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EDITED BY

E. RAY LANKESTER, M.A., LL.D., F.R.S.,

HONORARY FELLOW OF EXETER COLLEGE, OXFORD; CORRESPONDENT OF THE INSTITUTE OF FRANCE,
AND OF THE IMPERIAL ACADEMY OF SCIENCES OF ST. PETERSBURG, AND OF THE ACADEMY
OF SCIENCES OF PHILADELPHIA; FOREIGN MEMBER OF THE ROYAL BOHEMIAN
SOCIETY OF SCIENCES, AND OF THE ACADEMY OF THE LINCEI OF ROME;
AND OF THE AMERICAN ACADEMY OF ARTS AND SCIENCES OF BOSTON
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OF THE NEW YORK ACADEMY OF SCIENCES, AND OF THE
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PHYSICAL SOCIETY OF EDINBURGH; HONORARY
MEMBER OF THE BIOLOGICAL SOCIETY
OF PARIS;
DIRECTOR OF THE NATURAL HISTORY DEPARTMENTS OF THE BRITISH MUSEUM; LATE FULLERIAN
PROFESSOR OF PHYSIOLOGY IN THE ROYAL INSTITUTION OF GREAT BRITAIN.

WITH THE CO-OPERATION OF

ADAM SEDGWICK, M.A., F.R.S.,

FELLOW AND TUTOR OF TRINITY COLLEGE, CAMBRIDGE;

W. F. R. WELDON, M.A., F.R.S.,

LINACRE PROFESSOR OF COMPARATIVE ANATOMY AND FELLOW OF MERTON COLLEGE, OXFORD
LATE FELLOW OF ST. JOHN'S COLLEGE, CAMBRIDGE;

AND

SYDNEY J. HICKSON, M.A., F.R.S.,

BEYER PROFESSOR OF ZOOLOGY IN THE OWENS COLLEGE, MANCHESTER.

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MEMOIRS:

The Development of Lepidosiren paradoxa.
Part II.

With a Note upon the Corresponding Stages in the Development of Protopterus annectens.

By

J. Graham Kerr.

With Plates 1—4.

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Early Stages in Development:

INTRODUCTION.

THE following pages constitute a further instalment of my description of the developmental phenomena of Lepidosiren paradoxa.[1] I have devoted much time and

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[1] The first instalment, containing a description of the "External Features in Development," is to be found in 'Phil. Trans. Roy. Soc.,' B, vol. cxcii, p.

labour to making a very detailed investigation of the stages in development here treated of, and I had originally intended in my description to go into something like corresponding detail. I have, however, altered my original intention in this respect, for various reasons: amongst others because in the interpretation of minute details of early development one is necessarily much influenced by preconceived ideas; and in the second place, because I find that these details vary to an extraordinary extent in different eggs—some of the variations being apparently due to variation in technical methods of investigation, but many being certainly true individual variations. So potent are these disturbing factors that I doubt very much whether a description going into very minute detail must not necessarily be to a great extent misleading, and so do harm. I therefore propose to limit myself in regard to the early stages of development to the endeavour to give an adequately complete general description of the phenomena observed, with only so much detail as may seem necessary to make the description clear.

The investigation of a holoblastic egg 7 mm. in diameter and packed with yolk involves great technical difficulties, as the whole of each egg has to be converted into thin sections. The full extent of these difficulties will only be appreciated by embryologists who have essayed a similar task. In order to help future workers I devote a few paragraphs to a general account of methods. Then follows an account of the phenomena observed, in which, as in my first paper, I reserve remarks of a general nature embodying views rather than facts for a concluding section, so that any reader may obtain the facts, which are naturally of greater importance, with a minimum of trouble.

299. As in that paper I naturally did not make precise statements regarding the interpretation to be put upon surface features without having assured myself first by the examination of sections that they were correct, it is unnecessary for Prof. Semon to feel the doubts about the behaviour of the blastopore in Lepidosiren which he expresses in his latest contribution on the development of Ceratodus (Semon, 'Zoologische Forschungsreisen,' Band i, S. 327).

In conclusion I have to record the gratitude which I owe to my friend Mr. J. S. Budgett for the generous way in which he has placed his store of Protopterus embryos at my disposal. By his kindness I am able to interweave with my description, references to what takes place in the only other Dipneust still surviving, and consequently to greatly increase its value.

METHODS.

The eggs and larvæ on being brought in from the swamp were first studied alive. For permanent preservation two fluids were used—formalin and alcohol. Of the former solutions in water of from 5 per cent. to 10 per cent. were used, and I found formalin an admirable preservative for the early stages. It caused practically no shrinkage either of capsule or embryo. It further left the former transparent as in the fresh condition. The material of early stages fixed and preserved in formalin was found to be in admirable condition, both as to fixation and as to consistency for section work. This, however, only applies to the early and heavily yolk-laden stages.

The alcohol material was fixed in a variety of ways. Practically all the ordinary fixing agents were tried, but the best all-round results were obtained by corrosive sublimate and acetic acid, and Flemming's chrom-aceto-osmic solution (strong formula). Perenyi's solution proved to be unreliable.

For section cutting, after many weeks of failure, the following three stock methods were adopted :

I. Thick sections of early eggs, where the cell elements were very large, were cut with a "Jung" microtome after soaking for three days in thin celloidin, three days in thick celloidin, and thirty minutes in chloroform, followed by treatment with cedar oil until clear. The block was kept saturated with cedar oil, and the sections were transferred in order to a shallow tray containing the same fluid. The sections were then arranged upon strips of tissue-paper 3 inches by 1 inch within a space equal to the size of the cover-slip used. The paper strips with the sections lying on them were now laid in a bath of absolute alcohol, to remove the cedar oil, and then taken up and laid sections downwards upon slides coated with a layer of dry collodion. A finger was now passed lightly along the paper, giving a gentle pressure, just sufficient to cause the celloidin of the sections to adhere to the collodion on the slide. The slide was now removed to 90 per cent. alcohol and the ordinary process of staining carried out. In the subsequent dehydration previous to mounting a mixture of chloroform and absolute alcohol was used for the final stage of the process.

II. To obtain thin sections of yolk-laden eggs, it was necessary to embed in both celloidin and paraffin. The preliminary embedding in celloidin was done as before. The egg was taken from celloidin solution and dropped bodily into chloroform for 15—30 minutes. At first I was in the habit of transferring the celloidin block to cedar oil before embedding in paraffin, but latterly I have frequently embedded at once by the chloroform-paraffin method. It is of great importance to keep the temperature of the water-bath as low as possible, and also to diminish the length of time during which the object is on the water-bath to the shortest possible.

Sections were cut with a Cambridge rocking microtome, and flattened with warm water on a slide coated with glycerine and egg albumen. The water was drained off and the slides put aside to dry in an atmosphere containing vapour of alcohol and ether. It was found that drying in an ordinary atmosphere over the water-bath caused the celloidin-infiltrated section to dry, curl up, and break away from the paraffin: this was avoided by drying in the manner described. It is important, however, not to use an atmosphere completely saturated with ether and alcohol vapour, as this, by causing the celloidin to swell, may cause wrinkling of the sections.

III. Older embryos were embedded in paraffin in the ordinary way and cut with the rocking microtome.

Orientation.—For the accurate orientation of embryos during the embedding process I use a special apparatus[1] in which a pool of paraffin in contact with the block holder of the microtome is kept melted by a small loop of platinum, nickel, or other wire of high resistance and not easily oxidisable, heated by the current from one or two ordinary bichromate cells.

Staining.—After many trials of different staining fluids I adopted two stock methods.

I. Early eggs rich in yolk were stained in Grübler's "Safranin 0"—a saturated solution in absolute alcohol, diluted with an equal volume of distilled water. In regard to formalin eggs, difficulty was found in obtaining a good chromatin differential stain. This difficulty was completely got over by treating the eggs with corrosive sublimate solution for a couple of hours before transference to alcohol.

II. Later embryos were stained in Heidenhain's iron hæmatoxylin followed by faint staining with eosin. By this stain beautiful preparations were obtained showing minute nuclear detail to perfection.

Mounting Medium.—When sections of early eggs did not stain successfully they were mounted in colophonium, which on account of its lower refractive index shows up feebly stained structures better than Canada balsam.

Reconstruction.—In working out the organogeny of Lepidosiren I have found the following method of reconstruction from serial sections extremely useful. Sections 10 μ thick are drawn with the Abbe camera lucida at a magnification of 100 diameters upon finely ground sheets of glass 1 mm. in thickness. Sheets of glass bearing drawings of consecutive sections are then piled in position on top of one another, a fluid of the same refractive index as the glass being run in between adjacent sheets. The result of this is to convert the whole into a transparent block, in which the structures drawn are seen occupying space of three dimensions, forming a kind of model. Different organs are drawn in different colours, lead pencil or coloured crayons

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[1] Made for me by the Cambridge Scientific Instrument Company.

(not anilins) being used. It is best, I find, only to do one or two systems of organs at a time, the process being so rapid compared to ordinary modelling by Born's method that it can easily be repeated if necessary. When I first devised this method I used a chemical solution having the exact refractive index of the glass, but latterly I have used ordinary clove oil, which is near enough for practical purposes. With clove oil ordinary water-colour pigments may be used.[1]

The above method is not meant to give a permanent model of the structures investigated, as does the Born method of reconstruction from sections; but, on the other hand, it involves far less expenditure of time, and is to be strongly recommended for purposes of research. The main principle of the method—the using sheets of glass or other transparent plates on which to draw the consecutive sections—has been used by other workers, e. g. Strasser and Dixon, and more recently by Vosmaer. I have not, however, come across any mention in literature of the two details upon which to my mind the chief beauty of the method rests, viz. the using sheets of ground glass to draw upon, and the subsequent rendering these transparent by an interposed fluid of high refractive index. The first of these details provides a particularly suitable surface upon which to draw; the second gives a perfect transparency to the mass of superimposed plates, quite unattainable where there are numerous alternating layers of substances differing so much in refractive index as do glass and air.

EARLY DEVELOPMENT OF LEPIDOSIREN.

Segmentation and Origin of Segmentation Cavity.—A vertical section through a mature egg of Lepidosiren shows that the interior is filled with a mass of yolk granules, the protoplasmic substance between being so small in quantity as to be quite invisible. The yolk granules are rounded or occasionally subangular in form. Through the greater

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[1] Mr. Budgett, who has been recently using my method of reconstruction, strongly recommends the use of moist water-colours.

part of the egg there are large granules, measuring, as a rule, between ·015 mm. and ·02 mm.[1] in diameter, and of the characteristic salmon-pink colour, while the interstices between these are filled with smaller granules. There is no indication of a region of specially coarse-grained yolk in the centre of the egg, but towards the surface of the "animal" portion the large granules are absent, and there is present a superficial layer in which the yolk is entirely broken up into very minute particles, whose innumerable reflecting surfaces give to this part of the egg a snowy white appearance when seen by incident light. In the middle of this cap of fine-grained yolk lies the germinal vesicle, the details of whose structure I have not been able to make out satisfactorily.

As segmentation proceeds, the fine-grained yolk spreads downward towards the centre of the egg—the smaller blastomeres being distinguished by their fine-grained yolk from the larger lower blastomeres, where the yolk remains in large granules.[2] Even in this latter region, however, the division planes become marked out by a septum of fine-grained yolk.

As mentioned in my former paper, the segmentation cavity begins to appear very early, in the form of chinks between the micromeres. In an egg of Stage 8[3] (Pl. 1, fig. 1) the cavity within the egg still remains in the form of such

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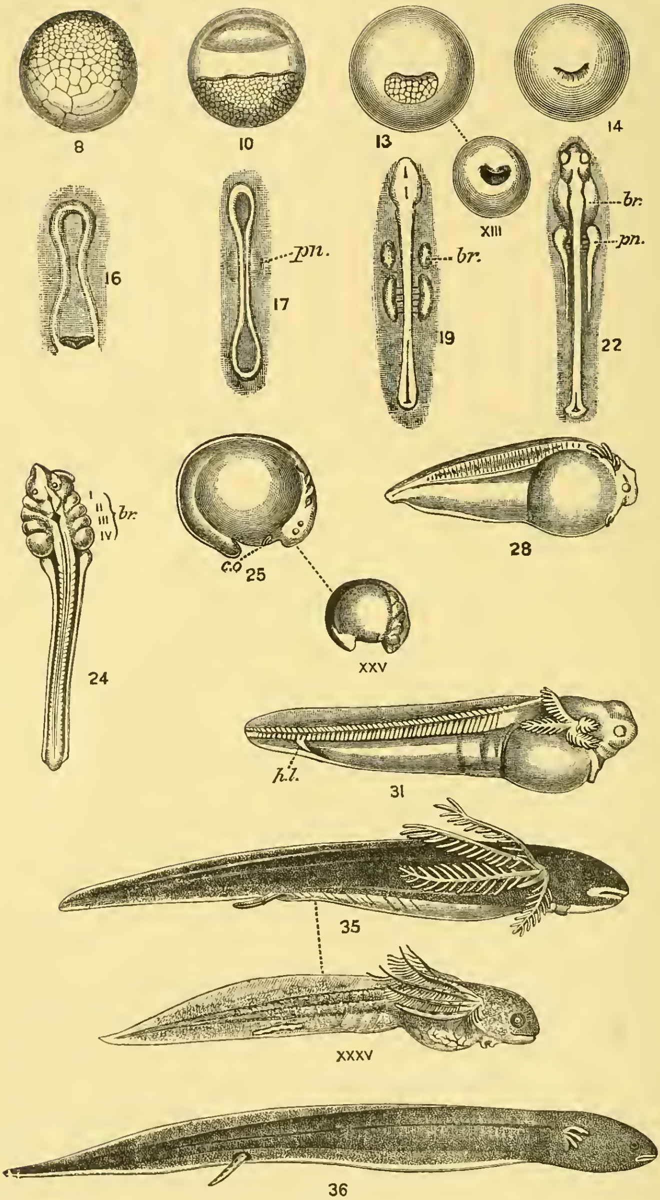
[1] Although the eggs laid by one female may be said to be on the whole more coarsely grained than those of another, yet there is much variation even amongst the eggs laid by a single female; e. g. in four eggs taken from one nest the large yolk granules averaged ·018, ·018, ·020, and ·022 mm. in diameter respectively; in three eggs taken from another nest the corresponding dimensions were ·015, ·015, and ·02 mm.

