermis (islands) (*hi*). *lh*, Larval hypodermis.

The formation of the **head** is very peculiar. It is (as œsophagus and optic vesicles connected with the œsophagus) invaginated into the thorax, and is later evaginated anteriorly out of the thorax during the pupal stage. The anterior part of the œsophagus becomes in this process the neck, which after the evagination of the head connects it with the thorax.

Of the inner organs, the **heart** and the rudiments of the **sexual organs** seem to pass direct into the corresponding organs of the pupa.

The whole **musculature** of the larva except a few muscles of the second thoracic segment **disappears.** The imaginal connective tissue and the greater part of the imaginal musculature are formed anew from the mesoderm elements, which early appear on the inner side of the imaginal discs. Perhaps the imaginal discs themselves yield, besides the thoracic hypodermis, the mesodermal layers belonging to them as well ; this point, however, needs further investigation. Certain dorsal muscles of the second thoracic segment of the larva do not disappear, but are transformed during a temporary loss of their transverse striation into the wing muscles of the imago.

A large part of the larval **tracheal system** disappears. The imaginal tracheal system seems to be regenerated out of scattered cells and cell groups of the larval tracheal hypodermis. In the **digestive tract** the greater part of the mid-gut disappears. The imaginal mid-gut forms anew out of persistent epithelial islands of the larval mid-gut. Parts of the fore- and hind-guts proceed direct from the fore- and hind-guts of the larva, while other parts arise out of circular islands or formative centres, the so-called **imaginal rings**, of the larval fore- and hind-guts.

The central portion of the **nervous system** (brain and ventral chord) and probably also the beginnings of the larger peripheral nerves proceed by means of peculiar alterations and transformations from the corresponding parts of the larva.

The **salivary glands** of the larva fall to pieces and disappear, falling victims to the leucocytes. The imaginal salivary glands are regenerated out of imaginal rings of the larval glands. The larval **fat body** is gradually devoured by the leucocytes.

As already pointed out, the **disintegration of the larval organs and the new formation of the imaginal organs** do not belong to two distinct periods. Both processes go on side by side, so that in general there is no discontinuity either in the outward form or in the structure of the organs. Physiological discontinuity prevails only in this sense, that the organs cannot, during transformation, perform their respective functions.

Parthenogenesis—Cyclic Reproduction—Pædogenesis.

Parthenogenesis occurs in many insects, and especially frequently in the plant lice (*Rhynchota*) and in many *Hymenoptera*, though here also, most probably, it is not the only method of reproduction, but merely alternates with reproduction by means of fertilised eggs. In the colonial *Hymenoptera* only males come from unfertilised eggs. In the *Aphides*, in summer, several generations of parthenogenetically reproducing, viviparous, generally wingless females succeed one another. The last viviparous summer generation, however, produces winged males, and either winged or wingless females, whose fertilised eggs remain through the winter. From these latter the first summer generation of parthenogenetically reproducing females is again produced. The reproductive cycle of *Phylloxera* is similar, with this distinction only, that all the generations are wingless, except that one out of whose eggs the sexual (male and female) generation is produced. *Phylloxera* is not viviparous.

The reproductive arrangements of *Chermes* are very peculiar; the males of this fir louse were, till recently, altogether unknown.

A **wingless** generation (I.) of *Chermes abietis* hibernates on the fir-tree, and in the spring lays unfertilised eggs, out of which a second **winged** generation (II.) of females is produced. Some of these females migrate from the fir to the larch. From their unfertilised eggs a third **wingless** generation (III.) of females comes, which winter in the larch, and in the spring of the second year lay unfertilised eggs, from which a fourth **winged** generation (IV.) of females comes. These fly back to the fir tree, and from their unfertilised eggs a fifth generation (V.) of **males and females** is developed. **The sixth generation** (VI.) which comes from the fertilised eggs of this generation, again corresponds with the first hibernating generation with which we started. Some of the second winged generation (II.) of females, however, remained on the fir-tree. From the unfertilised eggs of these females which remained arises an unwinged generation of females, and these, again, are succeeded by a winged summer generation, and so on. In this second parallel series of generations of *Chermes* individuals which remained on the fir-tree, two generations of females appear yearly, alternately winged and wingless, both reproducing parthenogenetically. Now it is probable that in this parallel series the generations do not thus reproduce (parthenogenetically) *ad infinitum*, but rather that, sooner or later, the parallel series re-enters the original series, so that then a generation of males and females again appears. The different generations differ considerably from each other in form, even apart from the alternating absence or presence of wings.

The *Aphides* afford an example of a kind of cyclic reproduction (**heterogeny**) in which the parthenogenetically reproducing females are viviparous. The unfertilised eggs here develop within the mother body. A similar phenomenon occurs in the *Diptera* (*Cecidomyia*) also; here, however, in the generation of females which reproduces parthenogenetically, the germarium which corresponds with the ovary becomes mature very early, *i.e.* in the larval stage. The unfertilised eggs are here developed within the larval body; thus, in the cycle of reproduction of *Cecidomyia*, an imaginal generation reproducing sexually by means of fertilised eggs alternates with several generations of parthenogenetically reproducing viviparous larvæ. This special kind of heterogeny is called **Pædogenesis.** In one species of *Chironomus* also the pupa may occasionally lay eggs, which develop just in the same way as the fertilised eggs of the imago.

D. Development of the Myriapoda.

The embryonic development of the *Myriapoda*, as far as it is known, does not greatly differ from that of *Insecta*. Embryonic envelopes, however, do not appear to form.

When the young *Myriapoda* are hatched, they are either provided with the definitive number of segments and legs, as is the case in the *Scolopendridæ* and *Geophilidæ* (*Chilopoda*), or they possess a smaller number, to which the missing ones are gradually added posteriorly during the many moults undergone by the animal. The young of the *Scutigeridæ* and *Lithobiidæ* (*Chilopoda*) have 7 pairs of legs. The number then increases to 15. The young *Diplopoda* (Fig. 357), on the contrary, have only 3 pairs of feet on the 3 anterior trunk segments, and a few posterior segments still limbless. They thus recall the type of the Insect larvæ. New segments gradually appear posteriorly and the number of legs increases. After each moult the number of rings is greater; the increase generally takes place very irregularly, so that (*e.g. Polydesmidæ*) stages with 7, 9, 12, 15, 17, 18, 19, and finally 20 rings, succeed one another. From the above we see, firstly, that a sort of metamorphosis takes place in many *Myriapoda*, and, secondly, that the body there differentiates from before backward, a point which can no longer be made out in the *Insecta*.

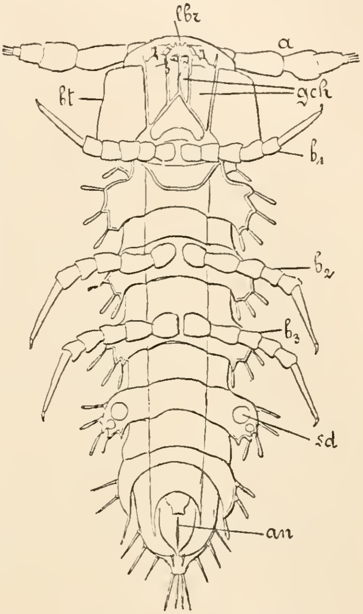


FIG. 357.—**Larva of Polydesmus complanatus**, just hatched (after **v. Rath**). *lbr*, Upper lip; *a*, antenna; *bt*, sides of the head (cheeks); *gch*, gnathochilarium; b_1, b_2, b_3, the three pairs of legs of the larva; *sd*, glands (saftdrüsen); *an*, anus.

XIV. Phylogeny.

Of the Antennata now living, the *Symphyla*, perhaps, stand nearest the common racial form. Yet even they are one-sidedly developed, and many of their organs, and above all, the tracheal system, by no means show a primitive arrangement. From the common racial form of the Antennata, the *Myriapoda* branched off to the one side, and the *Hexapoda* to the other. The different orders of *Myriapoda* perhaps developed polyphyletically, while for all *Hexapoda* we can assume one common racial form, resembling the now living *Apterygota*, and especially the *Thysanura*. There is thus no special reason for considering the *Apterygota* as originally winged insects, which became sexually mature at progressively earlier stages of development, and finally at a larval stage. At least one reason against such a supposition is the occurrence of the protrusible vesicles in the abdomen of the *Thysanura*, which is present in the *Myriapoda* (*Lysiopetalidæ* and *Symphyla*), but almost entirely wanting in the *Pterygota*, only one pair appearing temporarily on the foremost abdominal segment in the embryo.

The racial form of the Pterygota is to be derived from the Apterygota-like racial form of all *Hexapoda*, from which the various orders of insects have been produced. These have of course developed independently of one another. Those orders, however, whose members undergo a gradual or incomplete metamorphosis, have retained the original characteristics to a larger extent than the rest. Of the remaining orders, again, it is the *Lepidoptera*, *Hymenoptera*, and *Diptera* which are furthest removed from the racial form, and which reach the highest development among the *Insecta*.

Regarding the **relation of the Antennata to the Protracheata**, there can be no doubt that the two classes are racially connected, and that *Peripatus* has, far more than any member of the whole class of the Antennata, retained the original Annulatan characteristics.

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Class III. **Arachnoidea** *sive* **Chelicerota—Spider-like Articulata.**

Systematic Review.

Order 1. **Scorpionidæ** (Fig. 359, p. 512).

The body is divided into a compact unsegmented cephalo-thorax and a long segmented abdomen. In the abdomen again a thick and broad pre-abdomen of 7 segments is marked off from a long slender post-abdomen of 5 segments. The terminal segment of the latter carries a poison sting. On the ventral side of the 2d abdominal segment there is on each side a comb-like appendage. The jaw-feelers (cheliceræ) and jaw-palps (pedipalps) are provided with pincers. The pedipalps are leg-like, with large pincers. There are 4 pairs of book-leaf tracheæ (lungs), whose stigmata lie on the ventral side of the 3d to the 6th abdominal segments. *Euscorpius, Buthus, Androctonus.*

Order 2. **Solpugidæ** (Fig. 358, p. 511).

Head separate. Thorax of 3 segments, hind body cylindrical, of 10 segments. Cheliceræ with pincers, pedipalps long and leg-like. Tubular tracheæ. Stigmata in pairs on the 1st thoracic, and 2d and 3d abdominal segments. *Galeodes, Solpuga.*

Order 3. **Pseudoscorpionidæ (Chernetidæ)** (Fig. 360, p. 513).

Cephalo-thorax unsegmented or with two transverse furrows, abdomen broad, flat, of 11 segments. Neither poison stings nor caudal cerci present. Cheliceræ and pedipalps like those of the *Scorpionidæ.* Tubular tracheæ. Two pairs of stigmata, on the 2d and 3d abdominal segments. With spinning glands. Small animals. *Chernes, Chelifer, Obisium, Chthonius.*

Order 4. **Pedipalpi (Thelyphonidæ)** (Fig. 364, p. 519).

Cephalo-thorax unsegmented, distinctly marked off from the hind body. The latter flattened, consisting of 11-12 segments. Cheliceræ claw-shaped. Pedipalps large, ending either in claws or pincers. First pair of legs with flagellate ends, like feelers. Two pairs of book-leaf tracheæ, whose stigmata lie on the ventral side of the 2d and 3d abdominal rings. *Thelyphonus* (last 3 abdominal segments form a truncated portion clearly marked off from the rest of the abdomen and carrying a long jointed caudal cercus). *Phrynus.*

Near the *Pedipalpi* are perhaps to be classed the small and insufficiently known divisions of the *Tartaridæ* and *Microthelyphonidæ.*

Order 5. **Phalangidæ.**

Cephalo-thorax unsegmented, hind body of 6 segments, compact, applied along its whole breadth to the cephalo-thorax. Cheliceræ pincer-like, pedipalps leg-like. Legs often extraordinarily long and thin. Tubular tracheæ with one pair of stigmata which lies ventrally at the junction of the cephalo-thorax and abdomen. Without spinning glands. *Phalangium, Leiobunum, Gonyleptus.*

Order 6. **Cyphophthalmidæ** (often placed as a family of Order 5).

Cephalo-thorax unsegmented, abdomen of 8 segments. Of the pseudoscorpionid type. Cheliceræ and pedipalps like those of the *Phalangidæ.* Tubular tracheæ. *Cyphophthalmus* (without spinning glands, with one pair of stigmata on the ventral side of the 1st abdominal segment). *Gibbocellum* (spinning glands at the base of the abdomen behind the sexual aperture ; 2 pairs of stigmata on the 2d and 3d abdominal segments) (Fig. 372, p. 529).

Order 7. **Araneidæ—Spiders.**

Both cephalo-thorax and abdomen unsegmented, the latter large and egg-shaped. Abdomen joined to the cephalo-thorax by a short narrow stalk, 4 to 6 pairs of spinning mammillæ at the end of the abdomen. Cheliceræ claw-like with poison glands. Pedipalps leg-like, terminal joint in the male transformed in a peculiar manner into an organ for transmitting the semen in copulation (Fig. 377, p. 535). Tracheæ either exclusively book-leaf, or book-leaf and tubular at the same time.

Sub-order 1. **Tetrapneumones.**

With 4 book-leaf tracheæ, without tubular tracheæ. The 2 pairs of stigmata, ventral, behind the base of the abdomen. Generally 4 (in *Atypus* 6) spinnerets. *Mygale* (*Avicularia*, Fig. 374, p. 531), *Cteniza*, *Atypus*.

Sub-order 2. **Dipneumones.**

With 2 book-leaf tracheæ whose stigmata lie at the base of the abdomen, and with tubular tracheæ emerging through an unpaired (less frequently paired, *e.g. Dysderidæ*) stigma behind those of the book-leaf tracheæ. The unpaired stigma of the tubular tracheæ is generally moved far back, so that it lies in front of the 6 spinnerets. This sub-order includes most of the web-spinning spiders. Fam. *Dysderidæ* (2 stigmata for the tubular tracheæ) : *Dysdera*, *Segestria*. Fam. *Saltigrada* : *Salticus*, *Attus*. Fam. *Citigrada* (*Lycosidæ*) : *Lycosa*, *Tarantula*. Fam. *Laterigrada* : *Micrommata*, *Philodromus*, *Xysticus*. Fam. *Tubitelaria* : *Dictyna*, *Tegenaria*, *Agelena*, *Argyroneta*, *Drassus*, *Clubiona*. Fam. *Retitelaria* : *Linyphia*, *Theridium*, *Pholcus*. Fam. *Orbitelaria* : *Epeira*, *Zilla*, *Meta*.

Order 8. **Acarina—Mites.**

Abdomen fused with cephalo-thorax. Body unsegmented. Mouth parts adapted for biting, or piercing and sucking. Respiratory organs (tracheæ) either present or absent. Many Mites are parasitic.

a. **Mites provided with tracheæ** :—Fam. *Trombidiidæ* : *Trombidium*. Fam. *Tetranychidæ* : *Tetranychus*. Fam. *Hydrachnidæ* : *Atax*, *Hydrachna*, *Hydrodoma*. The sub-families of the marine *Halacaridæ* : *Aletes*, *Halacarus* without tracheæ. Fam. *Bdellidæ* : *Bdella*. Fam. *Oribatidæ* : *Oribata*, *Leiosoma*. Fam. *Gamasidæ* : *Gamasus* (Fig. 361, p. 514), *Uropoda*. Fam. *Ixodidæ* : *Ixodes*, *Argas*.

b. **Mites without tracheæ** :—Fam. *Tyroglyphidæ* (cheese Mites) : *Tyroglyphus*. Fam. *Dermaleichidæ* : *Listrophorus*, *Analges*. Fam. *Sarcoptidæ* : *Sarcoptes*. Fam. *Demodicidæ* : *Demodex*. Fam. *Phytoptidæ* : *Phytoptus*.

Appendage to the Class of the Arachnoidea.

The Linguatulidæ (Pentastomidæ)

Body vermiform, generally flattened, and ringed externally. No oral appendages. Two pairs of movable hooks near the mouth. Without sensory organs, tracheæ, Malpighian vessels, or diverticula of the mid-gut. Male aperture in front, behind the mouth ; female aperture at the posterior end of the body. Parasites, *Pentastomum*, *P. taenioides* (Fig. 378, p. 537). Parasitic in the nasal and throat cavities and in the cephalic sinus of the dog and wolf. The embryos, enclosed in their egg envelopes, reach the exterior with the nasal mucus. If they are taken into the intestine of a rabbit or a hare (or of a few other mammals) the embryos become free, pierce their way through the enteric wall and enter the liver or lungs. They here become encysted and undergo a remarkable metamorphosis, passing through many moults; the final result is a larva which has been named *Pentastoma denticulatum*. This larva finally breaks through its cyst and moves about. If it in any way (most often with the flesh of its host) reaches the mouth and throat of the definitive host, it chooses its future place of location, and through a series of moults develops into the adult *Pentastomum*.

I. Outer Organisation.

A. The Body.

If we compare the body of the Arachnoidea with that of the *Antennata*, the most important difference that strikes us is that in the former no head distinctly marked off from the thorax, or, what is the same thing, on thorax separated from the head, can be distinguished.

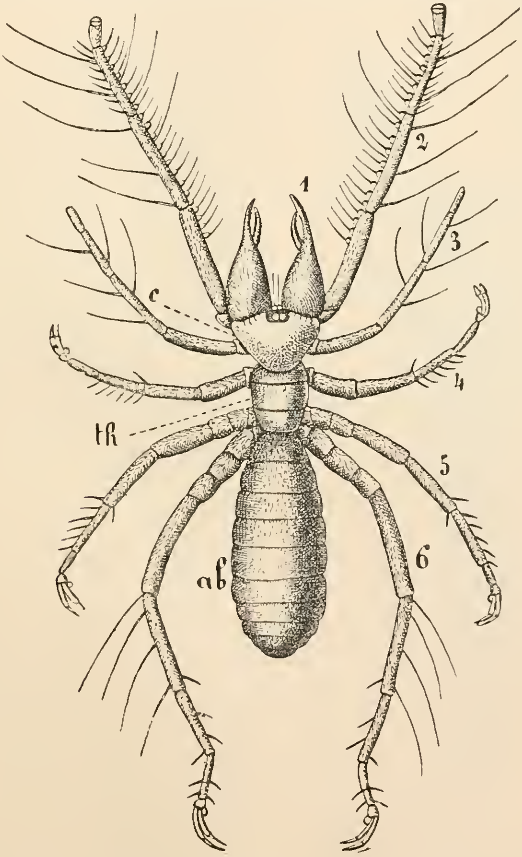

Fig. 358.—**Galeodes Dastuguei** ♀, natural size. 1-6, The six pairs of extremities; 1, cheliceræ 2, pedipalps; *c*, head; *th*, the thorax of 3 segments; *ab*, the abdomen (after **L. Dufour**).

In the body of the Arachnoidea we find almost always a number of anterior segments, probably 7, fused to form a generally unsegmented **cephalo-thorax.** Following upon this cephalo-thorax there is an **abdomen** consisting of a varying number of separate or fused segments, which may again fuse with the cephalo-thorax, as is the case in the *Acarina* and *Linguatulidæ* (?) and thus the body appears neither segmented nor divided into regions. We thus, within the class of the Arachnoidea, have not only fusing of segments and an obliteration of segmentation, but also a progressive concentration of the whole body; there can be little doubt that the Arachnoidea are no exception to the rule that the more richly and completely segmented the body is the better has it retained the primitive arrangement. The segmentation is richest in the *Scorpionidæ* and *Solpugidæ*, but is very different in the two groups. The segmentation in both these forms claims special attention.

The *Solpugidæ* (Fig. 358) vividly recall the *Insecta* in the metamerism of the body. In opposition to all other Arachnoidea, not only is the anterior division of the body, answering to the cephalo-thorax, distinctly segmented, but it even falls into two parts, an **anterior unsegmented head,** which may be compared with the head of the *Antennata*, and a **posterior thorax,** consisting of three segments, which may be compared with the thorax of the *Insecta* and with the three anterior trunk segments of the *Myriapoda.* An **abdomen of ten segments follows the thorax.**

There are considerable difficulties in the way of comparing the segments of the body of the *Solpugidæ* with the head and a corresponding number of trunk segments of the *Antennata*; these difficulties arise chiefly in comparing the extremities and nervous system, and will be discussed later on. The ontogeny of the *Solpugidæ* is unfortunately almost unknown.

Fig. 359.—**Scorpio africanus** (after **Cuvier,** *Règne animal*).

In the *Scorpionidæ* (Fig. 359) the **cephalo-thorax** is, in the adult condition, **unsegmented**; in the embryo, however, a segmentation into seven somites, including the frontal lobes, may be recognised. The **abdomen,** on the contrary, is distinctly segmented and consists of twelve segments. In it, again, we can distinguish two divisions, distinctly marked off from each other. The anterior division, the broad **pre-abdomen**, consists of 7 segments; the posterior, slenderer, tail-like division, the **post-abdomen**, of 5 segments. At the end of the post-abdomen is found the **poison sting**, which is often included as one of the segments. It ought, however, probably to be considered as an articulated appendage of the last segment, the latter being recognised, as in all Arthropoda, by the position of the anus.

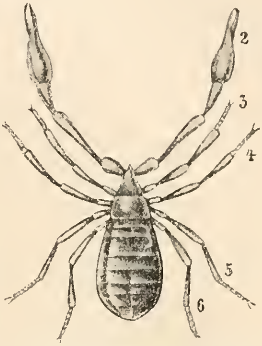

Fig. 360.—**Chelifer Bravaisii** (after **Cuvier**, *Règne animal*). 2-6, Second to sixth pairs of extremities.

Two small, insufficiently known groups of Arachnoidea, the *Tartaridæ* and *Microthelyphonidæ*, appear, as far as the metamerism of the body is concerned, to occupy in some respects an intermediate position between the *Solpugidæ* and the *Scorpionidæ*, and in others between the latter and the *Thelyphonidæ*. In the *Microthelyphonidæ* an anterior and a posterior division can be distinguished in the cephalo-thorax, and again, the latter shows on its dorsal surface indistinct division into three parts which recalls the arrangement of the cephalo-thorax of the *Solpugidæ*. The abdomen consists of ten segments, the last three being much narrower and smaller than the rest and representing a sort of post-abdomen, whose terminal segment carries a long, thin, jointed caudal filament. In the *Tartaridæ* the thorax is divided by a distinct circular constriction into an anterior and a posterior division. The abdomen consists of seven or eight segments followed by a small, short, truncated post-abdomen, formed of a few (four) segments and carrying a variously-shaped caudal appendage.

In the *Pedipalpi* the cephalo-thorax is unsegmented. The abdomen consists of 12 segments (*Thelyphonus*) or of 11 (*Phrynus*). In *Thelyphonus* the last 3 segments are very small and narrow, and form a sort of post-abdomen, which carries an anal filament.

The cephalo-thorax of the *Chernetidæ* (*Pseudoscorpionidæ*), which recall the *Scorpionidæ* in their general type, is unsegmented or else has 2 dorsal transverse furrows. The abdomen consists of 11 (less often 10) segments. A pre-abdomen and a post-abdomen cannot be distinguished, and a poison sting or a caudal or anal filament is wanting.

The cephalo-thorax of the *Phalangidæ* (including the *Cyphophthalmidæ*) is unsegmented. The abdomen, which is sometimes clearly, sometimes indistinctly segmented, is applied to the cephalo-thorax along its whole breadth. There is no separation of the abdomen into pre-abdomen and post-abdomen, and no caudal filament.

In the *Araneidæ* (the true spiders) the cephalo-thorax as well as the abdomen is unsegmented. The two are separated by a deep constriction.

In the *Acaridæ* the segmentation of the body as well as its division into regions is suppressed. It is rightly assumed that the unsegmented body has here come from the fusing of an unsegmented cephalo-thorax with an unsegmented abdomen. It only rarely occurs that the limbless abdomen is distinctly marked off from the limbbearing cephalo-thorax. An anterior portion of the body, often distinguished as the "head," and carrying the oral aperture, can certainly not be regarded as an original division of the body, *i.e.* a

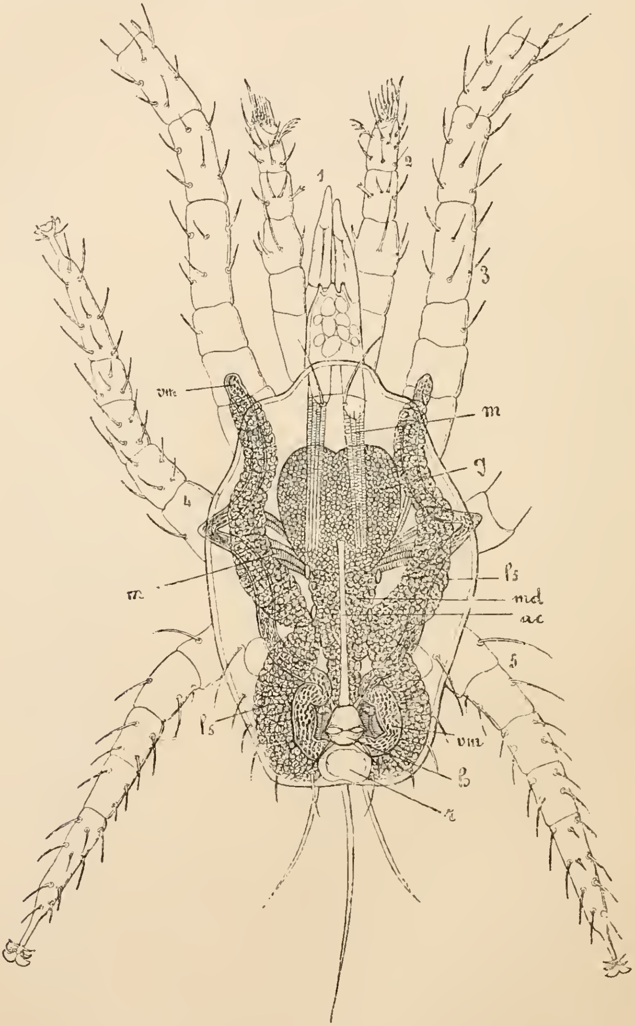

Fig. 361.—**Larva of Gamasus fucorum** (after **Winkler**). 1-5, The 5 pairs of extremities of the larva (the sixth still wanting); 1, the cheliceræ = mandibles; 2, the pedipalps = maxillæ; *m*, muscles; *vm*, Malpighian vessels; *g*, brain = supra-œsophageal ganglion; *ls*, diverticula of the mid-gut (hepatic tubes); *md*, mid-gut; *h*, heart; *ac*, aorta-cephalica; *r*, rectal vesicle.

division derived from ancestors. It is also very doubtful whether a ringing of the body, which can here and there be recognised, has anything whatever to do with a true segmentation.

The body of the parasitic *Linguatulidæ* is elongated, vermiform, and ringed. But this ringing has again nothing to do with a real segmentation.

B. The Extremities.

The Arachnoidea are typically provided with six pairs of extremities exclusively belonging to the cephalo-thorax. The abdomen is everywhere limbless.

Of the 6 pairs of extremities the most anterior pair is known as the **cheliceræ (mandibles, jaw-feelers, claw-feelers, falces)**, the second as the **pedipalps (underjaws, maxillæ)**. The other 4 pairs are mostly similar in form and serve as ambulatory legs for locomotion.

The **First Pair of Extremities**—the **cheliceræ**—lie in front of and above the mouth. They are either 2- or 3-jointed, and serve for seizing, and often also for killing, prey. The terminal joint is claw-like. The cheliceræ are chelate, when the terminal claw is, as in the chelate feet of *Astacus*, movable against a process of the preceding joint; they might be called **claw-jaws** when the terminal claw can merely be bent round upon the preceding joint, as in the seizing feet of the *Stomatopoda*.

The **Second Pair of Extremities**—the **pedipalps** or **maxillæ**—lie on the two sides of the mouth, and everywhere function as oral appendages, being nearly always provided with masticatory ridges at their bases. The masticatory ridges, which elsewhere can move freely against one another, have in the *Pedipalpi* (*Thelyphonidæ*), *Cyphophthalmidæ*, and *Acarina*, grown together in the middle line as an adaptation for sucking. As opposed to the masticatory ridge, the remaining part of the second extremity is called the **palp** or **feeler**. The many-jointed palp (originally 6-jointed) everywhere serves as an organ of touch, but may perform very different functions as well, and in correspondence with these functions may be very variously modified. In the *Scorpionidæ*, *Chernetidæ*, and in many mites it ends in pincers and functions as a seizing organ. In the *Pedipalpi* it ends as a **claw feeler** with a movable claw. The feelers of the *Phalangidæ* and of many *Acarina* have a terminal claw. In the male *Araneidæ* the terminal joint of the feeler is transformed into a copulatory organ. The feelers of the *Solpugidæ* serve, like the 4 subsequent pairs of extremities, for locomotion, and are formed much like the rest. The same is the case in the *Microthelyphonidæ*, where the second pair of extremities not only resembles those which follow it, but is even devoid of the masticatory ridges.

The **Third Pair of Extremities** lies behind the mouth, and is in most Arachnoidea more or less like the 3 following pairs, and serves, like them, for locomotion. In the *Scorpionidæ* and *Phalangidæ* the basal joint is provided with a masticatory ridge. The third pair of extremities is differently shaped in the *Pedipalpi*; it is long and thin, with long flagellate ringed terminal joints. Here it is principally or exclusively used as an organ of touch.

The **Fourth, Fifth and Sixth Pairs of Extremities** are, as a rule, similarly shaped—6-jointed locomotory organs. In the *Scorpionidæ* the fourth pair of extremities also carries a masticatory ridge.

In the *Linguatulidæ*, which are regarded as Arachnoidea degraded by parasitism, the limbs are reduced in number and form. Only two pairs of clinging hooks are found near the mouth. Definite data for a comparison of these clinging hooks with any special pairs of the limbs of typical Arachnoidea are, however, wanting.

The homologies of the Arachnoidean limbs with those of other Arthropoda are difficult to establish. If we compare the Arachnoidea with the *Antennata*, and especially the cephalo-thorax of the former with the head and 3 anterior trunk segments (thorax) of the latter, we find that the Arachnoidea possess one pair of extremities less than the *Antennata* in the corresponding regions.