[2] This statement must be taken as true only in a general sense; every now and then one meets with a few coarse granules within the micromeres; while in the region of the macromeres irregular patches of comparatively fine-grained yolk frequently appear.

[3] By "Stage *n*" I mean an egg whose external features have reached the stage of development represented by fig. *n* of my previous paper. At Prof. Lankester's suggestion I have had a figure (Text-fig. 1) prepared to illustrate the chief stages, and so to obviate the necessity of frequent reference to the plates of my previous paper.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XXV
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h.l.
35
XXXV
36

Text-fig. 1.

chinks. The extent of these cavities varies considerably in different eggs of the same age, the blastomeres in some being more rounded, in others less rounded and more flattened against one another. The more rounded condition of the blastomeres in the former case does not appear to be associated with the nuclei being in a state of karyokinetic activity, as has been asserted to be the case in other forms.

Text-fig. 1, illustrating the course of development of the Dipneumona.—The stages are numbered in accordance with my earlier paper. Roman numerals indicate figures of Protopterus (after Budgett, 'Trans. Zool. Soc.,' vol. xvi). The remaining figures refer to Lepidosiren. In figs. 16—24 the embryo is for convenience shown spread out in one plane and viewed from the dorsal aspect. The magnification is slightly over two diameters. *br.* Rudiment of external gills. *c.o.* Cement organ. *h.l.* Rudiment of hind limb. *pn.* Pronephros. 8. Egg during segmentation. 10. An early stage of invagination, the invagination groove stretching round about one third of the egg's circumference. 13. A later stage of invagination, the large yolk-cells being now for the most part covered in by small cells. XIII. Corresponding stage in Protopterus. 14. Egg at the close of invagination, showing the crescentic blastopore. 16. Dorsal view of an embryo in which the medullary folds have just become visible, diverging posteriorly to embrace the blastopore. 17. Later embryo where the folds have met behind the blastopore, and are approximated in the middle region of the embryo; the rudiment of the pronephros is now visible as a slight bulging on either side. 19. The medullary folds are nearly completely fused; the branchial rudiment is visible as a bulging in front of the pronephros; indications of the myotomes are seen between the pronephros and the neural rudiment. 22. The branchial rudiment has greatly increased in size, the optic rudiments are conspicuous, the pronephric ducts have grown considerably backwards. 24. Embryo in which the branchial rudiment has become completely segmented on the right-hand side; the central cavity of the neural rudiment has appeared as a dark shadow. 25. Side view of a slightly older embryo in its natural position on the egg; the rudiments of the four external gills now form distinct projections; the rudiment of the cement organ has appeared ventrally. XXXV. Corresponding embryo of Protopterus. 28. Larva three days after hatching. 31. Larva (thirteen days) in which the external gills have become pinnate, and the rudiments of the limbs have appeared (anterior hidden by external gills). 35. Larva with external gills at their maximum; the cement organ, now in course of atrophy, is seen beneath the throat. XXXV. Corresponding larva of Protopterus. 36. Young Lepidosiren with external gills in process of atrophy.

As already mentioned, the yolk in the micromeres is reduced to the condition of fine granules. These also become reduced in number, and the nucleus tends to be surrounded by an area of finely granular reticular protoplasm, almost free from yolk granules. The transition from the finely granular micromeres to the coarsely yolked macromeres is perfectly gradual.

Between Stages 8 and 9 there appears an irregular chink of larger size than the others amongst the lower micromeres (Pl. 1, fig. 2). This, the definite segmentation cavity, increases in size, spreading laterally, and at the same time approaching close to the upper surface of the egg, being eventually covered in by a roof of comparatively regular thickness throughout. This roof soon becomes composed of two regular layers of cells (figs. 3 and 4). As the segmentation cavity further increases in size these become flattened out, until the roof forms a thin translucent membrane through which in the entire egg the segmentation cavity appears as a dark shadow. The characters of the completed blastula may be sufficiently gathered from fig. 4.

The blastomeres on the floor and sides of the segmentation cavity are rounded, almost spherical in form, and project into the cavity. Usually, some of these spherical blastomeres appear to float quite free in the fluid of the segmentation cavity. This appearance does not of course prove that they are not really connected up to the other blastomeres by delicate protoplasmic strands; but such connecting threads if present are too delicate to be seen by ordinary observation.

Gastrulation.—The process of gastrulation in Lepidosiren may for convenience of description be divided into three periods, which I will call A, B, and C.

A. In this period, which marks the beginning of gastrulation, we have to do with a process of true invagination. The commencement of this process is indicated, as I have shown in my previous paper, by the appearance of a row of little depressions of the egg's surface arranged in a latitudinal direction a few degrees below the equator. These depressions soon become joined up to form a continuous groove stretching through about one third of the circumference of the egg at this latitude (cf. Text-fig. 1, fig. 10). A section through the whole egg at this stage is given in fig. 6 (Pl. 2), and sections through the groove itself under a higher magnification in figs. 5 and 7 (Pl. 1).

In the cells lining the groove much of the yolk has passed into a state of fine subdivision, thus pointing to cell activity. From the open character of the groove during this stage it is obvious that we have to do with a process of true invagination. In some series of sections one can see very well (fig. 7) how the groove, although to the naked eye apparently coincident with the boundary between the cells with small and those with large yolk granules, lies really just within the region of the latter. The invagination in Lepidosiren is thus essentially a lower cell phenomenon.

The groove, as mentioned in my previous paper, gradually becomes more limited in extent by its lateral portions becoming flattened out. Had it extended at any period of ontogeny completely round the exposed area of large cells, we should have been able to speak of a yolk-plug. As it is probable that the disappearance of a yolk-plug bounded all round by an invagination groove is due to increase in size and richness of yolk in the egg, I had hoped to find it present in Protopterus. In this I have been disappointed, the condition in this respect being just as in Lepidosiren.

While the lateral parts of the groove flatten out and disappear, the middle part is deepening to form the archenteric cavity.

B. The exact method by which this takes place in its earlier stages forms a problem of considerable general interest, but at the same time one the final solution of which is attended with great difficulties.

The appearance of sections during this period is illustrated by fig. 8 (Pl. 2). The archenteric cavity runs obliquely inwards from the surface of the egg, and at its inner end turns upwards so as to run roughly parallel to the surface. The whole cavity is slit-like in form and is eminently suggestive of having been formed by a process of splitting amongst the large yolk-cells, after the manner described by Robinson and Assheton in the case of the frog. Further evidence is afforded in this direction by the fact that many sections show the archenteric slit to end in a perfectly sharp edge (fig. 9), which may even appear to be prolonged by division planes along which the cells have not yet separated. Had I had to rely upon a small amount of material, I should almost certainly have described the archenteric formation during this stage as being carried on by a process of splitting. I have, however, examined now a very large number of series of sections, and I am disposed to think that the process is by no means one of simple splitting. In the first place, by looking through complete series of sections, one as a rule finds that, in certain sections, the archenteron terminates in a clear rounded end (fig. 10). It appears impossible to me to imagine that this can occur if the cavity is only extending by a splitting process. Further, it is usual to find that, round the tip of the archenteron, the cells have assumed a triangular shape in section, with their tips towards the archenteron, which strongly suggests the existence of a compressing force acting round the tip of the cavity, and of such a nature as would be caused by growth of either roof or floor of the cavity. On the whole, I conclude that increase of the archenteric cavity does take place mainly by true invagination during this stage also. The slit-like appearance in many sections may conceivably be an artefact due to the roof of the archenteron being squeezed down against its floor by the action of the fixing agent, or possibly the process of invagination may be aided by one of splitting. There seems nothing improbable and indeed little of importance in this, notwithstanding how much has been written on the subject. If it does occur it is only another example of a very common phenomenon in yolky eggs,—the formation by splitting of a cavity elsewhere formed by invagination.

As regards the probable cause of the invagination—beyond the use of the vague phrase "differential growth"—nothing can be said. The absorption of the fluid in the segmentation cavity which is associated by Samassa with the invaginatory process of Amphioxus is excluded as an explanation of the phenomenon here, as the first obvious result of such absorption would be the collapse of the very thin and delicate roof of the segmentation cavity, and such collapse is conspicuously absent.

In transverse section the archenteron is seen to be, in this stage, a tube rounded in section—in other words, showing no signs of splitting laterally, and about ·2 mm. in diameter, strikingly narrow in proportion to the diameter of the egg as compared with most holoblastic forms.

Towards the end of period B the archenteron approaches the margin of the segmentation cavity, and now we have very distinct evidence that the growth of the archenteron is not due to splitting, for the cells round its tip become pushed definitely into the segmentation cavity forming a rounded bulging into it (Pl. 2, fig. 8). As the process goes on the large-yolk cells become laid up against the original roof of the segmentation cavity, which, already two-layered, alters little in character and will later become definitive epiblast. The further stages in the obliteration of the segmentation cavity I will deal with later.

C. In the later stages of gastrulation we have certainly to do with a process of true invagination, the end of the archenteron being always quite smooth and rounded, with cuticular lining, and there being never any trace whatever of splitting (cf. Pl. 3, figs. 11 and 12). The precise character of this invagination could only be settled definitely by experiment upon the living egg, and such experiments, though attempted, proved absolutely fruitless on account of the tough egg capsule and the soft nature of the egg contents. From the study of sections[1] of the eggs I am disposed to believe that

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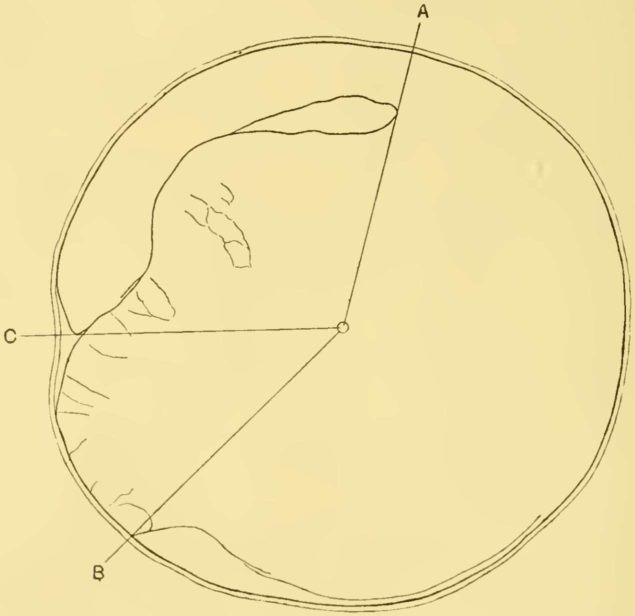
[1] In my account of the external features I pointed out that against the probability of such a backgrowth taking place, was the fact of the blastoporic lip not assuming the form of an arc of gradually diminishing radius with its

we have to do with an invagination of the large yolk-cells of the lower lip of the blastopore by the upper dorsal lip growing bodily down over them. The evidence upon which this belief rests is as follows :

(*a*) A sagittal section through an egg of this stage fixed in such a way as to avoid shrinkage of the capsule is shown in outline in Text-fig. 2. It is obvious that the general outline of the section suggests strongly that the dorsal lip of the



TEXT-FIG. 2.—Camera outline of sagittal section through an egg in its capsule at a late stage of gastrulation. The lines O A, O B, and O C are drawn from the centre of the section so as to touch respectively the tip of the archenteron (O A), the edge of the small-celled area (O B), and the dorsal lip of the blastopore (O C).

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concave side downwards. As a matter of fact this objection is done away with by the fact that in Protopterus frequently the lip does become concave downwards just as we should expect (cf. a forthcoming paper by Mr. Budgett in 'Trans. Zool. Soc. Lond.,' vol. xvi). The blastoporic lip becoming convex downwards in Lepidosiren I attribute now to the backgrowth being more active in the middle line than laterally.

blastopore is growing bodily downwards, wedging itself in between the capsule and the large yolk-cells, and causing as it does so the latter to invaginate into the floor of the archenteron.

(β) The frequency of mitotic figures in the region overlying the archenteron, and more especially in the dorsal lip, appear to indicate active growth of this region, and consequent backward migration of the blastoporic lip.

(γ) During the later stages of gastrulation I find that the angle between the lines O A and O B (passing from the centre of the section to the tip of the archenteron and to the margin of the small-celled area respectively) remains nearly constant, and the increase in the angle A O C corresponds fairly closely with the diminution in the angle C O B.