In the *Solpugidæ*, in which the section of the body which corresponds with the cephalo-thorax of other Arachnoidea is, as in the *Antennata*, segmented, the head carries 3 pairs of extremities, viz. the cheliceræ, pedipalps, and the pair of limbs which follow these. Each of the thoracic segments following the head possesses a pair of limbs. Since the *Antennata* carry typically 4 pairs of limbs on the head, viz., the antennæ, mandibles, anterior and posterior maxillæ, it follows—presupposing that the head of the *Solpugidæ* really corresponds with that of the *Antennata*—that the wanting limbs belong to the head. Various facts, chiefly ontogenetic, make it probable **that it is the antennæ of the Antennata which are wanting** in the *Solpugidæ* and in the Arachnoidea generally,[1] while the other limbs correspond according to their order of succession. In this way we reach the following homologies between the Arachnoidean and Antennatan limbs.—

	Antennata		*Arachnoidea*		
Head	Antennæ		wanting[2]	Head of the *Solpugidæ*	Cephalo-thorax of the *Arachnoidea*
	Mandibles	=	Cheliceræ		
	Anterior Maxillæ	=	Pedipalps		
	Posterior Maxillæ	=	3d pair of limbs		
3 Anterior trunk segments = thorax of *Insecta*	first Trunk foot (thoracic legs of *Insecta*)	=	fourth Pair of Limbs	3 thoracic segments of the *Solpugidæ*	
	second	=	fifth		
	third	=	sixth		

If these homologies are correct, then the cheliceræ especially, but also the pedipalps and the 3d pair of extremities of the Arachnoidea, differ very greatly from the corresponding cephalic limbs of the *Antennata*, *i.e.* the mandibles and anterior and posterior maxillæ. The mandibles of the *Antennata* are never jointed and the maxillæ never elongated like legs, as in the Arachnoidea. Now since it is not conceivable that the 3 anterior pairs of much-jointed limbs of the Arachnoidea have proceeded from the reduced and specialised oral appendages of the *Antennata*, we are compelled to assume that if there is any near relationship between the two groups,

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[1] While these sheets are passing through the press it is announced that the embryo of a large spider (*Trochosa singoriensis*, Laxm.) shows distinct rudiments of antennæ which disappear later; and further, that more than 4 pairs of rudimentary abdominal limbs are visible, with traces of several pairs of stigmata. (*Zool. Anzeiger*, 11th May 1891.) [Tr.]

[2] *Ibid.*

the Arachnoidea branched off from the common Tracheatan stem at a time when the oral appendages were still much jointed, and elongated like legs.

In connection with the assumed complete absence of the Antennatan feelers in the *Arachnoidea* or *Chelicerota*, it is a striking fact that no rudiments which can be proved to be those of antennæ appear, as far as we know, at any stage of development, even temporarily.[1] And yet we must assume, keeping *Peripatus* in mind, that the ancestors of the *Tracheata* possessed well-developed antennæ.

In recent times the near relationship of the *Arachnoidea*, and especially of the *Scorpionidæ*, with the fossil *Gigantostraca* and the *Xiphosura* has been zealously maintained. It cannot be denied that the 6 pairs of limbs of the Scorpion show greater agreement with the 6 pairs of limbs of the cephalo-thorax of *Limulus* than with the limbs of the *Antennata*. There are, however, other serious objections to the assumption of a nearer relationship between the *Arachnoidea* on the one hand and the *Xiphosura* and *Gigantostraca* on the other (see p. 541).

Rudiments of Abdominal Limbs in the Arachnoidea.

1. In various Arachnoidea rudiments of abdominal limbs appear temporarily during embryonic development ; 6 pairs on the 6 anterior abdominal segments in the *Scorpionidæ* (Fig. 379, p. 538), 4 pairs in the *Chernetidæ* and 4 pairs in the *Araneidæ* (Fig. 380, p. 539). Such rudiments of abdominal limbs will probably also be found in the embryonic stages of other Arachnoidea, whose development has been hitherto not sufficiently investigated.

2. The *Scorpionidæ* possess in the adult condition on each side of the second abdominal segment ventrally a comb-like organ (Fig. 362, *k*), whose function is not yet fully known. These two "combs" are said to come from embryonic rudiments of the limbs of the second abdominal segment.

3. It is in the highest degree probable that the spinning mammillæ of the *Araneidæ*, which, 4 or 6 in number, rise on the hind body, represent rudimentary abdominal limbs. This is supported by the following facts : (*a*) they are for the most part jointed ; (*b*) they, as recently observed, develop from the embryonic rudiments of abdominal limbs ; (*c*) the fact that they are spinning mammillæ, *i.e.* that the spinning glands open on them. These facts gather weight when we remember the coxal and spinning glands of the *Protracheata* and *Antennata*, and particularly the slime papillæ of *Peripatus* and the spinnerets of *Scolopendrella*. The assumption that the spinning mammillæ of the *Cyphophthalmid* genus, *Gibbocellum*, also represent rudimentary limbs, is open to the objection that the two pair of mammillæ lie in one and the same, *i.e.* the 2d abdominal segment.

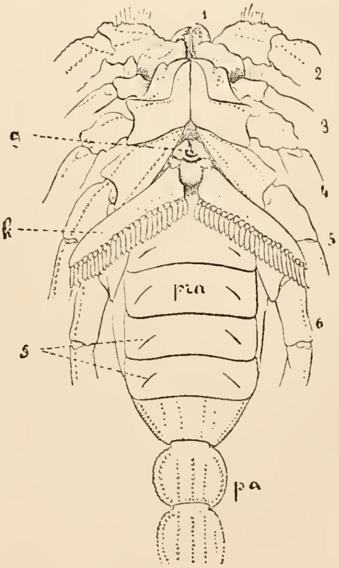

FIG. 362.—**Buthus occitanus** (*Règne animal*). Cephalo-thorax, pre-abdomen (*pra*), and the first segments of the post-abdomen (*pa*), from the ventral side. Limbs (1-6) not fully drawn. 1, Cheliceræ ; 2, pedipalps (jaw-feelers, chelate-feelers) ; *g*, genital aperture ; *s*, stigmata ; *k*, combs.

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[1] See note on p. 516.

The occurrence of rudimentary abdominal limbs in the Arachnoidea proves that the ancestors of these animals possessed extremities on the abdomen (at least on 6 abdominal segments).

II. The Nervous System.

The segmentation of the body is reflected in the segmentation of the nervous system. The *Scorpionidæ*, which of all Arachnoidea show the richest segmentation of the body, also possess the greatest number of ganglia in the ventral chord, while on the other hand in the *Araneidæ* and *Acaridæ* concentration both of body segmentation and of nerve chord reaches its highest point. As in other *Arthropoda* concentration of the nerve chord is due to displacements, fusings, and to reductions of originally separate segmentally-repeated pairs of ganglia; these processes may be directly observed during ontogenetic development.

The **brain** is connected with the ventral chord by a short œsophageal commissure. **From the brain arise the optic nerves, and also, in most cases, the nerves of the cheliceræ.** The fact that the cheliceræ are innervated from the brain seems to oppose the assumption that they are homologous with the mandibles of the *Antennata*, since the latter always receive their nerves from the infra-œsophageal ganglion. It has been found, however, that in the earlier stages of development that portion of the brain from which the nerves of the cheliceræ arise, and which is often still distinctly separate in the adult animal, begins to form in the embryo as the first post-oral pair of ganglia. These later take part in the formation of the œsophageal commissures, or else even fuse with the ganglionic rudiments of the segment of the frontal lobes, *i.e.* with the rudiments of the actual brain. This process is evidently similar to the fusing of the ganglia of the posterior antennæ with the brain in the Crustacea. In the *Phalangidæ*, however, in opposition to the other Arachnoidea, the nerves of the cheliceræ are said to arise out of the anterior part of the great thoracic ganglionic mass. A similar observation has recently been made in the *Acarina* (*Gamasidæ*), where "the mandible nerves arise out of two spherical ganglionic masses of the infra-œsophageal ganglion, and pass through the supra-œsophageal ganglion."

Throughout the Arachnoidea, even in the ventral chord of the most richly segmented *Scorpionidæ* and *Solpugidæ*, all the ganglia of the cephalo-thorax, and a number of the anterior abdominal ganglia, fuse to form **one great thoracic ganglionic mass**, from which arise the nerves for the second to the sixth pairs of extremities and for the anterior abdominal segments. In the abdomen there may be several separate ganglia (*Scorpionidæ*, Fig. 363), or only one or two (*Thelyphonidæ*, Fig. 364, *Solpugidæ*, *Chernetidæ*, *Phalangidæ*, *Mygalidæ* among the *Araneidæ*, Fig. 374, p. 531). In the *Dipneumones* (*Araneidæ*) and the *Acaridæ* (Fig. 365) on the contrary, the whole central nervous system, the brain and ventral chord, form a single mass

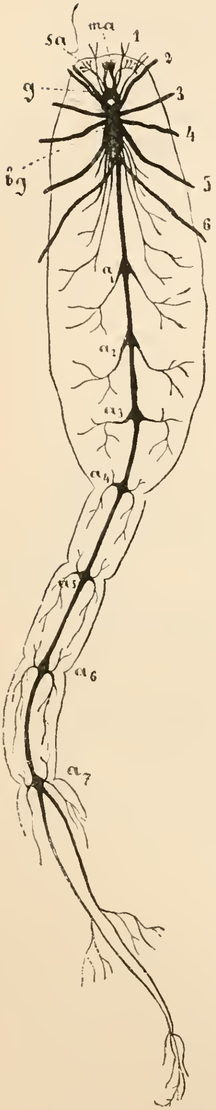

FIG. 363.—**Nervous system of the Scorpion** (after **Newport**). 1-6, Nerves of the 6 pairs of limbs; *ma*, middle eyes; *sa*, lateral eyes; *g*, brain; *bg*, large infra-œsophageal ganglionic mass; a_1-a_7, ganglia of the abdomen.

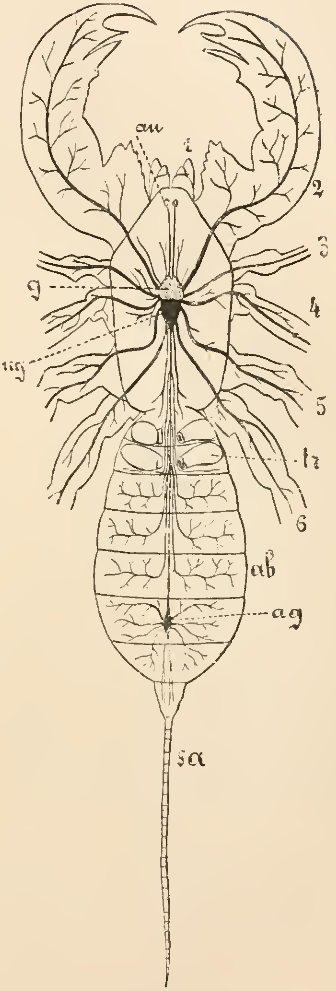

FIG. 364.—**Nervous system of Thelyphonus caudatus** (after **Blanchard**). 1-6, First to last pairs of limbs with the corresponding nerves from the thoracic ganglionic mass; *au*, eyes; *g*, brain; *ug*, thoracic ganglionic mass; *ab*, abdomen; *ag*, abdominal ganglion; *sa*, jointed caudal appendage.

pierced by the œsophagus; the greater part of this mass, which lies behind the œsophagus, represents the fused ventral chord, from which the nerves radiate.

The **disappearance of a segmented abdominal ganglionic chain** in the Arachnoidea may have been brought about by various co-operating factors: (1) by a forward displacement of the ganglionic masses, and the fusing of the same with the thoracic mass; (2) by the fusing of several abdominal ganglia to form one or two abdominal masses; (3) perhaps also by the running of the ganglia into the nerve trunks which, paired or externally unpaired, run through the abdomen; and (4) by the concentration of the whole ventral chord into one single thoracic ganglionic mass.

In the *Scorpionidæ*, where the nervous system in the abdomen is still most richly segmented, there are 7 abdominal ganglionic masses, 3 in the pre-abdomen, 3 in the post-abdomen, and 1 on the boundary between the two, which as yet cannot be certainly assigned to the one or the other.

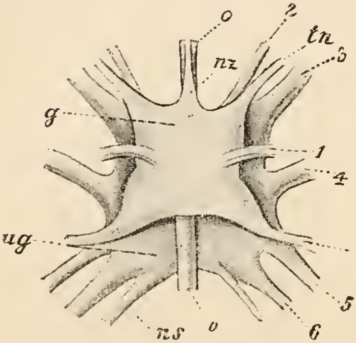

Fig. 365—**Central nervous system (thoracic ganglionic mass) of Gamasus,** diagrammatic (after **Winkler**). *g*, Portion lying over the œsophagus (*o*) = brain; *ug*, portion lying under the œsophagus (infra-œsophageal ganglionic mass); 1-6, nerves of the 6 pairs of limbs; 1, of the chelicerae (mandibles); 2, of the pedipalps (maxillæ); *nz*, nerve of the tongue; *ns*, visceral nerve; *tn*, nerve of the maxillar palp.

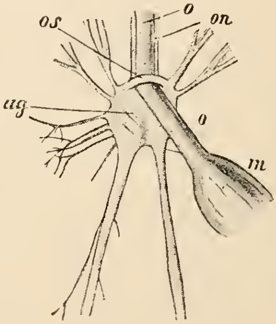

Fig. 366.—**Nervous system of Pentastomum tænioides** (after **R. Leuckart**). *o*, œsophagus; *m*, anterior portion of the chylific stomach; *on*, œsophageal nerves; *os*, œsophageal ring running over the œsophagus; *ug*, infra-œsophageal ganglionic mass.

The longitudinal commissures of the Arachnoidean ventral chord are, almost everywhere where they are distinguishable, fused in the middle line into an externally single median longitudinal strand.

The nervous system of the endo-parasitic *Linguatulidæ* (Fig. 366) is much reduced. It is restricted to one ganglionic mass lying beneath the œsophagus and an apparently double commissure embracing the œsophagus, in which no special cerebral swelling can be made out. This great reduction of the brain is chiefly due to the degeneration of the eyes.

A **sympathetic nervous system** has been proved to exist in various Arachnoidea (*Scorpionidæ, Araneidæ, Acaridæ*), and consists of an unpaired nerve connected with the brain by paired nerves and running along the œsophagus and stomach. Ganglia connected with the ventral chord have also been described as belonging to the sympathetic nervous system.

III. The Eyes.

Most Arachnoidea possess eyes. These are unicorneal and are, except in the middle eye of the *Scorpions*, constructed on the same general plan as the ocelli of the *Antennata*. The hypodermis is nearly always continued under the cuticular lens to form the so-called vitreous body.

Number and Position of the Eyes.—The eyes of the Arachnoidea are sessile and from 2 to 12 in number; they lie symmetrically arranged on the upper side of the cephalo-thorax.

Solpugidæ: 2 large ocelli on one common prominence. *Scorpionidæ*: 2-6 pairs of eyes, one pair of which, the great middle eyes, are placed close to the median line, and the rest at the anterior edge of the cephalo-thorax. *Chernetidæ*: 0, 1 or 2 pairs of eyes. *Pedipalpi*: 4 pairs of eyes, the largest lying in the middle, the other 3 on the anterior edge of the cephalo-thorax. *Phalangidæ*: usually 1 pair of eyes in the middle of the cephalo-thorax on a prominence. In *Cyphophthalmus* there is an eye on each side on a prominence; in *Gibbocellum* 2 eyes on each side at the edge of the cephalo-thorax, each on a prominence. *Araneidæ*: generally 8, less often 6 or fewer eyes, symmetrically arranged, generally in 2 transverse rows on the cephalo-thorax. The special arrangement is of value for classification. *Acarina*: eyes are wanting, or present in 1 or 2 pairs. *Linguatulidæ*: eyes wanting.

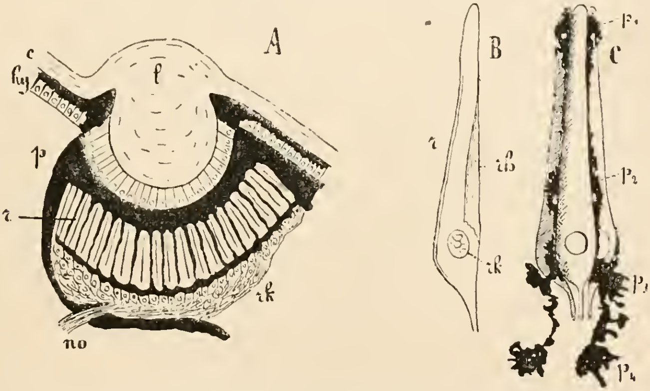

FIG. 367.—A section through a **middle eye of Euscorpius italicus** (after **Carrière**). *c*, Chitinous carapace; *l*, chitinous lens; *hy*, hypodermis, continued as so-called vitreous body under the chitinous lens; *p*, pigment cells; *r*, retinulæ; *rk*, the proximal nucleated portions of the retinulæ; *no*, optic nerves. *B*, A single retinular cell (*r*), with the rhabdomere (*rh*), and the nucleus (*k*). *C*, A retinula with the pigment cells p_1, p_2, p_3, p_4. (*B* and *C*, after **Ray Lankester.**)

The Structure of the Middle Eye of the Scorpionidæ (Fig. 367).—The middle eye of the *Scorpion* takes, according to its structure, an intermediate place between a simple eye (ocellus) and a compound or facet eye. It agrees with the ocellus in possessing one single cuticular corneal lens, and with the facet eye in its retinal cells (understanding these cells in Grenacher's sense) which form groups, the so-called retinulæ.

Under the cuticular lens an epithelial layer lies as a continuation of the hypodermis; this represents the matrix of the lens and is called the vitreous body. Under the vitreous body lies the layer of the retinulæ. Each retinula is separated from its neighbours by pigment cells and consists of 5 retinal cells. One rhabdomere belongs to each retinal cell. The 5 rhabdomeres fuse in the axis of the retinula into one rhabdome.

IV. Glands Opening on the Outer Integument.

These are very numerous in the Arachnoidea. Many of them are insufficiently known, especially as far as their constitution and the physiological significance of their secretions are concerned. We shall divide the different sorts of glands into two principal groups: (1) such as open upon limbs, and (2) those whose ducts have no apparent connection with limbs.

1. **Glands opening on Limbs.**—Among these we have in the first place the **spinning glands of the Araneidæ**, since the 2 or 3 pairs of spinning mammillæ on which they open are very probably rudimentary abdominal limbs. There are on each side several variously constructed spinning glands, whose secretion, which hardens by exposure to air, serves for forming the various sorts of webs. Among these different pairs of glands there is one pair which only seems to occur in the female and to serve for the spinning of the egg cocoon. Immediately in front of the anterior pair of the spinning mammillæ there is found in some *Araneidæ* a paired glandular region, the so-called **Cribrellum**, in which extremely numerous spinning glands open through fine pores. The cribrellum perhaps also represents the last remains of another (4th) abdominal pair of limbs.

The spinning glands of the *Araneidæ* are rightly reckoned among those variously developed integumental glands (coxal glands, spinning glands, protrusible sacs), which must be finally traced back to the segmental setiparous glands on the parapodia of the *Annelida.*

In *Gibbocellum* (*Cyphophthalmidæ*) there are found on each side ventrally on the 2d abdominal segment 2 spinning mammillæ, on which several spinning glands open.

Glands which open on the 4 pairs of ambulatory legs (either on one or on several) have often been observed. One large gland is found on each side of the cephalothorax of the *Scorpionidæ.* It emerges, at least in the embryo and in young animals, on the coxal joint of the 3d pair of ambulatory legs. On the 1st and 2d pair at the place where the glandular apertures lie in the 3d pair, there are bulgings which suggest that there were once glandular apertures here also. The apertures of these coxal glands are usually not demonstrable in adult animals.

Similar glands having apertures on the coxæ of the 3d pair of legs are found in the *Araneidæ* also, in the *Tetrapneumones* (*Mygale, Atypus*) as well as in some *Dipneumones.* Here also it is often difficult to prove the existence of the outer apertures in the adults, and here also slits may appear on other legs which correspond in position with the glandular apertures of the 3d pair of legs.

The fact that the coxal glands of the *Scorpionidæ* and *Araneidæ* are unmistakably similar to the coxal glands of the *Xiphosura* in position (on the 5th pair of extremities), in structure, and in manner of opening, has been used as a further argument in favour of the relationship of these latter with the Arachnoidea.

In the *Solpugidæ* and *Phalangidæ* also coxal glands are said to occur, in these cases on the bases of the last pair of legs. Their ducts have, however, not been observed. The occurrence of coxal glands in the *Acaridæ* has also been described. In the *Oribatidæ*, for example, they lie at the bases of the 2d pair of legs; in the *Gamasidæ*, it appears, between the coxal muscles of all the legs. It is not yet known if certain stigma-like pores near the bases of the 1st pair of legs of the *Halacaridæ* belong to the category of coxal glands. In *Trombidium* a gland with its opening lies on the terminal joint of each leg.

Glands of the pedipalps (the 2d pair of extremities) have been observed in various Arachnoidea (*Atypus* and other *Araneidæ*, *Solpugidæ*, *Scorpionidæ*, *Phalangidæ*, and *Tetranychus* among the *Acaridæ*). They have been classed somewhat arbitrarily, some as salivary glands, others (*Galeodes*) as poison glands, and others again as spinning glands (*Tetranychus*).

Glands emerging on the cheliceræ are also somewhat widely distributed. The best known and most investigated are the **poison glands of the Araneidæ**, which mostly lie in the cephalo-thorax, but often partly project into the chelicerae themselves and always open outward on their terminal claws. In the *Gamasidæ* also there are glands at the bases of the cheliceræ. According to recent observations, the webs prepared by the *Pseudoscorpionidæ* are said to be formed by glands lying in the cephalo-thorax, whose ducts penetrate into the cheliceræ and open on the terminal joint. Earlier observers had asserted that the spinning glands and their apertures were to be found on the ventral side of the first abdominal segment. In the *Linguatulidæ* there are glands emerging at the bases of the 4 clinging hooks.

We thus find in the Arachnoidea a striking number of limb glands. This number will no doubt be still further increased on more thorough investigation, and it may perhaps be established, that many of these glands, especially those emerging on the coxal joints of the extremities, belong, like the spinning glands of the *Araneidæ*, to the category of segmental coxal glands homologous with the setiparous glands of the *Annelida*.

2. **Glands not emerging on the Limbs.**—Here belong the integumental glands emerging through pores in the chitinous cuticle at various parts of the surface of the body; these have been observed in different divisions, with special frequency, however, in the *Acaridæ* and *Linguatulidæ*, and have been called oil glands, stigmatic glands, stink glands, etc. The poison gland of the Scorpion also belongs to these. It is paired, lies in the swollen terminal segment of the post-abdomen and emerges by 2 separate apertures at the point of the sting with which the tail is armed. In the *Phalangidæ* and *Cyphophthalmidæ* (*Gibbocellum*) there is in the cephalo-thorax one pair of glands (the so-called **Krohn's** glands), the 2 ducts of which are said to emerge through 2 apertures on the dorsal side of the cephalo-thorax.

V. The Intestinal Canal.

This has as a rule a straight course through the body. We can again distinguish in it the three well-known divisions, fore-gut, mid-gut, and hind-gut.

The Fore-gut.—The mouth or buccal cavity is followed by the muscular **pharynx,** which functions chiefly as a suction pump, as it can be expanded by means of special groups of muscles attached to it, and contracted by circular muscles. The pharynx passes into the narrow **œsophagus.** This passes through the œsophageal ring and enters the mid-gut. Before entering the latter it swells, in the *Araneidæ*, into a special **sucking stomach.**

The **mid-gut** forms by far the largest portion of the digestive tract. **In the Arachnoidea it shows in a very high degree the tendency to form cœcal invaginations** which surpass all the rest of the viscera taken together in size and importance. Where the cephalo-thorax and abdomen are distinctly separate, these invaginations may be repeated in each. The whole mass of the mid-gut with its invaginations represents the digesting chylific stomach, and has glandular walls. The liquid nourishment reaches to the very extremities of these diverticula, which have been inaccurately called hepatic tubes.

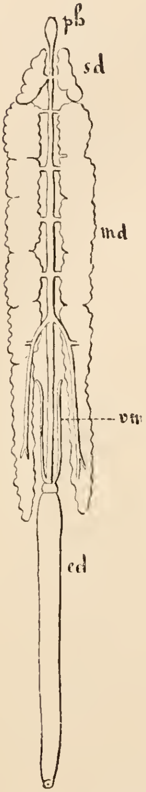

Fig. 368. — **Digestive tract of the Scorpion** (after **Newport**). *ph*, Pharynx; *sd*, salivary glands; *md*, diverticula of the mid-gut; *vm*, Malpighian vessels; *ed*, hind-gut.

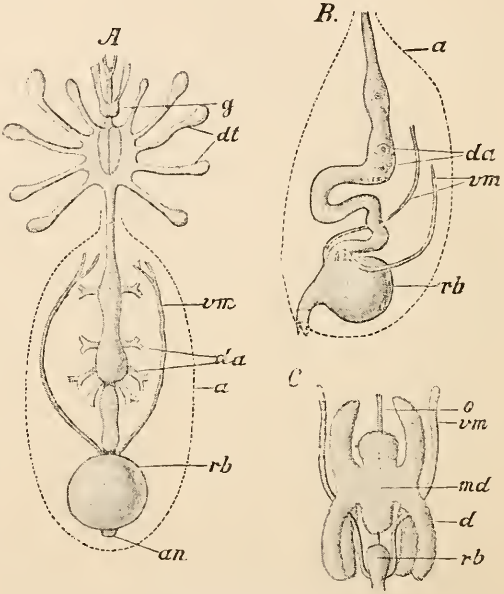

Fig. 369.—*A*, **Digestive apparatus of Mygale caementaria** (after **Dugès** in **Cuvier's** *Règne Animal*). *B*, **The abdominal portion of the same**, from the side. *C*, **Digestive apparatus of a Gamasus**, diagrammatic (after **Winkler**). Lettering the same in the 3 figures: *g*, brain; *dt*, enteric diverticula of the thorax; *da*, enteric diverticula (liver) of the abdomen (*a*), only the portions entering into the abdominal mid-gut drawn; *md*, mid-gut with diverticula (*d*) of *Gamasus*; *vm*, Malpighian vessels; *rb*, rectal vesicle (cloaca) into which both the digestive tract and the Malpighian vessels enter; *o*, œsophagus.

The **hind-gut** is generally very short. It opens externally through the anal aperture which is placed ventrally at the posterior end of the body. Into the hind-gut enter **tube-like excretory organs, corresponding with the Malpighian vessels of the Antennata.** There is generally one pair of these, less frequently several pairs. In the *Acarina* an unpaired excretory tube is often found.

The fact that the Arachnoidea like the *Antennata* have Malpighian vessels, while these vessels are not found in the *Crustacea* and *Xiphosura* and *Pycnogonidæ*, is of great importance in deciding the question of their systematic position.

The dorsal wall of the hind-gut is often bulged out in the form of a muscular sac. It then looks as if the Malpighian vessels on the one hand and the mid-gut on the other entered a common terminal sac, not at its blind end but near the anal aperture. In the structure of its walls this rectal vesicle, which is also often called the cloaca, agrees with the Malpighian vessels, and not with the mid-gut. This favours the view that the excretory tubes of the Arachnoidea, like the Malpighian vessels of insects, are invaginations of the hind-gut, and consequently ectodermal formations.

Salivary glands have often been described in the Arachnoidea, but our knowledge of them, especially of their manner of emerging, is very inadequate. The glands which open on the pedipalps are also often regarded as salivary glands. In certain *Acarina* (*Oribatidæ*) a pair of glands emerging at the boundary between the fore-gut and the mid-gut has been observed. In various Arachnoidea there are groups of glands in the upper lip.

The anatomy of the diverticula of the mid-gut varies greatly in the different orders. In the *Scorpionidæ* (Fig. 368) they form a 5-lobed mass on each side in the pre-abdomen, this mass being connected with the mid-gut by means of 5 canals (hepatic ducts). In the mid-gut of *Solpuga* (*Galeodes*) numerous branched diverticula are said to enter both its anterior and its posterior ends. In the *Pseudoscorpionidæ* there are 3 diverticula of the mid-gut, 2 lateral, and 1 unpaired ventral. The two lateral diverticula again subdivide at their outer edges into 8 lobes. The mid-gut here forms a double loop. In the *Microthelyphonidæ* 5 pairs of shallow bulgings have been observed in the mid-gut. In the mid-gut of the *Araneidæ* (Fig. 369, *A*, *B*) we must distinguish a cephalo-thoracic and an abdominal division. The former often has 5 pairs of diverticula. The first two diverticula may anastomose with each other over the sternal side of the thorax and so form a ring. The lateral diverticula often bend round from the side towards the middle line of the body under the thoracic ganglion, first, however, giving off a blind branch to the coxal joint of each limb (*e.g.* in *Epeira* and many other *Araneidæ*). In *Atypus* the thoracic portion of the mid-gut has only 3 pairs of diverticula, the most anterior pair in this case not forming a ring.

In the anterior portion of the abdomen of the *Araneidæ* the mid-gut, which is here somewhat expanded, forms a considerable number of diverticula varying in size and much branched; these are united by connective tissue to the mass which is erroneously called the liver. The coloured secretions occurring in some of the cells of these diverticula distinguish them from the non-coloured diverticula of the cephalothoracic mid-gut.

The mid-gut of the *Phalangidæ* is a tolerably spacious sac covered laterally and dorsally by numerous (30) blind tubes. These blind tubes enter the mid-gut through 6 lateral and 1 anterior pair of apertures.

The mid-gut of the *Acarina* (Fig. 369, *C*) also has longer or shorter bulgings, invaginations, or cœcal diverticula, whose number varies. There are often 2 or 3 pairs.

The mid-gut of the *Linguatulidæ* is a straight tube without diverticula.

The **Malpighian Vessels.**—In the *Scorpionidæ*, 2 Malpighian vessels enter the hind-gut. In one species (*Sc. occitanus*) 4 vessels are said to occur, 2 of them being branched. In the *Araneidæ*, the Malpighian vessels consist of numerous fine branched and anastomosing tubes which finally unite on each side into two collecting ducts. The two ducts of one side enter the rectal vesicle by a common terminal portion.