This seems to suggest that the line O C is gradually swinging through the arc between A and B. Otherwise we must believe that the lines O B and O A are swinging with equal velocity in a clockwise direction. It appears to me from study of my sections that this is not the case, the forward movement of the point B being very slow compared with the advance of the archenteric tip.

(δ) The cells of the ventral wall of the archenteron are continuous, without any visible change in character, with the large yolk-cells lying exposed on the outer surface of the egg below the blastopore.

On the whole, then, I believe that the evidence, such as it is, points to the view that the main factor of the increase in length of the archenteron during this last stage is the downgrowth of the blastoporic lip.

While these processes of formation of the archenteron have been going on the area of yolk-cells exposed has been gradually reduced, dorsally by the growth of the blastoporic lip, elsewhere by the gradual encroachment of the small-celled area. This spreading of the small cell margin over the yolk-cells is most rapid in the neighbourhood of the blastoporic lip, least so at the point opposite to this. In this latter region the superficial layer of small cells passes into a thickened rim, which at first I called the growing edge of the epiblast. Further investigation showed, however, that the chief characteristic of this rim is not its growth, which is comparatively small, but the fact that it represents the mass of small cells on which the roof of the segmentation cavity rested at its margin. The thin two-layered epiblast, in fact, from this rim for a considerable distance is nothing else than the persistent roof of the segmentation cavity. This is shown to be the case by the fact that within a short distance of the rim one frequently finds the small blastomeres beneath the epiblast retaining their rounded form with chinks between, or we may even find the segmentation cavity still present as a continuous slit.

What spreading of small cells over the large yolk-cells does take place is brought about by addition to the margin of small cells cut off from the yolk. This is well shown by sections such as that in fig. 13, where there can be no question of true epibole or sliding of the small cell layer over the surface of the yolk-cells.[1]

The slight extent of the movement over the yolk of the small-celled margin at the point opposite the blastopore rim is of importance as providing a nearly fixed point in the interpretation of sagittal sections. The evidence of these sections is, on the whole, that the dorsal roof of the archenteron is formed mainly by backgrowth of the dorsal lip, and as the medullary plate at its first appearance is practically coincident with the extent of the archenteron, Lepidosiren is brought into line with the Selachians, where almost the whole of what is commonly called the "embryo" is formed from a similar backgrowth.

The Segmentation Cavity.—I now return to the consideration of the segmentation cavity, which was left at a period when it was beginning to be encroached upon by the bulging wall of the archenteron. The further obliteration of the segmentation cavity, although it takes place

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[1] By an error the word "epibole" was used in my former paper at one place (p. 322) when delamination was actually meant.

during the process of gastrulation, does not by any means keep time with the latter—a further support to my assertion that the former is not the direct cause of the latter.

What takes place may be said to be in general terms that the floor of the segmentation cavity is brought up against its roof. During this process, however, a transient phase occurs which is not without interest. While the cavity is still at its full development we notice a tendency for large-yolk blastomeres to become arranged round the segmentation cavity, and in close contact with its roof (cf. Pl. 2, fig. 8; or better, figure of Protopterus VIII); following this, the smaller blastomeres lying in and near the floor of the cavity push out processes, become irregular and angular in shape, and, attaching themselves to one another by their corners, form a loose and irregular sponge-work traversing the cavity completely (Pl. 3, fig. 11). As will be gathered from the figures, the segmentation cavity during this process, although broken up by the sponge-work, really extends through a much larger volume than it did before. As, however, gastrulation proceeds, the fluid filling the meshes of the sponge-work becomes absorbed, and the blastomeres resume their spherical or, as they become pressed closer together, polyhedral shape. We may still for a long time, however, observe chinks persisting here and there, especially laterally. The roof cells of the segmentation cavity remain all through the stages we are now describing sharply marked off from the large yolked elements which have been laid up against them.

Origin of the Mesoblast and Notochord.—Pl. 3, fig. 14, illustrates a section through an egg of Stage 12 and transverse to the axis of the medullary plate region. Lying over the archenteron and tapering off on each side is a mass of cells distinguished from the remainder of the inner cells by their smaller size, more finely granular yolk, and by their rounded form. Immediately over the archenteron these small cells are aggregated closely together, but laterally as a rule they are separated by wide chinks—the remains of the segmentation cavity. At its outer edge this mass of small cells passes gradually into the large inner cells. The sum of small cells in question is the rudiment of notochord and mesoblast. It is perfectly continuous across the middle line, and is separated from the cavity of the archenteron by a definite archenteric roof composed of cells closely fitted together.

The cells of the notochordal-mesoblastic rudiment are the small blastomeres which are seen in earlier stages lying below the floor and round the edges of the segmentation cavity, or penetrating that cavity as a sponge-work.

A little later—in Stage 14 (cf. Text-fig. 1)—a transverse section (Pl. 3, fig. 15) exhibits very similar features, only now the mesoblastic cells are in close contact with one another, and the mesoblastic rudiment is found to be growing at its edges by delamination from the underlying large yolk-cells. The rate of this growth varies much. As a rule, in an egg of Stage 14 the mesoblast extends very little below the level of the archenteron on each side, though in one case I found that it had grown right round the ventral side of the egg. The process is in any case usually completed by Stage 18 or 20. For example, in an egg of Stage 18 I find that, although the actual splitting off of the mesoblast has taken place only to a level slightly below that of the archenteron, the superficial layer of yolk has become fine-grained all round the egg, and here and there a small mesoblast cell has separated off the large yolk-cells beneath. Such mesoblast cells are often split off far beyond the edge of the sheet of continuous mesoblast, so that when I speak of the mesoderm spreading over the hypoblast I must guard against giving the impression that the sheet is necessarily continuous up to a definite margin. Finally, in eggs of Stage 21 the stratum containing fine-grained yolk has been cut off the underlying hypoblast all over, as a definite layer, somewhat irregular in places, of rounded mesoblast cells.

Where the mesoblastic rudiment has in its early stages largely developed intercellular spaces, the boundary between it and the large yolk-cells is sharply marked very early (except in the middle line and at its outer margin). Where the cells composing the rudiment are in close contact the line of demarcation may be for a time indistinct. But in any case by Stage 14 the mesoblastic rudiment on each side becomes separated definitely from the underlying hypoblast (except at its outer edge), and a little later (Pl. 4, fig. 16, and Text-fig. 3) it becomes separated in a similar way from the axial portion which will give rise to the notochord. This latter remains in the meantime attached to the hypoblast.

Text-fig. 3.—Section through a complete egg of stage transverse to axis of embryo. *ent.* Enteron. *m.* Mesoblastic rudiment. *m.p.* Ectodermal thickening of medullary plate. *n.* Rudiment of notochord.

It should be mentioned incidentally that the cells added to the edge of the mesoderm sheet tend to take on a rounded form as soon as they become separated from the hypoblast. It consequently often happens that, when the sheet is continuous up to its edge, this edge with its rounded cells is very sharply marked off from the hypoblast beyond. With only such sections to go by one might well believe that the sheet of mesoblast was quite independent of the hypoblast, and growing inwards over its surface from the blastoporic rim after the manner described for various forms by Lwoff, Brauer, and others. It is at once seen from the study of a complete series of stages, such as the above account is based upon, that any appearance of the kind is quite secondary, and that originally mesoblast and hypoblast rudiments are perfectly continuous. I will return to this question later on.

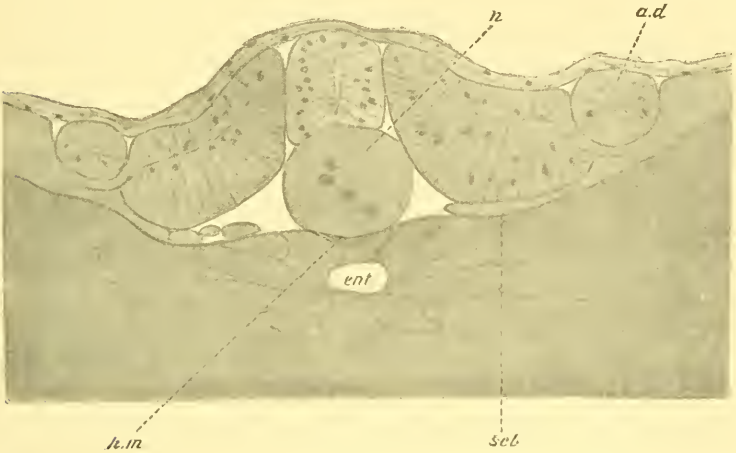
With the formation of the medullary keel the mesoderm sheet becomes thickened out to each side of it in the region where the myotomes are to be formed.

On account of the yolk-laden character of the mesoblastic rudiment it is difficult to make out when its segmentation begins. Distinct protovertebræ were first found in about Stage 17, where there were six present. They were squarish in section and were solid.

Cœlom.—The first parts of the cœlom to appear are myocœlic. In Stage 21 (Pl. 4, fig. 21) a cœlomic cavity is seen to have appeared in the centre of the myotome. This appears to arise by simple breaking down of the central cells, the cavity not having at first any sharply-marked outline, and irregular masses of yolk-laden protoplasm projecting into it. A little later (Stage 23) the outline is quite definite and the cavity is walled in by a single layer of regular columnar cells. From this the cœlom spreads outwards by definite splitting.

Early Development of Notochord.—The Notochordal rudiment was left (Pl. 4, fig. 16) at a stage in which it remains attached to the hypoblast on the separation of the mesoblast from it on each side. It forms a median dorsal ridge running along the middle line above the archenteric cavity. The yolk in the cells of this ridge is usually in a state of comparatively fine subdivision, though much coarser than that of the epiblast.

A set of division planes now become so arranged as to mark off the notochordal part of the ridge from the comparatively thin basal layer next the cavity of the archenteron (fig. 17, *e. r.*). The cells of this latter frequently, though by no means always, retain their yolk in a coarse-grained condition.



TEXT-FIG. 4.—Transverse section through dorsal region of an embryo of Stage 23. *a.d.* Archinephric duct. *ent.* Enteron. *h.m.* Mesenchyme cells being directly split off from hypoblast. *n.* Notochord. *scl.* Sclerotome outgrowth from mesoblast.

They are part of the definitive hypoblast, and form the roof of the enteron. The enteric roof is thus differentiated in situ from the cells of the archenteric roof, without any trace of ingrowth from the sides such as has been described by Lwoff, Brauer, and others.

The notochordal rudiment thus laid down retains for some time its comparatively undifferentiated condition (figs. 20 and 21), showing no obvious change beyond assuming a rounder, more definite outline as it separates off the hypoblast. About Stage 23 the separation is completed, and the notochord, now circular in transverse section, develops a fine cuticular membrane which foreshadows the sheath, and in longitudinal section its cells are seen to be becoming flat and plate-like.

In due course the notochord becomes separated off from neighbouring structures by mesenchymatous tissue, partly directly cut off the subchordal region of the hypoblast (Text-fig. 4, *h.m.*), but for the most part arising by proliferation from the inner surface of the mesoderm at about the level of the nephric rudiment very much as in Selachians, except that there is no obvious trace of a segmental arrangement (Text-fig. 4, *scl.*). I propose to postpone further consideration of the mesenchyme till a later period.

Origin of the Central Nervous System.—Already in Stage 12, as has been mentioned (cf. Pl. 3, fig. 14), the epiblast has become somewhat thickened over the region of the archenteron, the thickening affecting the lower layer especially whose cells have become more regularly columnar. By Stage 14, when there runs forward from the blastopore a faint depression along the axis of the medullary plate, this thickening has become more marked, and in addition the deep layer of epiblast is becoming more than one-layered (cf. figs. 15 and 16). The medullary plate thickening of the epiblast, most marked along the mid-dorsal line, extends outwards for a considerable distance, gradually thinning away on either side. The axial portion of the medullary plate rapidly increases in thickness, forming a deep wedge-shaped keel, the rudiment of the neural cord. This medullary keel develops from before backwards, and in some eggs of Stage 14 it has already begun to be distinctly formed anteriorly. By Stage 16 (cf. Pl. 4, figs. 17 and 18), where the medullary groove is well formed but widely open, the keel has increased much in thickness, being about five cells thick posteriorly, and thickening out anteriorly to about three times as much. Just about the anterior limit of the archenteron the keel tapers off, first suddenly, then gradually, till the ordinary two-layered condition of the general ectoderm is reached. The whole thickening of the keel is confined to the deep layer of the ectoderm—the outer layer passing unaffected over the floor of the groove. As the medullary folds approach one another the groove shallows out and disappears. Occasionally, in places, the folds come in contact before the groove has disappeared, so that for a short time they remain separated by a vertical chink (Pl. 4, fig. 19). As before suggested, this may be looked on as a last trace of a former method of formation of the spinal cord by involution, but any trace of cavity that is so enclosed in Lepidosiren is purely temporary and soon disappears. The keel is now (fig. 20) absolutely solid, and there is no indication of the formation of a central canal until about Stage 20 (fig. 21), when the cells of the interior of the neural rudiment are seen to begin to assume a regular arrangement and columnar form on each side of the median plane.

Along this plane the cells finally split apart, apparently by the secretion of fluid, the cavity in preserved specimens showing an abundant coagulum. The split appears somewhat irregularly, but by Stage 23 it has become continuous, forming a well-marked cavity in the region of the fourth ventricle, and stretching back from this through about three fourths of the extent of the neural rudiment. Anteriorly and posteriorly the neural rudiment still is solid.

Note upon the Early Development of Protopterus.

The egg of Protopterus is much smaller than that of Lepidosiren, measuring only about 3·5—4 mm. in diameter (Budgett). Corresponding with this the yolk granules are smaller, averaging about ·015 mm. by ·01 mm. They have also a characteristic difference in shape, being very frequently lenticular or fusiform. The blastula of Protopterus differs from that of Lepidosiren in the relatively greater depth and volume of the segmentation cavity, and in the greater relative extent of the micromeric region of the egg. The roof of the segmentation cavity is also thicker.

Gastrulation.—The line of invagination appears nearer the lower pole of the egg than in Lepidosiren, about 30° below the equator instead of about 10°. It is consequently visible from the beginning when the egg is viewed from the lower pole, forming part of the circumference of the small circle bounded by the edge of the small-celled area. The condition is exactly as in a typical Urodele[1] or Anuran egg, only here the groove never extends round the whole circle to enclose a definite yolk-plug, but, as in Lepidosiren, shortens up, flattening out at each end. The examination of sections shows that here as in Lepidosiren the invagination groove is at its first appearance distinctly within the coarsely-yolked portion of the egg.

The general features of gastrulation closely resemble those in Lepidosiren, and it is therefore not necessary to describe them in detail. I give, however, figures illustrating three successive stages (Pl. 2, figs. VI, VIII; and Pl. 3, fig. XII). By comparison of fig. VI with fig. VIII, the vertical axis being marked by the position of the segmentation cavity, it will be readily seen how important a part is played by overgrowth of the blastopore lip. The orientation of the egg during these stages is rendered simpler than it is in Lepidosiren by the segmentation cavity retaining its original relations much longer.

At the close of gastrulation the appearance of the egg is practically identical with that of Lepidosiren. I notice, however, that very frequently an egg of Protopterus at this stage assumes an ellipsoidal form, with the blastopore either at one end or somewhat ventral to this. In Lepidosiren only pathological or unfertilised eggs assume an ellipsoidal shape.

As regards the further points of development treated of in this paper, there do not appear to be any noteworthy differences between what occurs in Protopterus and what has been described for Lepidosiren.

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[1] The Protopterus egg very frequently passes through a stage identical in appearance with the stage in the development of Triton figured by O. Hertwig in 'Jen. Zeits.,' Bd. xv, Taf. xii, fig. 1.

Size of Nuclei during Early Stages of Development of Lepidosiren.—Owing to the small scale of the figures it is not possible to indicate the relative sizes of the nuclei in different parts of the egg. These bear, as one might expect, a rough relationship to the volume of the cell territories over which they preside; e. g. in two eggs of Stage 16 the nuclei of the ectoderm averaged ·016 mm. and ·014 mm. in diameter, those of the mesoderm ·018 mm. and ·016 mm., and those of the large yolk-cells ·022 mm. and ·021 mm. Again, in an egg of Stage 13 the nuclei in the region of the dorsal lip of the blastopore measured ·015 mm., and those of the large yolk-cells ·019 mm.

The measurements are in all cases the average of ten measurements of whole nuclei as seen in thick sections.

General Remarks.

Segmentation.—In studying the segmentation of Lepidosiren I have been much struck by the readiness with which all trace of the division planes may be destroyed in the parts of the egg filled with large yolk-granules. The two commonest causes of this are, firstly, the use of a fixing agent of inferior penetrating power, the blastomeres running together into a continuous mass very soon after death if the fixing agent has not reached them; and secondly, the use of two thin sections. In cutting a section it would appear that the yolk-granules become very slightly displaced as they strike the edge of the knife, and if the section is very thin this is enough to completely obliterate the division planes. During segmentation in Lepidosiren thick sections will show an egg to be completely divided up into blastomeres, while in thinner sections the whole lower portion with coarsely-grained yolk seems to form a quite continuous unsegmented mass. The mass of uncleaved yolk figured by Semon in the middle of the Ceratodus egg, and upon which he bases the statement that this egg in its early stages of segmentation occupies a place intermediate between the telolecithal and centrolecithal types, may, I think, quite possibly be an artefact of this nature, due to the fixing agent not having penetrated sufficiently rapidly; and it also seems by no means impossible that the lower part of the egg of Gymnophiona may be only apparently uncleaved for the same reason.

Segmentation Cavity.—The segmentation cavity of Lepidosiren arises in the normal fashion from intercellular chinks. Amia, whose segmentation otherwise so resembles that of Lepidosiren, is said to develop its segmentation cavity from intra-cellular spaces (Whitman and Eycleshymer[1]).

The mode of disappearance of the segmentation cavity, the blastomeres permeating it as a sponge-work, and then later rounding themselves off so as to leave the diminishing cavity in the form of chinks between them, resembles closely what occurs in Petromyzon as described by Nuel.[2] It may quite possibly occur pretty generally, as in Lepidosiren this stage lasts such a short time that it might easily be missed.

The two-layered character of the roof of the cavity from an early stage is noteworthy. The roof, in fact, has taken on its definitive epiblastic character already in the blastula stage. In Ceratodus the roof is one-layered; and in other cases where it is two or three layers thick, it is usual for a one-layered condition to be passed through before it becomes definite epiblast (Petromyzon, Axolotl, Gymnophiona).

Blastoporic Lip Downgrowth.—In Amphioxus it has been shown that the blastopore occupies the hind end of the embryo. So it is with Lepidosiren, so that we may reasonably compare embryos of the two forms at the close of gastrulation.

It is commonly said that in a heavily yolked egg the macromeric part has become too bulky to allow of invagination. This is true only in a restricted sense, there not being room for the macromeric portion to be pushed bodily within the other as in Amphioxus. In such a form as Lepidosiren, however, new space is continually being provided by

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[1] 'J. Morphol.,' vol. xii, p. 336.

[2] 'Arch. Biol.,' t. ii, p. 436.

the continued increase in area of the small-celled outer layer of the egg due to the backgrowth of the upper lip, and under this invagination goes on in the ordinary way. This is, it appears to me, the real significance of the backgrowth. It is a phenomenon directly associated with the increase in bulk of the macromeres. If this were true, we should find it become more and more pronounced as a developmental feature with increase in the quantity of yolk. This is, I think, what we do find, and we can also understand on this view why recent observers have failed to find such a process taking place in Amphioxus.

I do not propose to enter at length into the controversy which has raged over the parts played by invagination, splitting, downgrowth of dorsal lip, etc., in the gastrulation of vertebrates. Much of the evidence that has been brought seems to me unreliable, resting as it does on such characters as size of cells, size of yolk-granules, presence of pigment—characters which appear to me to be in great part merely the expression of greater or less metabolic activity for the time being, and which cannot therefore safely be used as criteria in treating of morphological questions.

Apart from these, the evidence afforded by the study of sections is of such a character that its interpretation is liable to be seriously affected by the observer's preconceived ideas. As regards observations on the living egg, many of the methods also seem open to the influence of very serious disturbing factors, either of a traumatic nature or of a simple physical character, such as movement of the egg as a whole, brought about by shifting of the centre of gravity due to the change in the relative extent and position of archenteric and segmentation cavities. The only really reliable method of investigation appears to be that of Kopsch,[1] where the developing egg is submitted to prolonged photographic exposures, and the surface-cell movements worked out on the pictures so obtained.

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[1] 'Verh. Anat. Ges.,' 1895, p. 181; and 'S. B. Ges. naturf. Freunde Berlin,' 1895, p. 21.

My own conclusions with regard to the part played by backward movement of the blastopore lip agree closely with those reached by Kopsch for Amphibia, and my support of his views is strengthened by the fact that I had not seen his paper until I had finished my observations of the phenomenon in Lepidosiren.

As will have been gathered from the descriptive part of this paper, I am strongly of opinion that in Lepidosiren the main factor in the formation of the archenteron is a process of invagination. I am not at present, however, prepared to deny that during what I have called Stage B of gastrulation this process may not be aided to some extent by splitting.

Communication between Archenteron and Segmentation Cavity.—The view expressed by Kupffer in 1879,[1] that the enteron is formed by a fusion of the two originally separate cavities—archenteron and segmentation cavity—has recently been supported for the large eggs of Salamandra maculosa and Gymnophiona. It will be seen from figs. 8 and 11 how thin is the septum separating these cavities, and how easily they might be thrown into one by rupture of the intervening wall. In one or two eggs I have found this happen. I attribute it to the fixing fluid not having penetrated properly; but whether this be so, or whether it really existed in the living egg, it is in any case quite abnormal in Lepidosiren, and in all except these few exceptional cases the two cavities remain completely shut off.

Formation of Parts of Archenteric Roof from "Ectodermic" or "Animal" Cells.—In the preceding description I have made no statements regarding ingrowth of ectodermic or animal cells along the roof of the archenteron. Assertions that this occurs in other forms seem to me to be weakened by two fallacies. In the statement by Lwoff, Brauer, and others that the plate above the archenteron which gives rise to chorda and mesoderm is ecto-

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[1] 'Zool. Anzeiger,' ii, p. 594.

dermic, there appears to me to lurk a confusion of ideas between the two pairs of antithetical terms—ectoderm and entoderm (or epiblast and hypoblast), and micromeres and macromeres (or animal cells and vegetable cells). The latter pair of terms are purely descriptive, and may be applied to blastomeres at once upon the evidence of an isolated observation. The former, on the other hand, are terms associated with definite theory; they are not to be applied on mere observations of sizes and shapes of cells, but involve the fate of the cells. It seems to me quite impossible to define a layer as hypoblastic except by asking one or other of the two questions: (1) Does it form the lining of an archenteric cavity? and (2) Does it become a certain part of the definitive epithelial lining of the gut? And if during the early stages of development a certain set of cells become invaginated along a considerable extent of the archenteric roof, this seems to me in itself amply sufficient reason for calling such cells hypoblastic quite apart from what their special characters of size, shape, content, and so on may be. There is no justification at all that I can see for calling the small fine yolked cells towards the upper pole of the egg epiblast, and on their extension in along the archenteric wall to found the statement that "ectoderm becomes invaginated." Because these cells behave as they do they are not ectoderm, but entoderm.

Further, a main character upon which these cells along the archenteric roof are relegated to the category of "ectoderm" or "animal cells" is the finely granular character of their yolk. Size of contained yolk granules is a form of evidence which must be used with the greatest caution, for wherever metabolism is active there the large yolk granules are broken down into fine granules to facilitate assimilation. All the yolk is destined to be so broken down eventually, and the fact of its having done so in some particular part of the egg earlier than elsewhere seems to indicate merely that metabolism is there more active. Consequently I can attach little weight to statements on the morphological nature of particular cells based on the finely granular character of the yolk. I should attach much greater weight to the presence of large granules of yolk in cells, for when the yolk is in this form in a developing embryo it seems usually to indicate that it has remained so all through, it being at least very unusual for yolk to be secondarily built up again into large granules during embryonic development.

The finely granular character of the yolk frequently shown by the roof, as compared with that of the floor of the archenteron, I would look upon then as being merely a necessary accompaniment of the active growth of this region associated with the backgrowth of the blastopore lip.

What I have said regarding the unreliability of evidence of the morphological nature of cells from the finely granular character of their yolk contents applies equally well to the presence of black pigment in cells. I believe it to be one of the most general reactions to light stimulus for active but unspecialised cells to have their metabolism so affected as to cause the formation of this particular product.[1] Examples are seen in the case of comparatively undifferentiated cells wandering into a position where they are subjected to light stimulus, e. g. to the surface of the body, or into the vicinity of a special light-collecting organ (e. g. Arthropod eye). Where pigment occurs in the smaller cells of a frog's egg it is, I think, to be correlated simply with the more active metabolism going on in these cells, and it is rather the absence of pigment in special cases which demands explanation; in many cases this may be due to natural selection—as in the case of eggs which are laid in a floating mass of white foam, where their being black would render them extremely conspicuous.[2]

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[1] Which once produced may well be made use of as a protective agent for neighbouring tissues against the harmful influence of light rays.

[2] With the criticisms in the foregoing paragraphs are to be associated those on similar lines of Houssay ('Arch. Zool. exp.,' 2nd sér., t. viii) and Samassa ('Verh. Deutsch. Zool. Gesell.,' Strasbourg, p. 139; also 'Arch. Entw. Mech.,' Bd. ii and Bd. vii).

Formation of Secondary Enteric Roof.—Brauer has described in Gymnophiona the formation of the definitive enteric roof by a backgrowth of "vegetative cells" under the original archenteric roof. In Lepidosiren no such backgrowth takes place. It is to be noted, however, that there is much variation in the character of the yolk granules in the cells lining the archenteric roof immediately ventral to the chorda. Most usually these cells have fine granules, but very frequently, on the other hand, they are distinctly marked off from the chorda cells by their yolk remaining in much coarser granules (cf. Pl. 4, fig. 17). With only scanty material, in which the later stages happened to show this difference, one might well imagine it due to a secondary growth of large yolked cells in beneath the chorda rudiment. In view of this possibility of erroneous interpretation of sections I do not feel absolutely convinced that such a backward growth of large yolk-cells under the original cells of the archenteric roof as has been described by Brauer and also by Lwoff actually takes place.