The tubes of the *Phalangidæ*, formerly considered to be Malpighian vessels, are said by more recent observers to emerge at the mouth. In this case they can of course not be regarded as Malpighian vessels. They require further investigation.

In the *Cyphophthalmidæ*, and especially in the genus *Gibbocellum*, 2 long Malpighian vessels are found which enter the sac-like expanded rectum (cloaca). Each vessel begins with a blind terminal tube, which breaks up into a plexus of fine tubules, uniting again into a single vessel entering the rectum. Malpighian vessels have been found in many *Acarina*. They are generally in the form of 2 long, occasionally coiled tubes, entering the hind-gut. Sometimes the 2 tubes unite in a common duct which enters the hind-gut, and they thus assume the form of the letter Y (*Atax*). In other *Acarina* the excretory organ is an unpaired tube lying on the mid-gut. In *Hydrodoma* it emerges close behind the anus, but separate from it. In other cases numerous Malpighian vessels are said to enter the hind-gut near the anus (*Argas*). Here and there a rectal sac like that of the *Araneidæ* is found, and into this enter both the gut and the Malpighian vessels (*Gamasidæ*, Fig. 369, *C*, and *Halarachnidæ*). The arrangement of the long Malpighian vessels in the larvæ and the first nymph stage of the *Gamasidæ* is interesting. They here (Fig. 361, p. 514) reach far forward and form a loop at each leg which may reach into its third or fourth joint. The blind ends of the two vessels reach far into the first pair of legs. In some *Acaridæ* and in the *Linguatulidæ* no Malpighian vessels have as yet been found. Our knowledge of the Malpighian vessels of the Arachnoidea in general is exceedingly scanty.

VI. The Blood-vascular System.

Among the Arachnoidea this system shows very various stages of development. It is most highly developed in the *Scorpionidæ* and next in the *Araneidæ*. The blood nowhere flows entirely in blood vessels separated from the body cavity, but rather for a larger or smaller portion of its course enters blood sinuses and lacunæ, which represent the cœlome. In the Arachnoidea also distinct relations between the blood-vascular system and the respiratory organs can be established. Where the respiratory organs are very strictly localised, as in the book-leaf tracheæ of the *Scorpionidæ* and *Araneidæ*, the vascular system with walls of its own is most developed; where the respiratory organs are dispersed over the whole body, as they are in the *Antennata*, and also where there are no special respiratory organs, the peripheral portion of the vascular system is reduced, as in the *Antennata*, and even its central organ, the heart, may disappear.

The central organ, **the heart** (Figs. 370, 371), shows, like that of the *Crustacea*, various degrees of concentration, from the extended many-chambered dorsal vessel provided with numerous pairs of ostia (*Scorpionidæ*), to the short, one-chambered cardial sac with one pair of ostia (*Acaridæ*). This progressive concentration is evidently closely connected with the progressive concentration of the whole body.

That the heart lies in a pericardium has only been with certainty observed in a few cases. Muscles and strands of connective tissue, which are attached on the one side to the heart or the pericardium (the latter appears to be the case in the *Araneidæ*), and on the other to the integument, seem to occur pretty generally.

After the heart itself the most constant portion of the vascular system is a median anterior vessel-like prolongation of the heart, running on the dorsal side to the brain; this may be called the **aorta**

cephalica. It is perhaps the remains of an originally long tubular heart which reached as far as the anterior region of the body, and which ceased to develop ostia.

The heart lies in all Arachnoidea in the abdomen, or in that part of the body which corresponds with the abdomen.

Scorpionidæ (Fig. 370, *A*).—The extended tubular heart of the Scorpion lies in the pre-abdomen. It is **8 chambered,** and has **8 pairs of lateral openings.** From the posterior end of each chamber a pair of lateral arteries diverges. The heart is continued posteriorly into an **aorta of the post-abdomen,** and anteriorly into an **aorta cephalica** which runs through the cephalo-thorax. From the posterior aorta several lateral pairs of arteries arise. Immediately in front of the most anterior pair of ostia, and thus at the root of the aorta cephalica, a lateral artery is likewise given off on each side. A little further forward there are two more lateral arteries running downwards, and embracing the œsophagus, so forming an œsophageal ring. From this œsophageal ring arises a medio-ventral longitudinal vessel running backwards; this lies above the ventral chord, and is called the **supraneural vessel.** In front of the vessels forming the œsophageal ring the aorta cephalica gives off numerous other arteries, principally to the 6 pairs of extremities.

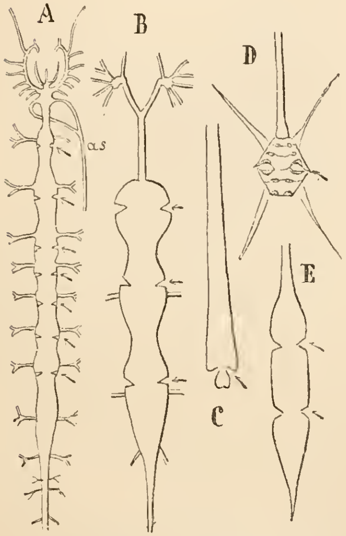

FIG. 370.—**The hearts of various Arachnoidea.** *A*, **Scorpion** (after **Newport**). *B*, **Araneid.** *C*, **Obisium silvaticum,** juv. (*Pseudoscorpionid*) (after **Winkler**). *D*, **Gamasus fucorum,** larva (after **Winkler**). *E*, **Young Phalangid** (after **Winkler**).

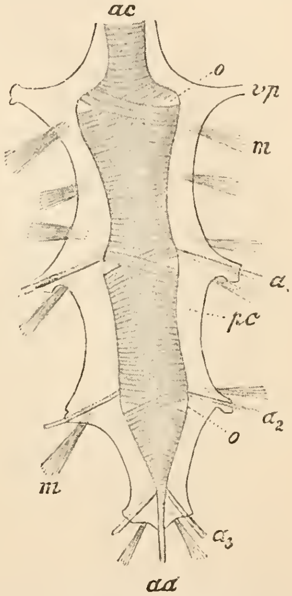

FIG. 371.—**Heart of a Spider** (*Pholcus phalangoides*) (after **Schimkewitsch**). *ac*, Aorta cephalica; *o*, ostia of the heart; *vp*, origin of the vena pulmonalis; a_1, a_2, a_3, lateral arteries of the heart; *aa*, aorta or arteria abdominalis; *m*, alary muscles, attached to the pericardium; *pc*, pericardium.

All the arteries apparently open into a lacunar system of the body, through which the blood flows in special currents, those of the pre-abdomen bathing the book-leaf tracheæ, again returning to the pericardium, and thence into the heart. This portion of the anatomy of the circulatory system, however, requires fresh investigation.

The circulatory system of the *Scorpionidæ* shows considerable similarity with that of the *Xiphosura*, which is increased by the occurrence of an œsophageal ring and a medio-ventral longitudinal vessel. It must, however, be particularly noticed that a medio-ventral longitudinal vessel (subneural vessel) occurs also in many *Crustacea* (*Malacostraca*), which further, in the *Isopoda*, is connected with the anterior end of the cephalic aorta by means of an œsophageal ring. In *Peripatus* also a medio-ventral vessel is said to have been observed.

Araneidæ (Figs. 370 *B*, 371).—After the *Scorpionidæ* the *Araneidæ* possess, as far as we know, the most richly developed vascular system. The heart, which runs along the dorsal side of the abdomen, is enclosed in a sac-like pericardium, which is itself again, as it appears, surrounded by a blood sinus. The heart has only 3 (in *Mygale* 4 ?) pairs of openings, and is continued anteriorly into an aorta cephalica and posteriorly into a short aorta or arteria posterior, and sends off laterally 3 pairs of inconsiderable arteries which soon open into the lacunar system of the body. The **arteria posterior** opens into a blood sinus placed near the anus. The **aorta cephalica** runs further forward into the cephalo-thorax, soon dividing into 2 lateral trunks, which bend downwards, and after a short course break up into several arteries which run to the eyes and extremities. All these arteries open into blood lacunæ or blood sinuses. In this definitely arranged system of lacunæ and sinuses the blood flows through the body in definite directions. The greater portion of it finally collects on the ventral side in the anterior part of the abdomen, here takes an upward direction, and thus round the book-leaf tracheæ, and then again finally enters the pericardium, whence it returns to the heart chiefly through the most anterior pair of ostia. From the book-leaf tracheæ (lungs) to the pericardium the blood flows through a special vein, formed by a continuation of the pericardial wall. Since, however, the pericardium itself is only a part of the cœlome, this vein also cannot be regarded as a genuine blood vessel, but only as a more sharply demarcated canal-like part of the cœlome, *i.e.* of the general lacunar system.

In the **Pseudoscorpionidæ** (Fig. 370, *C*), **Phalangidæ** (*E*), **Cyphophthalmidæ** and **Acarina** (*D*) the vascular system is reduced to the heart and the aorta cephalica. The heart itself, placed in the anterior part of the abdomen, becomes shorter and more compact. The number of its pairs of ostia diminishes, till finally there is only 1 pair (*Acarina*, and *Obisium* among the *Pseudoscorpionidæ*). This reduction probably is caused by the anterior part of the heart losing its ostia, becoming narrow and passing into the aorta cephalica, while only the posterior cardial chambers with their pairs of ostia remain as a sac-like organ of propulsion.

The heart of the *Pseudoscorpionidæ* lies in the 3 or 4 anterior abdominal segments, and in *Obisium* is said to have only 1 pair of ostia, in *Chernes*, however, 4 pairs. The heart of the *Phalangidæ* and *Cyphophthalmidæ* has 2 pairs of ostia. Among the *Acarina* a heart has so far been found only in the *Gamasidæ* and in *Ixodes*. It is probable, indeed almost certain, that many other *Acarina* have no heart, and in general no special blood-vascular system. The same is the case in the *Linguatulidæ*.

In the other Arachnoidea the blood-vascular system has either not yet been investigated or else not sufficiently investigated for a comparative study.

VII. The Respiratory Organs.

The respiratory organs of the Arachnoidea are **tracheæ**, whose 1 to 4 pairs of outer apertures or **stigmata** almost always lie ventrally and anteriorly in the abdomen. Two sharply distinguished forms of tracheæ occur: **tubular tracheæ** and **book-leaf tracheæ**. The former essentially agree with the tracheæ already known to us in the *Protracheata* and *Antennata*. The latter, which are also called **lungs, lung tracheæ, lung sacs,** or **leaf tracheæ**, have till now only been met with in the Arachnoidea.

Tubular tracheæ appear in three modified forms, between which, however, intermediate stages occur. (1) The principal trunk arising from the stigma is branched like a tree in the body, as in the *Insecta* and most *Myriapoda*. Separate tracheal trees are connected together by anastomoses. A spiral thread becomes differentiated in the chitinous cuticle of the tracheæ. Such branched tree-like tracheæ are found in the *Solpugidæ*, *Cyphophthalmidæ* (Fig. 372, s_1), *Phalangidæ*, a few *Pseudoscorpionidæ*, and a few *Acarina* (*Gamasidæ*, *Ixodes*).

(2) The principal trunk arising from the stigma generally divides only once into 2 chief branches. On each of these principal branches, at irregular intervals, are attached tufts of long finer unbranched tracheal tubules. Only one such tracheal tuft is sometimes found lying at the end of the principal trunk. Such tracheæ are found in many *Araneidæ*, many *Pseudoscorpionidæ*, and in most of those *Acarina* which are as a rule provided with tracheæ. This second tracheal form, and especially the modification of it last mentioned, leads over to the third form.

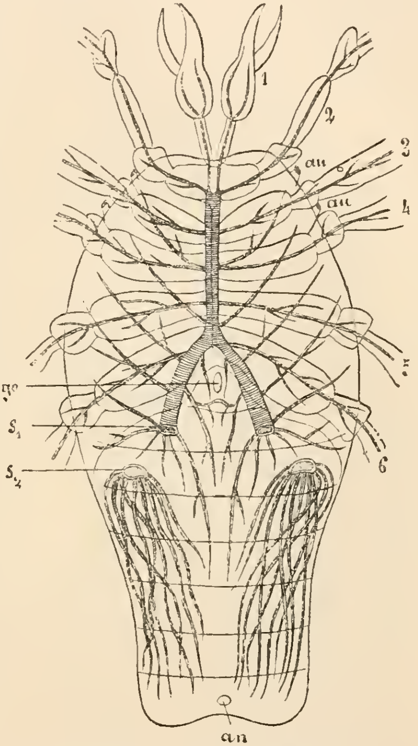

Fig. 372.—Diagrammatic representation of the **tracheal system of Gibbocellum Sudeticum** (after **Stecker**). 1-6, 1st to 6th pair of limbs, only the first (cheliceræ) drawn fully; *au*, eyes; *go*, genital aperture; s_1, anterior pair of stigmata (for the tree-like tracheæ); s_2, posterior pair of stigmata for the tufted tracheæ; *an*, anus.

(3) A common tracheal trunk, arising from the stigma, is wanting. The separate tubules of the tracheal tuft branch directly from the stigma. We are the more justified in tracing back this third form to a shortening and later disappearance of the common tracheal trunk, since the posterior tracheal tufts of a few Pseudoscorpionidæ (*Chernes cimicoides*) still rise from the end of a short tube. Such simple tufted

tracheæ are found in a few *Pseudoscorpionidæ* and a few *Cyphophthalmidæ* (*Gibbocellum*, Fig. 372, s_2). They show much similarity with the tracheæ of the *Scutigera* (p. 479). True spiral threads are not found in the second and third forms of tubular tracheæ.

Book-leaf tracheæ (tracheal lungs, lung sacs, Figs. 373 and 374). The stigma leads into a sac filled with air, into which there project from the anterior wall numerous leaves arranged like those of a book. They are, however, also attached by their side edges to the lateral walls of the sac, so that the latter may be compared with a letter-case divided by many partition walls into numerous compartments; the walls of the sac are internally lined with a chitinous cuticle, a continuation of the outer chitinous integument of the body; this is also continued on to the leaves, so that these consist of two somewhat closely contiguous lamellæ connected by (muscular ?) trabeculæ or transverse supports. Between the two lamellæ of a leaf the blood enters from the cœlome and the respiratory process takes place through the lamellæ.

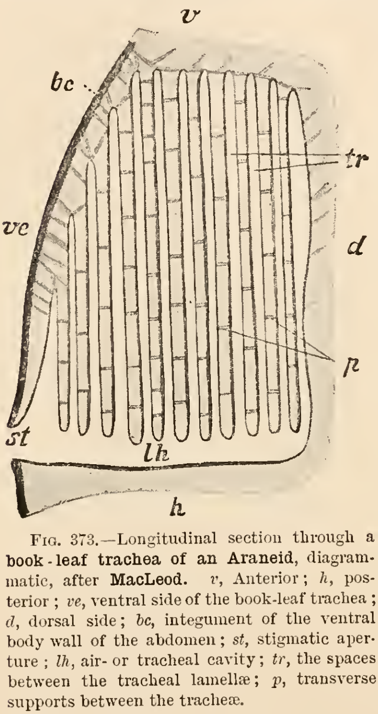

FIG. 373.—Longitudinal section through a **book-leaf trachea of an Araneid,** diagrammatic, after **MacLeod.** *v*, Anterior; *h*, posterior; *ve*, ventral side of the book-leaf trachea; *d*, dorsal side; *bc*, integument of the ventral body wall of the abdomen; *st*, stigmatic aperture; *lh*, air- or tracheal cavity; *tr*, the spaces between the tracheal lamellæ; *p*, transverse supports between the tracheæ.