In regard to Brauer's observations I might add that in my personal opinion the large-grained character of the cells figured by him as growing backwards makes it unlikely that they are multiplying with the activity which would be necessary on his view.

In regard to Brauer's fig. 59,[1] where the large yolked cells extend right to the blastopore, it is of importance to note that the author expressly states that it is not a median section. In Lepidosiren it is only the median part of the archenteric roof that is fine-grained.

In Ceratodus Semon has described the roof of the enteron as being formed by an ingrowth from each side under the chorda rudiment. There is no such ingrowth in Lepidosiren. Where it does occur it may be looked on as a cænogenetic modification bearing the same relation to the method of chorda formation in Amphioxus, as the method of separation of the neural rudiment from the

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[1] 'Zool. Jahrb. Anat.,' Bd. x, Taf. xxxvii.

ectoderm in Amphioxus does to the method occurring more usually by the formation of a neural groove. The method of chorda formation found in Lepidosiren may be compared, on the other hand, with the modification of the development of the neural rudiment occurring in Teleosts.

Growth of Epiblast.—In that the epiblast grows at its edge by delamination, Lepidosiren agrees with what has been found in various Amphibia (Houssay, Robinson and Assheton, Grönroos), but differs from what has been found by Brauer in Gymnophiona.

Mesoblast Formation.—In regard to the development of mesoblast there are two features of special interest. The first of these is the fact which cannot, I think, be doubted by anyone in Lepidosiren—that the so-called "gastral" mesoderm is formed directly out of the smaller blastomeres on each side of the archenteron. These masses are connected across the middle line, and the common rudiment of mesoderm and chorda is quite continuous. To go further than this and say, as has been done by others, that the notochord is derived from mesoderm, is quite unwarranted.

I do not see any possible phylogenetic explanation of this phase in the formation of the mesoderm.

The later phase in its development which is of interest is that in which we see the mesoderm as a sheet upon each side, segmented or not according to its age, free at its inner thicker edge next the chorda, and thinning away to become continuous with the large yolk-cells or primitive hypoblast at its outer edge, where it continues to grow by delamination. Here we have a condition of things upon which I think a ray of light is thrown if we regard it as a fleeting reminiscence of the primitive method of mesoderm development in the Chordata.

The phenomena, in fact, in Lepidosiren, closely paralleled by those in Petromyzon, suggest a scheme of the steps by which the method of mesoderm formation in the higher vertebrates may have been derived from that found in Amphioxus, differing somewhat from that due to Hertwig.

Figs. 101 and 102 in Hertwig's 'Lehrbuch'[1] are sufficient to illustrate his view of the derivation of the mesodermic rudiments in the higher vertebrates from the enterocœlic pouches of Amphioxus. This view, as is well known, rests mainly on Hertwig's observations on the development of Triton, in which he found pouches of the archenteric cavity projecting on each side of the notochord into the mesoblastic rudiment, which pouches he interpreted as vestiges of the original communications between the archenteron and the cavity of enterocœlic mesoderm pouches like those of Amphioxus. These observations of Hertwig appear to have failed to find adequate confirmation, and it seems to me that a scheme such as that represented below fits in better with the general facts of vertebrate development. Such a scheme, as will be seen, agrees in general principle with the theory suggested by Lankester and developed especially by O. Hertwig, that the mesodermal rudiments on each side of the vertebrate embryo represent the walls of the enterocœlic pouches of Amphioxus; it differs from the Hertwig development of the theory in the detail that it regards the continuity often found in vertebrate embryos between mesoderm and hypoblast on each side of the notochord (and necessarily also the similar continuity between mesoderm rudiment and notochord) as being a secondary fusion rather than as representing the original connection of mesodermic diverticulum with wall of the archenteron.

The adjoining figures (Text-fig. 5) represent transverse sections through the embryos of Amphioxus, Petromyzon, Lepidosiren, and chick. In the case of the last three I have, for convenience, represented only a small portion of the whole section. As will be seen, the condition in Petromyzon agrees very closely with that in Amphioxus, and is immediately derivable from it by reduction in the size of the archenteric cavity.

The disappearance of the cavity of the enteric diverticulum

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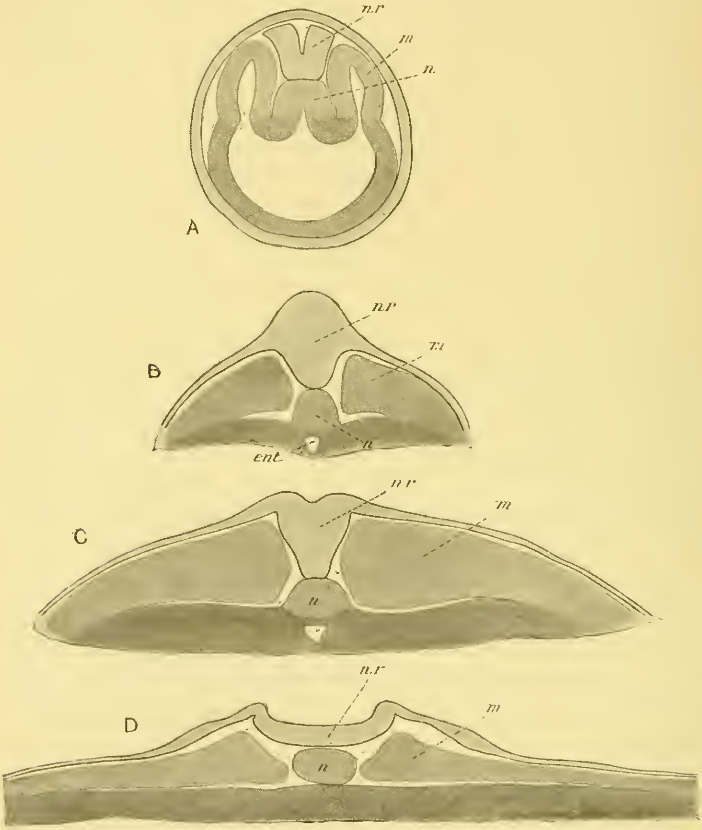
[1] 6te Auflage.

seems to me of no special weight; it is merely an additional example of a very common phenomenon, of the fact that hollow organs, formed primitively by involution of a cell-layer, tend, where the cells are burdened with yolk, to arise from a solid rudiment, and to develop their cavity secondarily.



Text-fig. 5.—Transverse sections through embryos of various vertebrates to illustrate the formation of mesoblast.—A. Amphioxus. B. Petromyzon. C. Lepidosiren. D. Sauropsida. *ent.* Enteron. *m.* Mesoderm rudiment. *n.* Notochordal rudiment. *n.r.* Neural rudiment.

Passing on to Lepidosiren, the difference between it and Petromyzon is seen to be quite insignificant, consisting, in fact, only of difference in relative dimensions.

Finally, the condition of the mesoblast in one of the higher Vertebrata, as indicated in fig. D, seems to me to hang on equally well to the earlier members of the series. What difference there is is merely difference in shape and relative size. I hold, then, that in the series of Vertebrata there exist passing phases in the development of the mesoblast which may be readily linked on to one another, and that the existence of these phases may be accounted for by regarding them as reminiscences of phylogenetic stages in the modification of the process of mesoblast development.[1]

Conclusion.—In general the phenomena described in this paper fully bear out what I referred to in my earlier communication—the extreme resemblance with corresponding features in the Urodela. As regards external features during the earlier periods of development this likeness is perhaps slightly less marked in Lepidosiren than in Protopterus, but as regards internal features of segmentation and gastrulation the most remarkable resemblance is seen.

The resemblance with Petromyzon is equally striking, and that with Ganoids only slightly less so. I do not feel it necessary to go into detail in this matter; it will only be necessary for the reader to turn to such figures as Houssay's[2] pl. xi, fig. 26 (transverse section of Axolotl, showing early stage of mesoblast); Calberla's[3] fig. 7 (similar section through Petromyzon); Eycleshymer's[4] pl. xx, fig. 8 (external view during early invagination of

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[1] It will be noticed that, on the above hypothesis, the growth of the mesoblast at its outer side by continued delamination from the hypoblast would correspond to a continued deepening of the groove between mesoblastic and chordal rudiments of Amphioxus, and is therefore easily understood. Were Hertwig's scheme the true one this growth of the mesoblast would be quite incomprehensible.

[2] 'Arch. Zool. exp.,' 2nd série, tome viii.

[3] 'Morph. Jahrb.' iii, Taf. xii.

[4] 'J. Morphol.,' vol. x.

egg of Rana palustris), or Dean's[1] pl. iv, fig. 62 (Acipenser, longitudinal section of egg during gastrulation), to see the remarkable unity which runs through these different types. Of the figures which I happen to have mentioned, the first three might have been used to illustrate the corresponding stages of Lepidosiren or Protopterus almost as well as the figures which I have given.

Looking at the broad facts in these three groups, and comparing them with what occur in other vertebrates, one cannot but be struck with the fact that in the only two groups in which it is almost certain that we have to do with poorly-yolked eggs in forms descended from richly-yolked ones, viz. the Teleostei and the higher Mammalia, we find that in neither has the process of gastrulation reverted to its original character. Rather by its profound modification from the normal type it bears witness to the changes which have taken place in its history. This being so, the comparatively simple type of gastrulation similar in Petromyzonts, Amphibia, Dipnoi, and Ganoids cannot but weigh strongly as evidence against the view propounded by Rabl, that any of these groups are descended from ancestors with large, richly-yolked meroblastic eggs.

There is one point which I should like, in conclusion, to draw attention to, and that is the shunting forwards in development of the rudiments of organ systems to an earlier period than that to which they normally belong. Thus by Stage 14, when gastrulation is just completed, the study of sections teaches us that the embryo is already a complicated triploblastic organism, with definite mesoblast and chorda.

I have obtained the small results recorded above only by prolonged work upon a most extensive material preserved with the greatest care and by the most approved methods. I have been greatly impressed by the variability observed amongst embryos of similar stages in development, much of it probably natural, much of it certainly due to differences

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[1] 'J. Morphol.,' vol. xi.

in methods of preservation, section cutting, etc.; so much so that my final description varies in many important respects from the rough draft made on a preliminary study of a few embryos. My experience convinces me of the futility of trying to give a fair description of the embryology of any type unless one has a very large material to go upon. Much of the discussion, involving often flat contradiction of distinguished observers' statements, which is constantly taking place appears to me to have a very probable cause in the small amount of material which has been made use of.

SUMMARY OF THE MORE IMPORTANT NEW FACTS.

1. The segmentation cavity arises in Lepidosiren from intercellular chinks.
2. The roof of the segmentation cavity early becomes two-layered, and assumes the character of epiblast.
3. Gastrulation takes place, for the most part, by a true invaginatory process.
4. Spreading of small cells over large takes place by delamination, there being no true epibole.
5. The disappearance of the segmentation cavity is inaugurated by its penetration by a sponge-work of small blastomeres from its floor and sides.
6. The notochordal and mesodermal rudiments are at first quite continuous across the middle line.
7. The notochordal rudiment remains attached to the hypoblast for some time after the mesoderm has separated off on each side.
8. The enteric roof is formed in situ directly from the archenteric roof.
9. The mesoderm grows outwards on each side by delamination from the large yolk-cells.
10. The myocœle arises by breaking down of cells in the middle of the myotome.
11. Later on the myotome wall is composed of a single layer of regular columnar cells.

12. The first-formed mesenchyme arises from sclerotomic outgrowths, assisted by proliferation to a slight extent from the subchordal hypoblast.

13. The solid neural keel arises by thickening of the deep layer of the epiblast.

14. The egg of Protopterus closely resembles in its early development that of Lepidosiren.

15. The roof of the segmentation cavity is, however, thicker.

16. And the invagination groove appears about 20° nearer the lower pole of the blastula.

17. The early development of Lepidosiren and Protopterus shows an extraordinarily close resemblance to that of Amphibia Urodela; a close resemblance to that of Petromyzon; and an only slightly less close resemblance to that of Ganoids.

EXPLANATION OF PLATES 1—4,

Illustrating Mr. Graham Kerr's paper on "The Development of Lepidosiren paradoxa," Part II.

As already pointed out, by "Stage *n*" I mean the stage represented by fig. *n* of my previous paper on the "External Features in Development." For the convenience of readers of the present paper I have copied and selected a number of these figures in Text-fig. 1 (p. 8). This will, I hope, obviate the necessity on the part of the reader of having to frequently refer to a separate publication.

Fig. 1.—Vertical section of egg of Stage 8, showing chinks between the micromeres. IV B 631.

Fig. 2.—Vertical section through egg, showing the commencing formation of the definite segmentation cavity, *s. c.* VII A 151.

Fig. 3.—Vertical section through the upper part of an egg slightly older than the last. The segmentation cavity has here begun to spread laterally. XXIV A 21.

Fig. 4.—Vertical section through an egg, showing the segmentation cavity at its full development. V 221.

Fig. 5.—Vertical section through the groove of invagination just after its first appearance. (Stage 10) *y* 511.

Fig. 6.—Sagittal section through a very slightly more advanced egg. *a.* Spherical blastomeres round floor of segmentation cavity. *i.g.* Invagination groove. *s.c.* Segmentation cavity. Va 371.

Fig. vi.—Similar section through egg of Protopterus. D 192.

Fig. 7.—Part of the section drawn in Fig. 6 under a higher power, showing the groove to lie within the region of coarsely-yolked elements.

Fig. 8.—Sagittal section of an egg during a later stage of gastrulation, showing folding up of coarsely-yolked elements against the roof of the segmentation cavity. VI C 222.

Fig. viii.—Corresponding section through egg of Protopterus. A 411.

Figs. 9 and 10.—Small portions of two sagittal sections through an egg of similar age to the last. The sections show the tip of the archenteron; the section drawn in Fig. 9 favouring the idea of "splitting," that shown in Fig. 10 negativing it. VI *b* 111 and VI *b* 221.

Fig. 11.—Sagittal section through an egg of Stage 12 to show the penetration of the segmentation cavity by a continuous sponge-work preparatory to its obliteration. 3* E 232.

Fig. 12.—Sagittal section through an egg of Stage 13 in which the segmentation cavity has become completely obliterated. ×x D 262.

Fig. xii.—Corresponding section through egg of Protopterus. C 263.

Fig. 13.—Portion of a similar section to that in Fig. 11, to show the characters of the small cell margin. 3* D 211.

Fig. 14.—Stage 12. R 441.

Fig. 15.—Stage 14. 7* 551.

Fig. 16.—Stage 14. XXXVII C 542.

Fig. 17.—Stage 16. XXXVII E 531.

Fig. 18.—Stage 17. XXXIII 632.

Fig. 20.—Stage 21. XXXIV B 531.

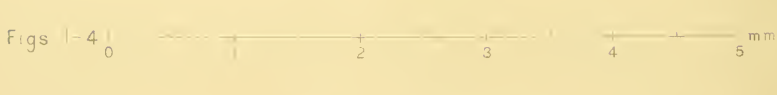
Fig. 21.—Stage 21. XXXIV C 432.

These figures form a series meant to illustrate the gradual differentiation of the mesodermal, notochordal, and other rudiments. *c.c.* Indication of split to form central canal. *e.* Epiblast. *ent.* Enteron. *e.r.* Elements of enteric roof, here with coarsely-grained yolk. *h.* Hypoblast. *m.* Mesoblast. *m.e.* Thickened ectoderm of medullary plate. *m.g.*

Medullary groove. *m.k.* Medullary keel. *m.s.* Spinal cord. *myoc.* Myocœle. *n.* Notochord. *p.n.* Pronephros.

Fig. 19.—Transverse section through neural rudiment. Stage 18.

n.c. Involution of outer surface of ectoderm to form a vestigial neural canal.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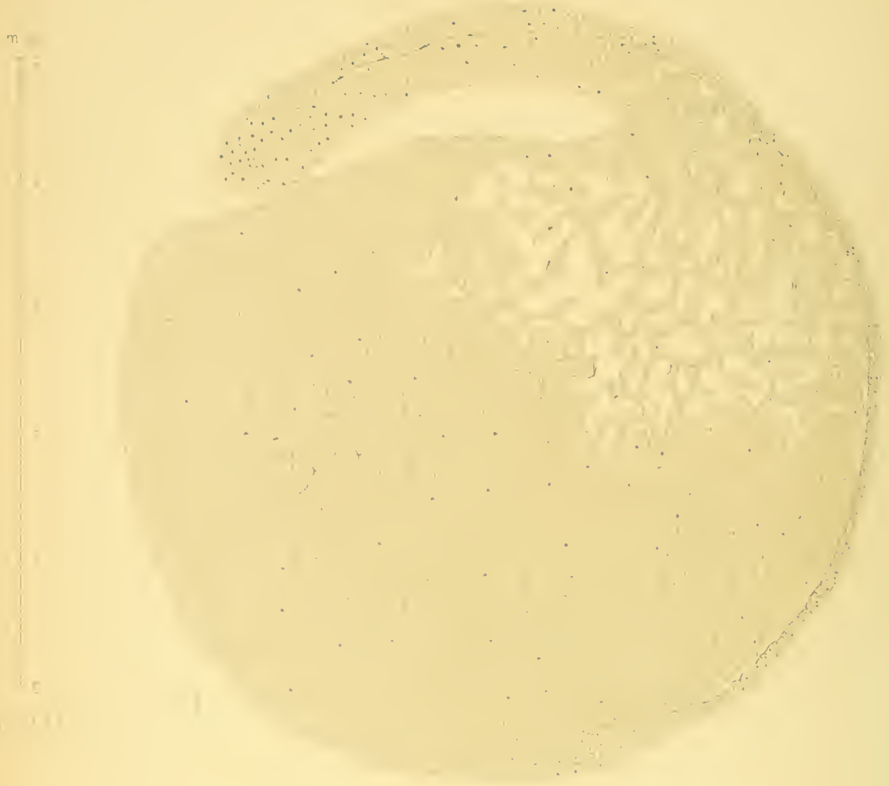
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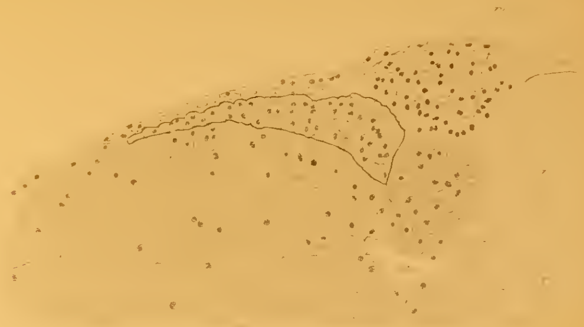

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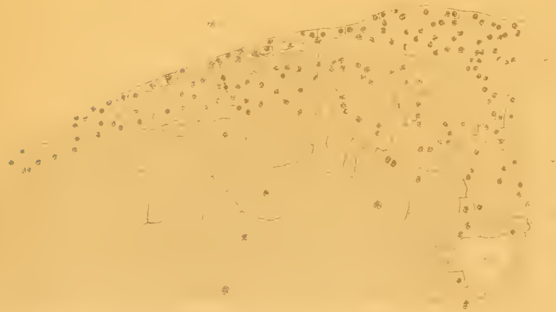

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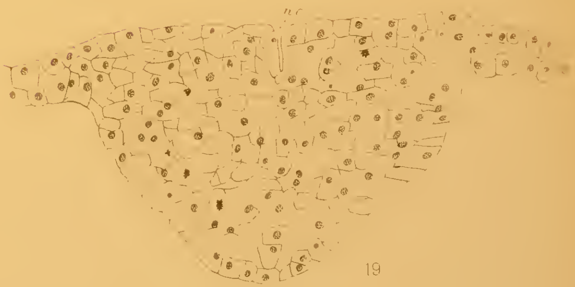

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Figs. 16, 17, 18, 20, 21 0 ——— 5 ——— 1 mm

Fig. 19 0 ——— 5 ——— 1 mm

F. Wilson, Cambridge.

On the Malayan Species of Onychophora.

Part II.—The Development of Eoperipatus weldoni.

By

Richard Evans, M.A., B.Sc.,
Of Jesus College, Oxford.

With Plates 5—9.

CONTENTS.

I. Introduction.

So much good work has been already done on the development of the Peripatidæ that it is necessary to justify the publication of another account. However, it is not difficult to do so, for not only is the development of the Malayan species still unknown, but even their very existence has been recently doubted. Their close anatomical relation to the neotropical forms renders an account of their development doubly interesting and highly desirable. For these reasons it is proposed to give a fairly complete account, and to pay special attention to those points which, hitherto, have not been sufficiently elucidated, and are still in dispute. It is not possible to give an account of the segmentation stages, owing to the material not being sufficiently well preserved. The ova being full of yolk, the younger stages in the development must be taken out of the uteri to preserve them properly; and even when this precaution has been taken, owing to the presence of a thick egg-shell, it will be difficult to ensure good preservation.

II. The Ovum.

When the germinal cells first appear in the splanchnic wall of the somites, they possess a highly granular nucleus, without a nucleolus, and their cytoplasm is in no way different from that of the remaining cells of the somite.

When the period of growth of the ovarian ovum commences the nucleus enlarges, its chromatic granules become, relatively to its size, less numerous, and are connected together through the intermediation of fine threads, which take up the chromatic stains. The nucleolus first appears, during the early stages in the period of growth, as a small spherical body. At first it presents no visible structure, but it soon becomes alveolar (Pl. 8, fig. 18 *a*). The cytoplasm, which at first resembles that of the surrounding cells, becomes clearly alveolar in character and remarkably uniform in appearance throughout the ovum. When the ovum has reached an intermediate stage in size, the small clear spaces or alveoli of the cytoplasmic network of the previous stages become darker than the intervening substance, a result probably brought about by the deposition in them of fine granules of food-yolk (Pl. 8, fig. 18 *c*). As the ovum increases in size the granules seem to run together, and consequently to form larger bodies, which in many cases appear to fuse so as to form structures which may be described as systems of granules which present several centres of deposition, as well as a common surrounding coat (Pl. 8, fig. 18 *d*).

The nucleus, at the commencement of the period of growth, is situated at or near the centre of the cell, and presents a regular oval outline; but towards the end of the period in question it moves nearer the surface. While this transference is being effected it presents an irregular outline, and seems to influence the general arrangement of the yolk bodies situated in its immediate vicinity (Pl. 8, fig 18 *d*).

The fully grown ovum possesses a fairly thick coat, presumably a vitelline membrane, and is furthermore surrounded by a layer of cells derived from the wall of the ovary: it is suspended, by means of a cord of cells, in the body-cavity. Dr. Willey used the term "exogenous" to describe this method of origin, in contrast to that found in the genus Peripatus in which the ova are formed "endogenously" (7).

The fully grown or mature ovum is oval in shape, provided it has sufficient space to assume its proper form; otherwise, under pressure exerted upon it by the neighbouring organs, it may become quite irregular in outline.

The difference existing between the modes of origin and structure of the ovum in the closely related genera Peripatus and Eoperipatus is worthy of note, and is probably the main cause of their divergence in development.

III. A General Account of the Development viewed externally.

In each uterus of Eoperipatus weldoni there may be as many as a dozen embryos, ranging in development from the segmenting ovum to an individual which measures from 25 to 27 mm. in length, and is coloured almost like the mother.

The description of the external features of the development will be limited to a number of embryonic stages, which are illustrated in the figures found on Pl. 5. The youngest embryo successfully taken out of the uterus is illustrated by the first figure on the above-mentioned plate. It seems to represent an early gastrula stage, which is oval in shape and provided with a slit-like blastopore possessing a somewhat irregular outline. The yolk masses situated in the interior are distinctly seen at the sides, but they are not so evident on the ventral surface round the blastopore, owing to the greater development of the germ layers in that position. In both shape and size the embryo under consideration substantially resembles the ovum.

The next stage of development to be described is represented in the second figure on Pl. 5. Besides being very different in shape, the embryo in question is actually shorter than the ovum. On the anterior end there are two pairs of thickenings situated one behind the other. The blastopore has been divided into two parts, one of which is situated immediately behind the first pair of thickenings mentioned above, but owing to the yolk which protrudes out of it and covers a considerable portion of the ventral surface, it cannot be seen in an external view; the other is placed further back, and may be similarly filled with protruding yolk. The quantity of external yolk present seems to be highly variable, and in some cases it appears to be wanting. When there is a great mass of external yolk spreading over the ventral surface, nothing can be seen save a botryoidal appearance, produced by the yolk embedded in a sparse reticulum of ectodermal cytoplasm. The presence of external yolk and its variability are points in which the development of Eoperipatus resembles that of Peripatoides (**6**).

The posterior portion of the blastopore presents the appearance of a square, the anterior side of which is absent. From in front it is being gradually encroached upon by the double layer of cells which has grown across the middle portion of the elongated opening found in the younger embryo. From the middle point of the posterior border of the blastopore, the primitive groove extends backwards for a considerable distance. The groove in question is not so evident in the immediate neighbourhood of the blastopore as it is some distance behind it. On each side of the groove and close to the blastopore there is a triangular-shaped thickening, in which very active proliferation is going on. These thickenings constitute the so-called primitive streak, and are the sources from which the mesoblastic bands are produced; in fact, they may be described as teloblastic spots from which the mesoderm is derived.

The next stage of development to be considered is represented by the third figure on Pl. 5. Unfortunately there is a considerable gap between this stage and the previous one. The posterior end of the embryo has grown round the head, so that it almost touches the rudimentary antennæ, which at this stage consist of three rings. The rudiments of perhaps all the appendages are visible; those of the jaws and oral papillæ being specially well developed in comparison with the others, which decrease in size from before backwards. The brain lobes constitute a marked feature of the embryo at this stage. Neither the body nor the rudimentary appendages exhibit ring-shaped markings.

The next stage to be described is illustrated by the fourth figure on Pl. 5. The posterior end of the embryo under consideration has grown over the head, and the antennæ, having increased in length, consist of about a dozen rings. The brain lobes are enormously large in proportion to the other parts of the body, and behind them are seen rows of papillæ, which represent the rudiments of the lips. The oral papillæ present at their free ends a marked depression, which represents the opening of the future slime-gland. Both the body and the appendages are provided with ring-like markings.