The most plausible view of the morphological signification of these lung sacs seems still to be that they are **modified tracheal tufts.** If we imagine that in a tracheal tuft which opens outwardly by means of a short tracheal trunk the separate tubules standing close together, mutually flatten each other out into hollow plates, and that these hollow plates become arranged in a row, we have before us a so-called book-leaf trachea or tracheal lung. The separate very narrow spaces lying between the leaves of the air sac would thus correspond with the lumina of the flattened tracheæ.

Ribbon-like flattened tracheæ are in fact to be found in the *Araneidæ*. Compare further the figures of the tracheal tufts of *Scutigera*, p. 479, which greatly facilitate a comprehension of the view here given of the rise of book-leaf tracheæ.

Another view as to the morphological significance of the book-leaf tracheæ of the Arachnoidea has been put forward by those who hold that the *Arachnoidea* and especially the *Scorpionidæ* are nearly related to the *Xiphosura*. According to this view the leaves or partition walls which project into the lung sac answer to the branchial leaves of the abdominal feet of *Limulus*, which have sunk below the body surface. The 4 pairs of book-leaf tracheæ in the *Scorpion* would thus represent rudiments of the 4 pairs of abdominal feet, *i.e.* of their branchial appendages. In comparison with the view first given, this view seems to us artificial and unsupported by comparative anatomy and ontogeny.

The *Scorpionidæ*, *Pedipalpi*, and the tetrapneumonic *Araneidæ* (*Mygalidæ*) have only book-leaf tracheæ. In the dipneumonic *Araneidæ* book-leaf and tubular tracheæ exist simultaneously.

Number and Position of the Stigmata.

The *Scorpionidæ* possess 4 pairs of book-leaf tracheæ and 4 pairs of stigmata, lying laterally on the ventral side of the 3d to the 8th abdominal segments (Fig. 362, p. 517).

The *Pedipalpi* have 2 pairs of book-leaf tracheæ with 2 pairs of stigmata on the ventral side of the 2d and 3d abdominal segments (Fig. 364, p. 519).

Among the *Araneidæ* the arrangements are different in the *Tetrapneumones* and the *Dipneumones*. The *Tetrapneumones* (*Mygalidæ*) have 2 pairs of book-leaf tracheæ and 2 pairs of stigmata (Fig. 374, *ft*, *s*) lying on the ventral side of the base of the abdomen. The *Dipneumones* have only one pair of book-leaf tracheæ, corresponding with the anterior pair of the *Tetrapneumones*. Besides these, however, they have, as the equivalent of the second pair of book-leaf tracheæ of the *Tetrapneumones*—tubular tracheæ, which generally open through an unpaired stigma in the shape of a transverse fissure placed far back on the abdomen. This unpaired stigma no doubt arises from a posteriorly placed pair of stigmata, which have united. This supposition is supported by the fact that in some *Araneidæ* (*Dysdera*, *Segestria*, *Argyroneta*) two separate more anteriorly placed stigmata for the tubular tracheæ occur (behind the pair for the book-leaf tracheæ), and also by the circumstance that in a few cases (*Dictyna*) the tracheal trunks which open through the unpaired stigma are distinctly recognisable as double.

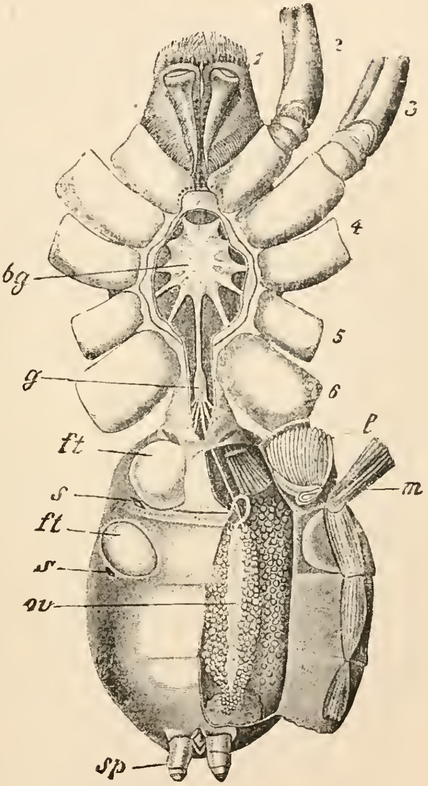

Fig. 374.—Mygale, from the ventral side. The ventral wall of the cephalo-thorax removed to show the large cephalo-thoracic ganglion (*bg*) and the 2d small ganglion at the base of the abdomen. The ventral wall of the abdomen on the left side opened out. *m*, Ventral muscles of the abdomen; *l*, lamellæ of the book-leaf tracheæ; *ft*, book-leaf tracheæ; *s*, stigmata of the same; *ov*, ovary; *sp*, spinning mammillæ; 1-6, 1st to 6th pairs of extremities. 2-6, not completely drawn (*Règne animal*).

The *Solpugidæ* have tubular tracheæ with tree-like ramifications, opening through 3 pairs of stigmata, the first pair lying in the first thoracic segment, the second and third pairs in the second and third abdominal segments. The position of the first pair of stigmata in the thorax deserves to be specially noted.

The *Pseudoscorpionidæ* have tubular tracheæ with 2 pairs of stigmata, which lie in the 2d and 3d abdominal segments. In *Cheiridium* there is only one pair of stigmata, which has perhaps arisen by the fusing of the two pairs found in other *Pseudoscorpionidæ.*

The ramified tracheæ of the *Phalangidæ* are said to open through a single pair of stigmata, lying ventrally at the anterior end of the abdomen, which is closely applied along its whole breadth to the cephalo-thorax.

Among the *Cyphophthalmidæ*, *Cyphophthalmus* is said to have only one pair of stigmata on the under side of the first abdominal segment. *Gibbocellum* (Fig. 372), on the contrary, has 2 pairs of stigmata lying laterally and ventrally in the 2d and 3d abdominal segments. The anterior pair of stigmata leads into richly branched tracheæ, whose two principal trunks unite into an unpaired median trunk in the cephalo-thorax. The posterior pair of stigmata lead into tufted tracheæ. Each stigma is covered by a plate pierced like a sieve, and each pore in this plate represents the aperture of a tracheal tubule.

In many *Acarina*, especially in the parasitic and marine *Acarina*, tracheæ are wanting. When they are present they open out through one pair of stigmata, which are placed very unusually. This pair of stigmata generally lies near the coxal joints of the last pair of extremities, but often much further forward. It occasionally lies on the dorsal side, and sometimes above the base of the cheliceræ. This arrangement is not at present understood. In certain *Acarina* short tubes or sacs connected with apertures in the outer chitinous integument have been considered as the rudiments of tracheæ.

The *Linguatulidæ* are devoid of tracheæ. The *Microthelyphonidæ* also are said to have no special respiratory organs. If this be established, it must not be considered in the *Acaridæ* the original arrangement.

The *Tartaridæ* are said to possess lateral apertures supposed to be stigmatic in the 2d, 3d, and 4th ventral rings, thus having 6 in all.

A review of the position of the respiratory organs and their apertures in the various divisions of the Arachnoidea shows us that not only do several abdominal segments possess stigmata, but that these may occur, as is shown by the example of the *Solpugidæ,* in the thorax also. Leaving out of consideration the anterior position of the stigmata in certain *Acarina*, which are a very one-sidedly developed Arachnoid group, and evidently, excepting the *Linguatulidæ,* the furthest removed from the racial form, we are justified in assuming that the, to us, unknown racial form of the Arachnoidea possessed a larger number of stigmata[1] and of tracheæ connected with them than any Arachnoid form now living. This presupposes that the book-leaf tracheæ are modified tubular tracheæ.

VIII. Sexual Organs.

In all Arachnoidea the sexes are separate. The sexual organs lie in the abdomen. The testes and ovaries are either paired or single. The paired condition must be the more primitive. The ovaries in very many Arachnoidea appear as tubes beset with spherules or sacs, and so have a grape-like appearance. The eggs arise only in the sacs, which may be called egg-follicles, and they thence enter the ovarian tube, which serves only as a duct.

With very rare exceptions the ducts of the sexual organs are paired. These unite in their terminal portion, and open externally

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[1] See footnote on page 516.

through an unpaired ventral genital aperture at the anterior end of the abdomen. Several organs, chiefly accessory, are connected with the terminal portion of the ducts, viz. receptacula seminis, vesiculæ seminales, glands, male and female copulatory organs. The anatomical structure of the sexual apparatus in the different Arachnoidea varies greatly in detail. The review which follows is incomplete, and only takes into account the better known forms.

Scorpionidæ. Female Apparatus (Fig. 375, *A*).—Three longitudinal tubes, beset with spherical ovarian follicles, lie in the pre-abdomen, one median and two lateral. The median tube is connected with the lateral by 5 transverse anastomoses, also beset with ovarian follicles, so that the ovigerous portion of the sexual apparatus forms a network of 8 meshes. From the anterior end of this there arises on each side an oviduct, which at once swells into a rather long tube (receptaculum seminis, or vagina?) The two tubes converge towards the ventral middle line, where they emerge on the first abdominal ring, in front of the combs, through an aperture which is covered by 2 valves. The *Scorpionidæ* are viviparous. The embryos develop in the ovarial tubes, which function as uteri.

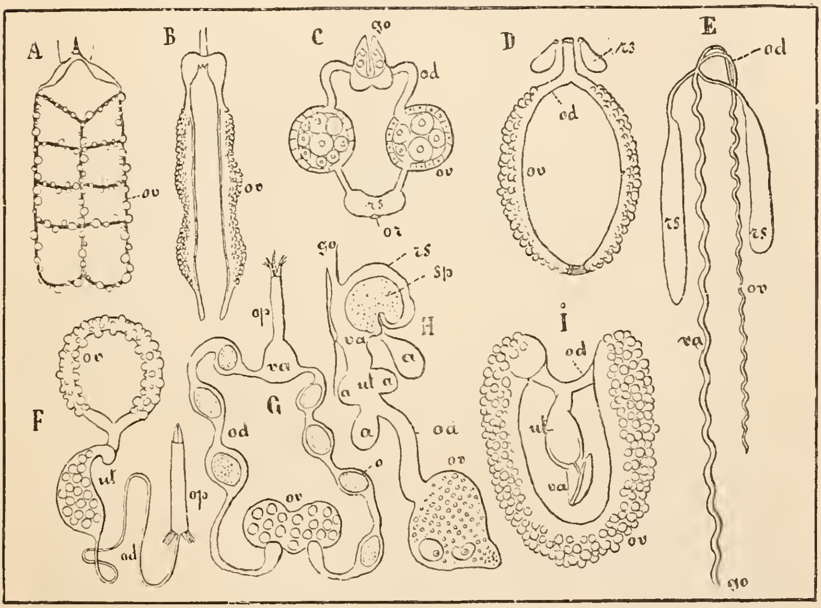

FIG. 375.—**Female sexual apparatus of various Arachnoidea.** Most of the figures are somewhat diagrammatic. *A*, **Scorpio occitanus** (after **Blanchard**). *B*, **Galeodes barbarus** (after **L. Dufour**). *C*, **Trichodactylus anonymus** (*Acarid*) female sexual organs of the nymph (after **Nalepa**). *D*, **An Araneid.** *E*, **Pentastoma tænioides** (after **R. Leuckart**). *F*, **Phalangium opilio** (after **Gegenbauer**). *G*. **Cepheus tegeocranus** (*oribatid*) (after **Michael**). *H*. **Gamasus crassipes** (*Acarid*) (after **Winkler**). *I*, **Trombidium fuliginosum** (after **Henking**). *ov*, ovaries; *od*, oviduct; *go*, genital aperture; *rs*, receptaculum seminis; *or* (in *C*), outer aperture of the same; *va*, vagina (in *E* also the uterus); *op*, ovipositor; *a*, glandular appendages.

Male Apparatus (Fig. 376, *A*).—The tubular testes are distinctly paired. There are on each side two testicle tubes connected together by anastomoses. These two tubes unite anteriorly to form a sperm duct, which, joining the duct from the other side, opens outwardly at the place where, in the female, the genital aperture lies. Paired accessory organs are connected with the ducts, viz. copulatory organs, seminal vesicles, and glands.

Pseudoscorpionidæ.—The ovary is an unpaired tube beset with follicles, which is continued into two oviducts entering a short vagina. Numerous unicellular, and 2 long tangled tubular glands are connected with the vagina.

The testes in *Chernes* and *Obisium* recall in their form the ovaries of the *Scorpionidæ*. In *Chelifer*, on the contrary, we find a single median testicle tube. There are everywhere 2 sperm ducts, entering a common copulatory apparatus, with which are connected glands similar to those in the female. The unpaired genital aperture lies ventrally in both sexes on the boundaries between the 2d and 3d abdominal segments.

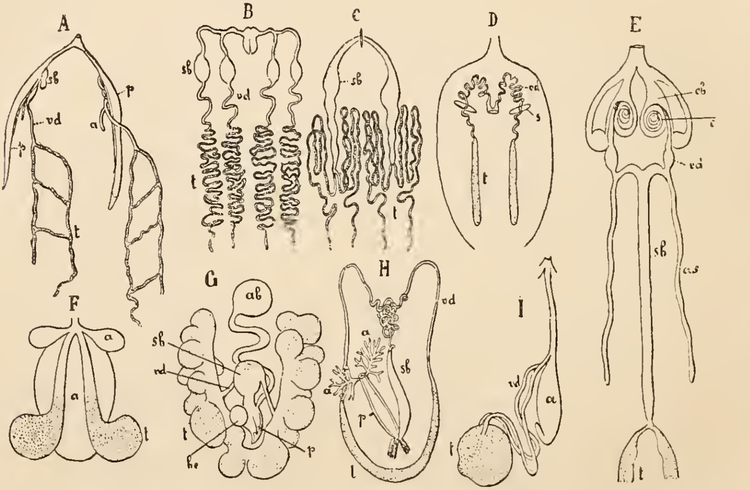

Fig. 376.—**Male sexual apparatus of various Arachnoidea.** Most of the figures are somewhat diagrammatic. *A*, **Scorpio occitanus** (after **Blanchard**). *B*, **Galeodes barbarus**. *C*, **Galeodes nigripalpis** (after **Dufour**). *D*, **Philoica domestica** (*Araneid*) (after **Bertkau**). *E*, **Pentastoma tænioides**, only the anterior end of the testes drawn (after **Leuckart**). *F*, **Uropoda** (*Acarid*) (after **Winkler**). *G*, **Trombidium fuliginosum** (*Acarid*) (after **Henking**). *H*, **Phalangium opilio** (after **Krohn**). *I*, **Gamasus crassipes** (*Acarid*) (after **Winkler**). The letters in all cases signify: *t*, testes (dotted); *vd*, vasa deferentia; *sb*, seminal vesicle; *p*, penis; *a*, glandular appendages; *as*, tubular appendages; *ab*, vesicular appendages; *bc*, bursa expulsatoria; *c*, cirrus; *cb*, cirrus pouch.