The next stage to be considered is represented by the fifth figure on Pl. 5. The most marked change that has been effected, as compared with the previous stage (shown in the fourth figure of the same plate), consists in increase in size, the embryo in its folded condition being two and a half times as long as the previous one. The posterior end of the embryo is passing from the strictly dorsal and median position to the left side of the head preparatory to unfolding itself. When the posterior end has slipped off the back it may become slightly coiled, so as to produce a short spiral, and, owing to both ends of the embryo simultaneously untwisting themselves in opposite direction, which sometimes happens, the whole body may for a time present the appearance of being spirally twisted. The ring-like markings occurring on the body and appendages are gradually becoming deeper.

The sixth figure on Pl. 5 illustrates the next stage of development to be studied. In the embryo under consideration the posterior end displays a curious twist, which it has acquired in passing from the left side and in becoming extended. The anterior end of the embryo is so placed that the ventral surface is turned towards the right side, but does not slip over to the side as the posterior end does. The flexed anterior end, besides being twisted laterally, is unfolding itself longitudinally; for in the embryo under consideration it carries only two pairs of the walking appendages, while in the one described in connection with the previous stage, and illustrated by the fifth figure on Pl. 5, it was provided with four pairs. The actual length of the embryo in its folded condition was 7 mm.

The next stage of development to be considered is represented in the seventh figure on Pl. 5. With the exception of the head, which is bent down towards the ventral surface, the body of the embryo has attained the extended condition of the older ones which occur in the uteri, and its colour is just beginning to turn brown. Only the first pair of walking appendages are in any way involved in the cephalic flexure. The actual length of the embryo in its folded condition was 17 mm.

The eighth figure on Pl. 5 illustrates the last stage in the development. The embryo is fully extended and presents nearly all the characters of the newly-born young. Even the colour is not very different, and the great length of the body is a most remarkable feature. In this latter respect it surpasses the embryos of the genus Peripatus by several millimetres. It may be worthy of note that the embryo under consideration, which is a male specimen taken out of the uterus of Eoperipatus weldoni, is five millimetres longer than one of the male specimens of E. horsti obtained from a dead tree trunk. Consequently there must be a considerable difference in length between the embryos of E. weldoni and of E. horsti at the time of birth.

This concludes what I have to say on the embryonic stages of Eoperipatus weldoni, viewed externally. There is nothing new or remarkable in the various phases of outward form through which the embryo passes in the course of development from the egg—heavily laden with yolk—to the young just before birth. The early stages in the development appear to be passed through very quickly, and the changes which occur appear to consist in the development and differentiation of parts at the expense of yolk stored up in the egg, the actual increase in volume being very small. It is not until the rudiments of all the most important organs have been developed that any appreciable increase in size takes place. Consequently the first five embryos in the uterus, counting from the ovary, present the appearance of being of the same size when examined through the uterine wall. The sixth embryo, however, is considerably larger than the fifth, the seventh than the sixth, and the difference between any two successive embryos goes on increasing to the end of the series.

The uterus may contain as many as a dozen embryos, the second, third, fourth, fifth, seventh, ninth, tenth, and twelfth of which are respectively represented on Pl. 5, and illustrate corresponding stages in the development.

IV. The Development of the Germ Layers, etc.

The First Embryo.—The sections obtained from the specimen illustrated in the first figure on Pl. 5 were not sufficiently good to admit of the structure being made out with any degree of accuracy and certainty. For this reason it is necessary to commence the description of the formation of the germ-layers from a slightly older embryo, of which four transverse sections are represented in fig. 9 (*a*, *b*, and *d*) on Pl. 6.

In the embryo under consideration there is no external yolk, and the blastopore is as yet undivided; but both the endoderm and mesoderm are already in process of formation. At this stage in the development there are no nuclei in the centre of the yolk.

The ectoderm consists of a single layer of cells except in front and at the sides of the blastopore on the ventral surface where the nuclei are already arranged two deep (Pl. 6, fig. 9 *a*). On the dorsal surface, especially towards the anterior end, the ectodermal layer seems to be incomplete. The ectodermal nuclei of the ventral surface are oval in shape, and are arranged close to one another; while those situated at the sides and on the dorsal surface are circular in shape, and placed at greater distances from one another. The doubling of the ectodermal layer, in front and at the sides of the blastopore, seems to represent the first rudiments of the nervous system, which is always developed from before backwards, a fact which explains the greater condensation of ectodermal nuclei in the position in question than elsewhere (Pl. 6, fig. 9 *a*).

The mesoderm is already in process of formation. It is derived from an area situated immediately behind the posterior end of the blastopore (Pl. 6, fig. 9 *d*). The first somite, already present, has not yet formed a cavity, though the nuclei are arranged in a ring (Pl. 6, fig. 9 *c*). In addition to the first somite, the rudiments of the second and third have already appeared, but their nuclei present no particular arrangement (Pl. 6, fig. 9 *d*). Even at this early stage in the development the first somite, preparatory to advancing along the side of the embryo towards its anterior end, is far removed from the median plane.

The endoderm is also forming, especially towards the posterior end of the embryo (Pl. 6, fig. 9 *c*, *en.*). In front of the blastopore there are no endodermal nuclei, but at its sides a few have already appeared. Towards the posterior end they are more numerous, and in the region in question an occasional nucleus may be seen halfway up the sides (comp. figs. 9 *a*, 9 *c*, 9 *d*). There seems to be no doubt that the endodermal elements in Eoperipatus are derived from the lips of the blastopore, with which the endodermal layer is continuous, and that they pass from that position through the outer layer of the yolk. While this process of invagination is going on, the layer of yolk in question, which is being gradually invaded by the endodermal elements, loses its deutoplasmic character and becomes more cytoplasmic. The central mass of yolk presents the appearance of containing compound systems as well as separate yolk bodies, between which there seems to exist a certain amount of cytoplasm. Simultaneously with the increase in number of the endodermal elements the cytoplasm grows at the expense of the deutoplasm.

Unfortunately the quantity of material at my disposal was not enough to enable me to form very decided conclusions on the formation of the blastula stage in Eoperipatus, and I do not wish, in any way, to question the accuracy of already published accounts of its formation in other genera of the Peripatidæ; but it is necessary to point out that the incomplete condition of the ectodermal layer on the dorsal surface of the very early gastrula stage, already described, tends to show that in Eoperipatus the circumcrescence of the yolk takes place after the same plan as in so many other Arthropoda; that is, by overgrowth from the future ventral surface towards the dorsal. It is well known that the various genera of the Peripatidæ differ from one another to a remarkable degree as regards the early stages in their development, and it is quite possible that the method by which the yolk becomes surrounded by the blastula cells in the young embryo of Eoperipatus conforms more closely to that existing in most Arthropoda than it does to that occurring in the other genera of the Onychophora. On this theory, Eoperipatus, which, from the point of view of external characters and internal anatomy, seems to be more primitive than the other genera belonging to the family Peripatidæ, would have to be considered more primitive, as regards the mode of circumcrescence of the yolk, unless it be admitted that the method in question has originated twice within the limits of the Arthropodan phylum, a view which is in no way probable.

The mesoderm seems to be formed exclusively from the primitive streak, but the endoderm develops from the lips of the blastopore by invagination.

The Second Embryo.—The next embryo which will be considered corresponds to the one represented in the second figure on Pl. 5, and is considerably more advanced than that described in the foregoing pages, for it possesses the rudiments at least of eight somites.

The ectodermal layer is complete on the dorsal surface, though thin, and possesses nuclei which appear either circular or oval in transverse section. When they are oval in shape their long axis lies parallel to the surface. The ectoderm, which covers the ventral surface, and is situated between the two portions of the divided blastopore, has similar characters (Pl. 7, fig. 10 *e*). Elsewhere the ectodermal layer is considerably thickened, and its nuclei are arranged three or four deep. The thickening of the ectoderm is most marked on the cephalic lobes, where the nuclei are arranged in three or four layers, and on the sides, where they are arranged in two layers. The cephalic lobes and the lateral bands, both produced by the thickening of the ectoderm, are continuous with each other, and probably represent the undifferentiated rudiments of the appendages, the nervous system, and the ventral organs. The upper moiety represents the rudiments of the appendages, while the lower one, later on in the development, splits into an inner and an outer portion, the forerunners respectively of the nervous system and ventral organs. In the region in front of the anterior portion of the blastopore, the ectodermal thickening is continuous across the middle line (Pl. 6, figs. 10 *a*, 10 *b*, and 10 *c*) ; but in the mid-region of the body, that is in the region where the blastopore has been obliterated, the two thickenings are widely separated from each other (Pl. 6, figs. 10 *d*, 10 *e*, and 10 *f*) ; while behind the blastopore in the region of the primitive streak they converge and fuse together (Pl. 6, fig. 10 *j*).

The disposition of these ectodermal bands presents another feature in which the development of Eoperipatus approaches that of P. novæ-zealandiæ (6).

The mesodermal bands, which originate from the triangular-shaped thickenings noticed in surface view, and situated immediately behind the blastopore, are placed exactly under the ectodermal bands above described (Pl. 6, figs. 10 *a*—*j*). At the sides they are broken up into several somites, which decrease in size from before backwards. In the anterior region, in which the cœlomic cavity has already appeared, every successive somite overlaps the one in front of it (Pl. 6, figs. 10 *c*, 10 *d*, and 10 *e*). The first somite has a well-developed cœlom, and is situated in the latero-ventral aspect of the cephalic lobes (Pl. 6, figs. 10 *a*, 10 *b*, and 10 *c*). The second somite is considerably smaller and overlaps the first one (Pl. 6, fig. 10 *c*). The third somite is slightly smaller than the second and passes forwards above it (Pl. 6, fig. 10 *e*). The same is true of the fourth and fifth somites, the remaining ones being so small in size as to be incapable of overlapping (Pl. 6, fig. 10 *g*).

As soon as the cœlom begins to form the two walls of the somite present distinctive characters. In the splanchnic wall the nuclei are placed at a distance from one another, and are flattened in the tangential plane ; but in the somatic wall, they are closely packed together and are oval in shape, their long axis being directed at right angles to the surface (Pl. 6, fig. 10 *e*, *som.*[3] and *som.*[4]). This rapid differentiation is prophetic of the changes which take place in the somatic wall at an early stage in the development; that is, of the formation of the myotome and the renal outgrowth.

In the embryo under consideration the endoderm is present as a layer which completely surrounds the central yolk. There are no cell outlines in it, and the nuclei are not always spherical in shape. The endodermal layer, however, is incomplete at two points, namely, the two portions of the divided blastopore through which the yolk protrudes and spreads itself over the ventral surface as the so-called external yolk. The inner limit of the endoderm is quite distinct from the central yolk, and at the edges of the blastopore it is continuous with the ectoderm. The endodermal nuclei are not situated in the outer layer of the yolk, but in a layer which seems to be new, and entirely different. It is true that it contains spherical masses, presumably stored-up food material, but there are no compound systems among them, and they stain much less readily. They probably consist of food masses, which the endoderm itself has elaborated at the expense of the central yolk, and stored up within its own substance. The endodermal layer possesses another characteristic which the central yolk completely lacks, namely, a great multitude of small refringent granules, which were not observed in the younger stages already described. The external yolk differs from the central yolk in that the masses of food material contained in it are smaller, while the amount of cytoplasm present is larger. It seems that the ectoderm is capable of acting on the external yolk in the same way as the endoderm does on the central yolk, and of building and storing up food masses for future use. This is done chiefly on the ventral surface, where the ectoderm and external yolk are in contact.

In the embryo under consideration there still remains to be described a most remarkable structure, the nature and significance of which must be discussed. It is the small somite (Pl. 6, fig. 10 *a*, *ce. som.*) situated in front of and above the somite usually described as the first. It has developed a cavity only on one side; on the other side it consists of a mere group of nuclei. This is all that can be said of its structure, and nothing is definitely known of its origin. It seems that it cannot have been separated from the first somite, which remains undivided until a much later stage in the development. If this be true, it follows that the small somite in question must be an independent structure, produced from the mesodermal bands at a late stage and disappearing early, and, as such, must have a very short existence. To judge from its position, its form and structure, and its late formation and early disappearance, it would seem that we are justified in concluding that it represents a somite which has been reduced to the merest vestige: so vestigial is it that it may not even develop a cavity at all, but remain as a group of nuclei lying in the undivided cytoplasm. It may, perhaps, be permissible to conclude, since it is not possible to regard any other metamerically arranged organs as corresponding to this somite—unless the dorsal lobe of the brain, that is the archicerebrum, be so considered—that the structure, the nature and significance of which is here discussed, is a true cerebral somite which up to the present has not been discovered.

The Third Embryo.—The third embryo, the internal structure of which will be considered, is the one shown in the corresponding figure on Pl. 5, and is represented by four drawings of sections, marked 11 *a*, 11 *b*, 11 *c*, and 11 *d* on Pl. 7, in which the first, second, third, and fourth somites are respectively illustrated.

On the ventral and dorsal surfaces the ectoderm forms a thin layer, in which the tangentially compressed nuclei are situated at some distance from one another, and, in the mid-region, as well as towards the posterior end, is still in contact with the endoderm (Pl. 7, figs. 11 *c* and 11 *d*).

The rudiments of all the appendages have appeared as outgrowths of the dorsal moiety of the lateral thickening of the ectoderm, and decrease in size from in front backwards. The common rudiment of the nervous system and ventral organs has been separated from that of the appendages, and in the region of the third and fourth somites the thickening in question has been divided into two, namely, an internal one, the primordium of the nervous system, and an external one, the forecast of the ventral organs. The ectodermal thickenings are continuous from the cephalic lobes backwards, —that is, the rudiment of the para-œsophageal cord is already formed.