Solpugidæ.—The female sexual apparatus (Fig. 375, *B*) consists of 2 long ovarial tubes beset at their outer edges with numerous ovarian follicles, and placed in the abdomen. From each ovary there arises an oviduct. The 2 oviducts unite, their ends swelling. The external genital aperture is a longitudinal fissure on the ventral side of the first abdominal segment.

The male apparatus (Fig. 376, *B*, *C*) consists of 2 thin and very long winding testicle tubes on each side of the abdomen, and quite separate from each other. These testicle tubes are continued into sperm ducts. The 2 sperm ducts of one side unite after a longer or shorter course into one duct, which, joining that from the other side, opens externally through a common aperture, which lies ventrally on the first abdominal segment. The ducts have either 4 or 2 swellings, regarded as seminal vesicles; if there are 4 they lie in the course of the 4 sperm ducts, if 2 in the course of the 2 common efferent ducts.

Pedipalpi.—The ovaries and testes are paired with paired ducts, and a common unpaired genital aperture on the ventral side of the first abdominal segment. The *Phrynidæ* are viviparous.

Microthelyphonidæ.—The germ glands (the ovaries at least) are said to be unpaired. There are probably 2 oviducts, which open outward by means of a common terminal piece on the ventral side of the first abdominal segment.

Araneidæ. Female Apparatus (Fig. 375, *D*).—There are in the abdomen 2 wide tubes, beset with numerous ovarian follicles, and looking like a cluster of grapes. The free ends of the ovaries sometimes fuse in such a way as to give rise to an unpaired circular ovary. There are always two short oviducts, uniting to form a short terminal portion (vagina), which emerges through the unpaired median genital aperture at the base of the abdomen, on the ventral side, between or somewhat behind the anterior pair of stigmata. All female *Araneidæ* possess receptacula seminis. There is either **one** receptaculum, or **two** lateral receptacula, less frequently **three**, one median and two lateral. These receptacula, into which, during copulation, the semen is introduced, are entirely separate from the sexual apparatus in many *Araneidæ*, and have separate outer apertures near the female genital apertures. In others they are accessory organs of the vagina. In *Epeira* each of the two receptacula has 2 apertures—an outer one, placed on the genital plate near the sexual aperture, and an inner one leading into the vagina.

Male Apparatus (Fig. 376, *D*).—Two testes lie as long tubes in the abdomen, and are continued as 2 long thin and often much coiled sperm ducts, these opening outward by means of a short wide common duct through the male genital aperture, which lies between the 2 anterior stigmata. The transition from the testes into the vasa deferentia is often gradual, so that it is difficult to say where the former leave off and the latter begin. Occasionally the blind ends of the 2 testes are united by connective tissue.

In the male sexual apparatus of the *Araneidæ* a special copulatory organ is wanting. The pedipalps of the male function as copulatory organs, their terminal joints (Fig. 377) being transformed in a peculiar manner. The inner side of this terminal joint carries an outgrowth, through which runs a spirally coiled canal emerging at the pointed end. This canal is filled by the male with sperm from the genital aperture. When copulation takes place the point of the outgrowth of the pedipalp is introduced into the receptaculum seminis of the female, and the semen discharged from the spiral canal into the receptaculum.

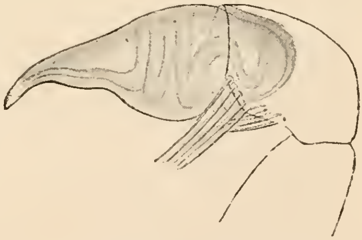

Fig. 377.—**Last joint of the pedipalp of Filistata testacea Latr. (after Bertkau).**

Phalangidæ (Fig. 375, *F*, Fig. 376, *H*).—Both the ovaries and testes are here unpaired. Each germ gland is a semicircular tube which, by analogy with the arrangement described in the *Araneidæ*, may well be considered to have arisen by the fusing of the blind ends of originally paired germ glands. The ovarian tube is superficially beset with ovarian follicles. The 2 ends of the germ glands are continued into 2 ducts (sperm ducts in the male, oviducts in the female), and these unite to form a common duct which enters the copulatory apparatus. This, in the male, is a rod-like penis, in the female, a long cylindrical ovipositor. Both the penis and the ovipositor are enclosed in special sheaths, and they can, together with their sheaths, be protruded and evaginated. The 2 vasa deferentia are very much coiled shortly before entering the common duct. Before the latter enters the penis, its wall becomes strongly muscular. This muscular portion of the duct evidently serves as a propelling organ for driving the semen out of the penis. A pair of accessory glands enters the end of the penis sheath.

In the female the common efferent duct has 2 divisions, the proximal division being enlarged into a uterus, which at maturity is filled with eggs, the narrow and long distal portion being a vagina which is continued into the ovipositor. The vagina has 3 lateral sacs, which are regarded as receptacula seminis. Accessory glands enter the end of the sheath of the ovipositor.

The genital aperture in both sexes lies ventrally, on the boundary between the cephalo-thorax and the abdomen.

It often occurs in the male *Phalangidæ* that eggs develop on the surface of the testes ; these apparently do not leave the body, but are reabsorbed.

Cyphophthalmidæ.—Here also the genital aperture lies ventrally at the base of the abdomen (on the first abdominal segment). The male has a long penis, the female a long ovipositor.

Acarina (Fig. 375, *C*, *G*, *H*, *I*, Fig. 376, *F*, *G*, *I*).—Great variety here prevails in the structure of the sexual organs. The following are 2 extreme cases. In the first there are 2 separate symmetrically-placed germ glands and 2 separate ducts, opening outwards through a common unpaired copulatory organ. We here see the more original arrangement. The other extreme is rare. It is found in the female of the *Gamasidæ* (Fig. 375, *H*), where a single unpaired ovary is continued into a single unpaired duct, which opens outwards through the copulatory organ. Transition forms between these 2 extremes are very commonly found. The 2 germ glands fuse in various ways to form one, which sometimes still shows traces of its originally double character ; the ducts, however, remain separate to a greater or smaller extent.

Accessory organs, glands, receptacula seminis are often connected with the ducts. The unpaired terminal portion of the ducts nearly always leads to the outer sexual apparatus, which in the male is the penis, and in the female may be developed as an ovipositor. There are often found near the genital apertures adaptations (*e.g.* suckers) which assist in copulation. The sexual organs are by no means limited in position to the posterior part of the body, on the contrary, the fact that they often run far forward shows the extent to which the concentration of the whole body and the obliteration of the boundary between the cephalo-thorax and the abdomen have taken place. The aperture of these organs often lies far forward also, in some cases as far forward as between the most anterior pair of legs. It has been observed in the *Tyroglypha* (*Trichodactylus anonymus*) that the genital aperture which in the adult female lies between the 2d pair of legs, in the last larval stage (before the last moult) still lies between the last pair. This observation also throws light on the anterior position of the stigmata in many mites, which must be attributed to displacement.

As in the *Araneidæ*, so also in certain *Acaridæ* there occur in the females receptacula seminis with apertures separate from the rest of the sexual apparatus. Trichodactylus thus has a receptaculum at the posterior end of the body, opening outward through a post-anal aperture. The penis is introduced into this aperture during copulation. The receptaculum is connected by 2 short tubes with the 2 ovaries. This arrangement and that found in *Epeira* recall to a certain extent the well-known arrangement in the *Trematoda* and *Cestoda*, where the female sexual apparatus is connected with the exterior not only by means of the usual genital aperture, but by **Laurer's** duct as well. In *Trichodactylus* the receptaculum arises independently by an invagination of the integument, and becomes connected with the ovaries only secondarily.

Some *Acarina* are viviparous, others ovoviviparous, *i.e.* the eggs develop to a certain extent within the mother body, so that the young is hatched soon after the laying of the egg. Most *Acarina*, however, are oviparous. The eggs or embryos collect often in great numbers in the expanded oviducts, which then function as uteri.

Linguatulidæ. Female Apparatus (Figs. 375 *E*, 378).—The ovary is a long unpaired tube, beset with ovarian follicles, which runs through the body over the intestine in a longitudinal direction. It is continued anteriorly into 2 oviducts, which surround the œsophagus, and under it enter the anterior end of the unpaired vagina. This serves at the same time as uterus, the first embryonic development of the eggs taking place in it. The vagina is an unusually long tube which runs backward with many windings, accompanying the intestine, and is often filled with several hundreds of thousands of eggs and embryos; it opens outward through a female genital aperture close to the anus. The ducts of 2 long receptacula seminis, which lie at the 2 sides of the mid-gut, enter the most anterior end of the vagina at the point where the oviducts join it.

Male Apparatus (Fig. 376, *E*).—The testes are paired or unpaired tubes placed like the ovary. The testis or testes are continued anteriorly into an unpaired efferent division, which has been regarded as a seminal vesicle. This vesicula seminalis divides anteriorly into 2 canals, the vasa deferentia, which encircle the œsophagus. Each vas deferens ends in a male copulatory apparatus. The male genital aperture common to the 2 copulatory apparati lies, in contradistinction to that of the female, in the anterior portion of the body, between the 2d pair of hooks. Corresponding with the receptacula seminis of the female there are in the male 2 blind tubes running backward, these are apparently organs for propelling the semen, and enter the 2 sperm ducts. The end of each sperm duct enters a very long chitinous cirrus, which at a time of rest is rolled up in a special sac.

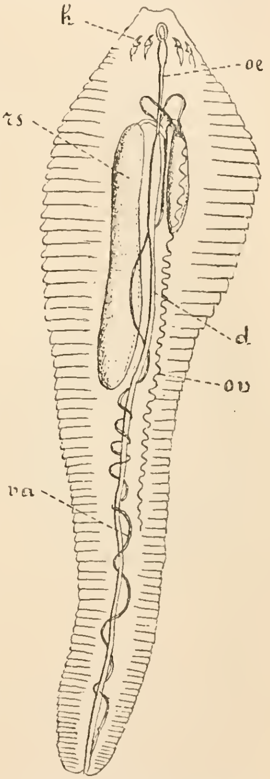

FIG. 378.—**Female of Pentastomum tænioides** at the time of copulation, with the viscera (after **Leuckart**). *h*, Hooks; *oe*, œsophagus; *rs*, receptacula seminis, one of which is still empty; *d*, gut; *ov*, ovary; *va*, vagina.

IX. Ontogeny.

We can only bring forward a few facts concerning the ontogeny of the Arachnoidea, chiefly such as are of most importance from the point of view of comparative anatomy.

1. The **segmentation** is in the main that of the centro- or mesolecithal eggs. A blastoderm is formed covering the yolk, in which, however, merocytes remain. The formation of the germ layers and of the rudiments of the most important organs proceeds, as in other *Arthropoda*, from a blastoderm plate, which may be called the embryonic rudiment. In the *Scorpionidæ*, however, the egg seems to be meroblastically telolecithal, and the furrowing takes a corresponding course, so that no blastoderm enveloping the yolk on all sides is formed, but a germ disc is developed at one pole of the egg.

2. **Embryonic envelopes** have till now only been found in the *Scorpionidæ*. The embryonic envelope here, as in the *Insecta*, consists of 2 membranes, the outer representing the serosa, the inner the amnion of the *Hexapoda*.

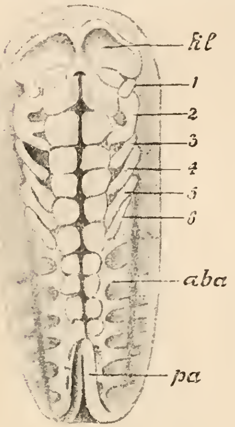

Fig. 379.—**Embryo of a Scorpion**, spread out flat, from the ventral side (after **Metschnikoff**). *kl*, Frontal lobes; 1, chelicerae; 2, pedipalps; 3-6, the 4 pairs of legs; *aba*, rudiments of the abdominal limbs; *pa*, post abdomen.

3. The **formation of segments** in the embryonic rudiments takes place as a rule from before backward, so that new segments are continually formed from the terminal segment behind those already developed. Frequently, however, the segment bearing the chelicerae, and sometimes that bearing the pedipalps, appear only after the formation of a few of the subsequent segments.

4. The **rudiments of the extremities** seem in various Arachnoidea to have different orders of succession. The permanent extremities, with the exception of the chelicerae, which begin to form later, often develop simultaneously. In the *Pseudoscorpionidæ* the rudiments of the extremities are even said to be recognisable before the marking off of the segments on the embryonic rudiments.

5. In all Arachnoidea, except the *Linguatulidæ*, **the body is, in its embryonic condition, more richly segmented than in the adult animal.** The cephalothoracic region especially shows embryonic metamerism. This region consists at certain embryonic stages of a cephalic or frontal lobe, in which the stomodæum and the definitive oral aperture form, and of 6 subsequent and thus post-oral segments, the 1st being that of the chelicerae, the 2d that of the pedipalps, while the 4 others are the segments of the 4 following pairs of extremities. In the abdomen also, even when there is no metamerism in the adult animal, segmentation is to be recognised in the embryo. The number of the embryonic abdominal segments in the various divisions of the Arachnoidea, however, differs greatly.

It is a specially important fact **that the segment bearing the chelicerae is in the embryo post-oral.** No extremities develop on the frontal lobe, where, in the *Crustacea*, *Protracheata*, and *Antennata*, the antennæ form.[1] From this fact it follows that there is no correspondence between the chelicerae of the Arachnoidea and the antennæ of the *Antennata*.

The appearance of rudimentary abdominal limbs in the embryos of many Arachnoidea has already been mentioned; some of these rudiments disappear later, some, however, are retained (*e.g.* the combs of the *Scorpion*, the spinning mammillæ of the *Araneidæ*).

6. What has been said about the relation of the embryonic metamerism of the body to the definitive metamerism of the same is also true of the nervous system. Investigations show that in the *Scorpionidæ* and *Araneidæ* a pair of ganglia forms in each embryonic segment. The embryonic pair of ganglia of the frontal lobe is the rudiment of the supra-œsophageal ganglion. **In the first post-oral segment a special ganglion for the chelicerae is developed**, which only secondarily joins the supra-œsophageal ganglion, forming with it the brain. In the *Antennata* and *Protracheata*, on the contrary, the antennæ are from the very first innervated from the preoral supra-œsophageal ganglion. Each of the following embryonic segments except the terminal segment in like manner possesses 1 pair of ganglia. The more or less

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[1] See footnote on page 516.

concentrated form of the nervous system of the adult animal arises in consequence of the fusing of pairs of ganglia which were separate in the embryo. The whole central nervous system arises in a manner similar to that in other *Arthropoda*.

7. The **Mesoderm** of the Arachnoidea at a certain embryonic stage is developed just as in the *Annulata*, *Protracheata*, *Antennata*, and perhaps also the *Crustacea*, in the form of 2 lateral segmented streaks or bands with segmental cavities.

8. The **fore-** and **hind-guts** develop in the well-known way as invaginations of the ectoderm (stomodæum and proctodæum). Opinions still differ as to the manner of formation of the **tube of the mid-gut.**

9. The first rudiments of the **lungs** (book-leaf tracheæ) appear as invaginations of the ectoderm, and thus in the same way as the tracheæ in the *Antennata*.

10. Most Arachnoidea when born or hatched from the egg resemble the adult. As far as we know, a post-embryonic metamorphosis occurs only in the *Pseudoscorpionidæ* and *Acarina*. The former are hatched in a very imperfect condition, but remain for some time (parasitically) attached to the body of the mother, who carries the eggs about with her. The young larvæ of the *Acarina* (Fig. 361, p. 514) are still devoid of the last pair of extremities, *i.e.* of the 4th pair of legs. The metamorphosis in the *Acarina* is often very complicated, and is accompanied by many moults. Sometimes several pupal and larval stages occur. In such cases the metamorphosis is accompanied by the same inner processes as in the *Insecta* with complete metamorphosis, *i.e.* by the breaking up and disappearance of larval organs, and by the formation of the definitive organs out of imaginal portions of the larva. The development and life-history of the *Linguatulidæ* were briefly described in the systematic review. The ontogeny of this group yields no data for deciding their systematic position.

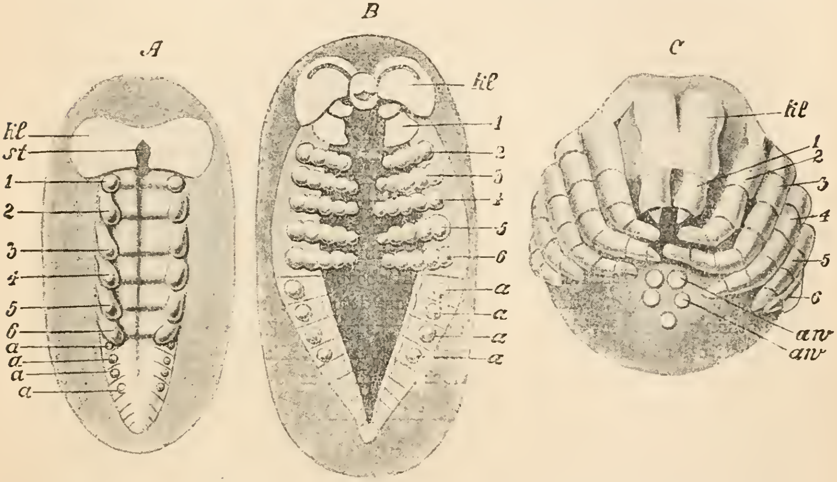

FIG. 380.—*A*, *B*, *C*, **Embryos of Agelena labyrinthica** at three stages of development; in *A* and *B* supposed to be spread out flat, in *C* in the natural form from the ventral side; *kl*, frontal lobes; *st*, stomodæum; 1-6, 1st to 6th pairs of extremities (of the cephalo-thorax); viz. 1, the cheliceræ; 2, the pedipalps; 3-6, legs; *a*, rudiments of abdominal limbs; *aw* in *C* spinning mammillæ (after **Balfour**).

X. Phylogeny.

The Arachnoidea form a sharply demarcated natural division of the *Arthropoda*. Leaving the *Linguatulidæ* out of consideration, there can be no doubt as to the relationship of the various orders united in this class. There is, further, no doubt that those Arachnoidea whose bodies are most richly segmented have best preserved the original character. These are the *Scorpionidæ*, on account of the rich segmentation of their abdomen and abdominal nervous system, and the *Solpugidæ*, on account of the segmentation of that part of the body which answers to the cephalo-thorax of other Arachnoidea ; this cephalo-thorax consists of an anterior section and three subsequent segments, which may be compared with the head and three anterior trunk segments of the *Antennata*. For such a comparison, however, further data as to the structure and development of the *Solpugidæ* are needed.

The *Acarina*, with their highly concentrated organisation, are evidently the furthest removed from the racial form of the *Arachnoidea*. The other divisions in various points take intermediate positions, and may be used as examples of progressive concentration.

It is by no means proved that the *Linguatulidæ* belong to the *Arachnoidea*. We are not even in a position strictly to prove that they are *Arthropoda*. It is, in any case, quite possible that the *Linguatulidæ* are mite-like animals greatly modified by parasitism, but they might just as well be degenerate descendants of other *Arthropoda*. Definite data are wanting for deciding whether the want of a respiratory and blood-vascular system is original, or has only arisen secondarily through parasitism. The presence of 2 pairs of hooks does not prove that they are Arachnoidea or indeed *Arthropoda* at all. The history of their development also affords us no assistance. The position of the female genital aperture at the posterior end of the body is unusual in the Arachnoidea. The diverticula of the mid-gut so common among the Arachnoidea are wanting here. The reduction of the central nervous system to an œsophageal ring with several œsophageal ganglia is probably connected with the reduction of sensory organs, extremities (?), etc., brought about by parasitism, but this does not help to decide the question whether they are descended from Arachnoidea and not from other animals provided with such a nervous system. There finally remains only the constitution of the ovarial tubes beset with ovarian follicles, which specially recall the Arachnoid arrangement, and opinions may differ as to the value of this point of agreement.

The question as to the systematic position of the Arachnoid class in the Arthropodan system is still a matter of discussion. There are two views on this subject. According to one of these views the Arachnoidea are nearly related to the *Xiphosura* and fossil *Gigantostraca* ; these three would then together form a third subphylum of the *Arthropoda*, distinct both from the *Crustacea* and the *Antennata*. According to the other view the Arachnoidea are racially connected with the *Antennata*, and form with these and the *Protracheata* the subphylum of the *Tracheata*. At present we prefer the latter view, and consider the Arachnoidea as *Tracheata* which have lost their antennæ,[1] while the first postoral pair of limbs, homologous with the mandibles of the *Antennata*, has been pushed forward, so that in all adult Arachnoidea they are inserted in front of the mouth. The cephalo-thorax of the Arachnoidea would then correspond with the fused head and thorax (3 anterior trunk segments) of the *Antennata*, and we thus perhaps find in the segmentation of the cephalo-thorax in the *Solpugidæ* a primitive arrangement. If this supposition should prove correct, then the comparison of the other organs presents no very great difficulties. In judging of the systematic position of the Arachnoidea, their relationship to the *Antennata* is strongly supported by the facts that **the Arachnoidea possess both Malpighian vessels and tracheæ, which are wanting in the Crustaceans as in the Xiphosura.**

In the *Antennata*, the mandibles and the 2 pairs of limbs of the head which

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[1] See footnote on page 516.

follow them are either not at all or very little like legs, they are changed into mouth parts. In the *Arachnoidea*, the appendages which probably correspond with them (the cheliceræ, the pedipalps, and the 1st pair of legs) have preserved far better the character of long-jointed extremities. Now, since we can find no justification in comparative anatomy or ontogeny for deriving long many-jointed extremities from abbreviated and specialised mouth-parts adapted for chewing, sucking, etc., but are, on the contrary, distinctly justified in assuming that the opposite process is the usual one, we conclude that the racial form of the Arachnoidea branched off from the racial form of the *Antennata* very early, at a time when the limbs lying directly behind the mouth were not yet changed into specialised mouth-parts. The *Arachnoidea* (*Chelicerota*) on the one hand, and the *Antennata* on the other, would thus represent two branches diverging early from the Tracheate trunk. The *Protracheata* cannot, it is true, be placed at the root of this trunk, but may still in many points of their organisation much more faithfully retain the primitive condition than do the Arachnoidea and *Antennata*, and may thus to a certain extent represent an offshoot from the root.

The above statements must make the relationship of the Arachnoidea and especially of the *Scorpionidæ* with the *Xiphosura* and *Gigantostraca* appear at present doubtful. At the same time it cannot be denied that the limbs of the cephalothorax in the Arachnoidea show a remarkable agreement with those of the *Xiphosura* and *Gigantostraca*, a much greater agreement than with the corresponding limbs of the *Antennata*. The want of preoral limbs comparable with the antennæ is also a point of agreement not to be underestimated.[1] But we may possibly have here only a phenomenon of convergence. The agreement in the rest of the organisation, leaving out of account characteristics common to all *Arthropoda*, appears to us not so great as to justify a nearer relationship based upon it. Even if the occurrence of rudimentary abdominal limbs forces us to assume that the ancestors of the Arachnoidea possessed abdominal limbs, the same is true of the *Hexapoda* also, the *Myriapoda* still possessing limbs on all the trunk segments.

The comparison of the book-leaf tracheæ with the book-like gills of the *Xiphosura* seems far-fetched compared with their derivation from the tufted tracheæ. The assumption that the tubular tracheæ in the Arachnoida have arisen independently of those of the *Protracheata* and *Antennata* can only be resorted to as a makeshift. Malpighian vessels are wanting in the *Xiphosura*. The sexual organs may emerge at very different regions of the body in the *Antennata*, as was seen as early as in the *Myriapoda*, and therefore no very great weight should be attached to the circumstance that their position is almost similar in the Arachnoidea and the *Xiphosura*. The presence of coxal glands, which emerge in the Arachnoidea and *Xiphosura* on the third pair of legs, does not bear much upon this question, since, on the one hand, coxal glands may occur on other pairs of legs as well in the Arachnoidea, and on the other, these glands are very widely distributed among the *Protracheata* and *Antennata* (especially *Myriapoda*), and apparently were originally found in all the pairs of legs, as is still the case in the *Protracheata*.

In any case further investigations as to the relations between the *Arachnoidea* and the *Xiphosura* cannot but be fruitful, and may throw much light upon the as yet by no means solved problem of the relationship of the two groups.

The *Pantopoda* (*Pycnogonidæ*) are also often considered as related to the Arachnoidea, a view which was arrived at originally in consequence of the great similarity in appearance of the two groups. This view had, however, to be abandoned when their organisations were more closely compared (*cf.* p. 424).

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[1] See footnote on page 516.

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Appendage to the Race of the Arthropoda.

The Tardigrada, or Bear Animalcule.

The body of these small animals, which does not exceed 1 mm. in length, is cylindrical or a long oval; it is outwardly unsegmented, and carries **4 pairs of short truncated appendages armed with claws,** and not marked off from the body by joints. The last pair of these appendages lies at the posterior end of the body. The most anterior portion of the body is either narrowed like a proboscis, or marked off like a head. The body is covered by a probably **chitinous cuticle,** which is thrown off from time to time (ecdysis). The **mouth** lies at the anterior, and the **anus** at the posterior end of the body. In the straight **digestive tract** which passes through the cœlome the 3 well-known regions, the fore-gut, mid-gut, and hind-gut (rectum) may be distinguished. The oral aperture, which is surrounded by papillæ, and in some cases by setæ, also leads into an oral cavity, into which project the pointed and sometimes calcified ends of 2 teeth. Two pear-shaped or tube-like glands (salivary glands? poison glands?) enter the oral cavity. The oral cavity is followed by a generally narrow oral tube, which swells out at its posterior end into a muscular, spherical, or egg-shaped œsophageal bulb (pharynx). Between the mid-gut (stomach)

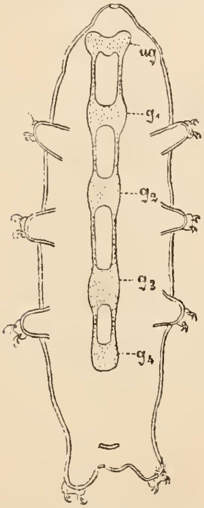

FIG. 381.—**Macrobiotus Hufelandii.** Outlines of the body and ventral chord. The supra-œsophageal ganglion is not represented. *ug*, Infra-œsophageal ganglion; g_1, g_2, g_3, g_4, the 4 following ganglia (after **Plate**).

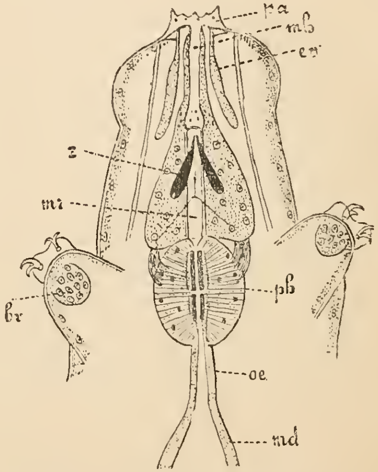

FIG. 382.—**Head of Doyeria simplex,** from the ventral side. The nervous system not drawn. *pa*, Oral papillæ; *mh*, oral cavity; *ev*, hypodermal thickenings near the mouth (glands?); *z*, teeth; *mr*, oral tube; *ph*, pharynx; *oe*, œsophagus; *md*, mid-gut or stomach intestine; *br*, hypodermal thickenings (leg glands? coxal glands?) in the feet (after **Plate**).

and the œsophageal bulb an œsophagus is intercalated. Two blind tubes enter the rectum, no doubt corresponding with the **Malpighian vessels** of the *Tracheata*.

The sexes are separate; the **germ glands** unpaired, and sac-shaped. In both sexes they enter the hind-gut, which thus becomes a cloaca. Special circulatory and respiratory organs are wanting. The **nervous system** consists of a brain, an infra-œsophageal ganglion which is connected with the brain by two œsophageal commissures, and 4 other ventral ganglia, which are connected by longitudinal commissures placed far apart from one another. There are two eye spots in the head, lying on two small ganglia connected by nerves with the brain. The **musculature** is richly developed. Various dorsal, ventral, and lateral longitudinal muscles run under the integument. Special muscles serve for moving the legs. All the muscles are smooth.

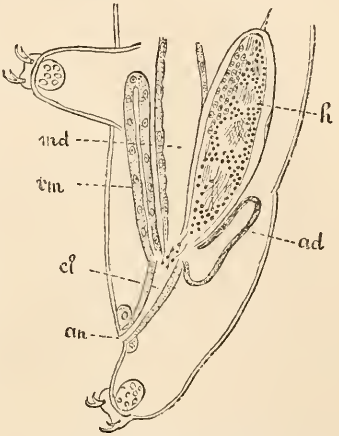

Fig. 383.—**Posterior portion of the body of Macrobiotus Hufelandii** ♂, from the side. *h*, Testis; *ad*, accessory gland of the male sexual apparatus; *cl*, cloaca; *an*, anus; *vm*, excretory tube (Malpighian vessel); *md*, mid-gut (after **Plate**).

The systematic position of the Tardigrada is uncertain. The three related facts that they possess accessory organs of the hind-gut comparable with the Malpighian vessels, tube-like oral glands, and truncated feet provided with claws, make it not improbable that they belong to the *Arthropoda*, and especially to the *Tracheata*. The want of oral limbs, the structure of the nervous system, and the manner of emergence of the sexual organs, stand in the way of a comparison of the *Tardigrada* with the *Acarina*. Although we may agree with the view that they are somehow related to the *Tracheata*, or to the ancestors of the *Tracheata*, we cannot in any case assume that they, in any way, resemble the primitive arrangements. The want of a blood-vascular system, the unpaired germ glands, the reduced and abbreviated condition of the whole body, the absence of nephridia and of coxal glands (?), rather make the *Tardigrada* appear as a one-sidedly developed lateral branch.

Most of the Tardigrada live among moss and lichens, a very few in fresh or salt water. They can stand desiccation, and remain apparently dead for a long time, reviving again when wetted. **Echiniscus, Macrobiotus, Milnesium, Doyeria.**

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