Owing to the way in which they develop from in front backwards, the mesodermal somites in the embryo under consideration illustrate in the most perfect manner the changes through which they pass in their development up to a certain stage, a result made possible by the most admirable series of sections into which the embryo was cut. But the general remarks I have to make on these will be reserved for another section of the paper, in which the cœlom and the mesodermal organs will be specially considered. At present it suffices to say that there are twenty-seven pairs of them, and that it is impossible to state with any degree of certainty whether one pair more would have been developed or not. There are no traces whatever of the germinal nuclei, either in the mesoderm or endoderm.

In the embryo under consideration the endoderm is very different from what it was in the second embryo described. It is no longer possible to speak of a peripheral layer of endoderm containing nuclei, and a central mass of food yolk devoid of nuclei. It would be preferable to speak of a peripheral layer and central mass of endoderm; for the endodermal elements of the peripheral layer of the previous stage have invaded the central mass and converted the central yolk into a number of nucleated masses, which present the same structure as the peripheral layer did in the previous stage. In both the peripheral layer and the central mass spherical masses of stored-up food materials, and almost innumerable granules small and refringent in character, are present;

but the compound systems of yolk-masses have totally disappeared, unless they are represented by the nucleated masses. The nuclei of the peripheral layer are almost invariably circular or oval in shape, and usually much larger than either mesodermal or ectodermal ones. Their larger size, most probably, is correlated in some way with the function of presiding over the transformation and elaboration of the yolk present in the central mass of the previous stage. This increase of size is quite comparable to that which takes place in the case of the nucleus of the ovarian ovum, which supervises the process of elaborating and storing up the deutoplasm in the egg-cell. The two processes seem to be comparable in every respect. The nuclei found in the central mass of amœboid wandering cells, may occasionally present an irregular form, but they seem never to break up and disintegrate. The wandering character of these cells more than suffices to account for the angular outline of some of their nuclei. In a slightly later stage in the development the angularity of the endodermal nuclei becomes much more marked, even those of the peripheral layer presenting the same characteristic (Pl. 7, figs. 11 *a*, 11 *b*, 11 *c*, and 11 *d*).

The Fourth Embryo.—The fourth embryo, the internal structure of which will be described, is the one illustrated by the corresponding figure on Pl. 5, and represented by drawings of ten transverse sections on Pl. 7 (figs. 12 *a*, 12 *b*, 12 *c*, 12 *d*, 12 *e*, 12 *f*, 12 *g*, 12 *h*, 12 *j*, and 12 *k*).

On the dorsal and ventral surfaces, the ectoderm presents the same characteristics as in the third embryo, already described, with the difference that they are still more emphasised, the layer being thinner, the nuclei more compressed, and the space—especially on the dorsal surface—over which it is in contact with the endoderm, being greater, the last result being brought about, not so much by the withdrawal of the mesoderm, as by the growth of the embryo, and consequently more highly arched condition of the dorsal aspect (Pl. 7, figs. 12 *e* and 12 *f*).

The nervous system has undergone only a very slight change, the differentiation that has taken place beyond what was observed in the third embryo being very small, but in spite of this fact, the growth in size of the nervous rudiment is considerable. Most marked of all is the increased thickness of the forecast of the brain, which so far shows no sign of demarcation into several ganglia or lobes, and is situated in front of the renal opening of the first somite (Pl. 7, figs. 12 *a*, 12 *b*, 12 *c*, and 12 *d*).

Both the stomodæal and proctodæal invaginations are well-formed structures, and communicate with the irregularly shaped enteron (Pl. 7, figs. 12 *e* and 12 *k*).

The mesodermal somites have attained, in a general way, a more advanced stage of development than they had in the previously described embryo, in which they were not divided into appendicular and median portions. In the present embryo the renal portion of the first somite communicates with the exterior, and the same portion of several other somites has reached the ectoderm, though the opening has not been actually formed (Pl. 7, figs. 12 *d* and 12 *e*, *ren. op.*). "Germinal nuclei" have already appeared in the splanchnic walls of several somites (Pl. 8, fig. 13).

In the embryo under consideration the endoderm seems in some respects to be in a less advanced state of development than in the third one. In connection with its structure there are several points which should be noticed. In the first place, the peripheral endoderm is not so well marked off from the central mass as it was in either the second or the third embryo, and it often contains within its substance a number of yolk-bodies belonging to the type referred to as compound systems, which was not the case in the third embryo (Pl. 7, fig. 12 *f*). In the second place, the presence of compound systems marks a decidedly less advanced state of development, unless they are regarded as the products of the metabolic activity of the endodermal elements themselves, and different from those, occurring in the second embryo, which were directly derived from the yolk-bodies originally found in the egg. It seems that this second alternative is more probable, because in the embryo under consideration they occupy a central as well as a peripheral position in the endoderm. If this supposition be correct, their formation from the spherical masses of deutoplasm, which occur in the endoderm of the third embryo, would have to be explained on the same principle as the building of compound systems from separate masses of deutoplasm in the case of the ovarian ovum. In the third place, the refringent granules found in the third embryo do not seem to occur in the present one. In the fourth place, nearly all the endodermal nuclei display an angular outline; while in the third embryo only a few of these, situated in the central endoderm masses alone, presented the characteristic in question. In the fifth place, the endodermal cytoplasm, apart from the difference arising from the change in character of the deutoplasm, is quite different in structure, in that in many places it appears distinctly fibrous, the fibres being arranged according to no particular plan (Pl. 7, fig. 12 *e*).

V. The Development of the Mesodermal Organs.

In the foregoing pages an attempt has been made to describe the formation of the Germ Layers, and to give a brief account of what happens during the early stages of the development; but in the following pages it will be my endeavour to give a more detailed account of the development of the Organs from the Germ Layers.

(1) The Development of the Mesoderm with its Cavities.

The development of the mesodermal somites has been followed both by von Kennel (**4**) and by Mr. Sedgwick (**5**). The description given by the former of their development in Peripatus edwardsii is so unsatisfactory as to deserve no further mention in this connection; while that given by the latter of the processes going on in Peripatopsis capensis is so good that, even now, after an interval of fifteen years it is almost impossible to improve upon it. However, the failure of Kennel's attempt to explain the mysterious phenomena in P. edwardsii hardly accounts for the whole difference between the two descriptions. But before proceeding any further a few words must be said regarding the terms which Mr. Sedgwick used in his description, and those which will be adopted in the present account. On page 493 of the third part of his account (5) Mr. Sedgwick uses the terms "dorsal" and "ventral," by which he means the dorsal and ventral portions of the almost unmodified somite, with its fully developed cœlom. On the following page he speaks of an "outgrowth" from the posterior part of the somite into the rudimentary limb, and describes it as the "lateral or appendicular portion" of the cœlom, in contrast with the "median portion." On the same page he labels the "median portion" as the "dorsal," and on page 496 the "lateral" or "appendicular" becomes, in Mr. Sedgwick's nomenclature, the "ventral division." In the passages referred to, each of the terms dorsal and ventral has been used in two different senses, for if I understand him rightly, Mr. Sedgwick does not apply the expressions dorsal and ventral on pages 494 and 496 as he does on page 493 (5). In the present account the expressions dorsal and ventral will be used in the same sense as was given them on page 493 of Mr. Sedgwick's account,—that is, to refer to the upper and lower portions respectively of the unmodified somite. The expressions median and appendicular, alone, will be applied to the portions of the cœlom resulting from its division into a portion situated in the body, and a portion placed in the appendage.

In treating of a mesodermal somite and its cœlomic cavity, it will conduce to clearness if I describe the development of a somite situated somewhere about the middle of the body before proceeding to consider the special modifications occurring at either end of the animal.

The first appearance of the somites and of the cavities situated in them has been considered in describing the second embryo (p. 49). A mesodermal somite which has reached the point of maximum development, but which is still unmodified, is crescent-shaped (Pl. 7, figs. 11 *a* and 12 *k*), the splanchnic wall always being less curved than the somatic. Though the somites situated on either side never meet either below or above the gut—except in the formation of the ovary,—at one period in the development they approach very near to one another, especially on the ventral surface, a condition which reminds us of that occurring in an adult Annelid, and at one time must have existed in the ancestral Arthropod.

By the time the somites have reached this stage, the rudiment of the nerve-cord has attained considerable development. The rudiment in question, together with the myotome which develops on the latero-ventral aspect of the somatic wall, exerts such a pressure on the somite that the two walls of its ventral portion are pressed together, resulting in the obliteration of the cœlom in that part of the somite. Only the dorsal portion of the cœlom, together with the small rudiment of the appendicular outgrowth, remains (Pl. 7, fig. 11 *b*). The growth of the appendicular portion for a time keeps pace with that of the leg, to the distal end of which the cœlomic outgrowth reaches. The ultimate separation of the appendicular from the median cœlom is brought about by the continued increase in size of the myotome, which extends both in front of and below the canal which places the two portions of the cœlom in communication with each other. I have been unable to observe the septum which Mr. Sedgwick describes as growing from the ventral wall, and finally dividing the cœlomic cavity into median and appendicular portions, and I am firmly convinced that the obliteration of the communication is brought about in Eoperipatus by pressure from without, the result of the continued growth of the myotome and nervous system.

The median portion of the cœlom persists for a short time after the appendicular part has been constricted from it, but it soon disappears, leaving absolutely no trace of its former existence, that is in the first eighteen to twenty somites. Mr. Sedgwick, in a foot-note to page 493 (5), seems to doubt his own description as to the origin of a layer of cells situated above and below the somite, during a particular stage in the development of P. capensis. In Eoperipatus, however, the ventral portion of the cœlomic cavity is obliterated in exactly the same way as is described by Mr. Sedgwick in the text, with the difference that the obliteration is more extensive, probably owing to the presence of a large quantity of food material in the interior—wanting in P. capensis,—which helps to intensify the pressure brought about by growth. The median cœlom of the later stage disappears in the same way as the ventral portion of the earlier stage, that is by the coming together of its two walls.

Now that the median cœlom has been absolutely obliterated, only the appendicular cœlom remains. It was mentioned above that the appendicular outgrowth for a time kept pace with the rudiment of the leg in which it is situated; but this arrangement is not long continued. Its distal end ceases to grow, and a spot on the ventral wall of the appendicular cœlom begins to proliferate, resulting in a downward growth which is situated near its proximal end. Its distal end projects into the leg rudiment. This condition is very well marked in the appendicular cœlom of the third appendage (oral papillæ, Pl. 7, fig. 12 *g*). But this distal projection of the appendicular cœlom, in later stages of the development, seems to be obliterated by the formation in its walls of the rudiments of the leg muscles, which appear to develop to a greater extent in Eoperipatus than in Peripatopsis. The downward outgrowth from the ventral wall of the appendicular cœlom soon reaches the ectoderm at the base of the rudimentary leg, and effects a communication with the exterior. The ectodermal indent is at first extremely slight, nearly the whole tube being mesodermal, and throughout the series of changes which give rise to the renal organ, consisting of renal duct and cœlom, I have seen nothing that would tend to make it necessary even to modify not to speak of abandoning, the view that the renal duct is almost exclusively mesodermal; that is, that the ectodermal portion is extremely short, though always present—a conclusion arrived at from the histology of the fully developed organ.

It will be observed that the above description of the development of the cœlom in Eoperipatus agrees with that given by Mr. Sedgwick of the processes occurring in P. capensis, save in a few details of no material importance, a confirmation which bears weighty testimony to the correctness of that embryologist's work. This correspondence in the development of the cœlom in these forms goes far to prove that the changes which take place in P. edwardsii would be found to agree, if only they were properly examined; for P. edwardsii and Eoperipatus are much more closely related to each other than either of them is to P. capensis.

(2) The Development and Disappearance of the First Somite (*som.*^{1}).

The early stages in the development of this somite have been already described, and are illustrated on Pl. 6, figs. 9 *c*, 10 *a*, and 10 *b*. In fig. 11 *a* on Pl. 7 it is represented at the zenith of its development, but still undivided. At the side of the stomodæal invagination, its inner wall, contrary to what occurs in the somites situated behind, has considerably thickened to produce the rudiment of the mesodermal portion of the fore-gut. In figs. 12 *a*, 12 *b*, 12 *c*, 12 *d*, and 12 *e*, on Pl. 7, the first somite is shown in its divided condition, the two portions being separated by a thin septum, which was probably produced in the manner described by Mr. Sedgwick as occurring in all the somites; but I have no evidence on this point. The two portions into which the somite is divided extend the whole length of the rudimentary antenna (Pl. 7, fig. 12 *a*, *som.*^{1}). Posteriorly they pass backwards almost to the level of the second pair of rudimentary appendages.

From the posterior inner corner of the renal portion a fine canal passes to the exterior, its external opening being situated immediately in front of the rudiment of the jaw and on the inner side of the forecast of the lip (Pl. 7, figs. 12 *d* and 12 *e*). It is only fair to point out that this communication with the exterior was discovered many years ago by Miss Sheldon in P. novæ-zealandiæ (**6**), and that the nephridium of the first somite had been seen and identified by Mr. Sedgwick in P. capensis (**5**). Consequently, the somite under consideration was clearly shown to have the same morphological value as any one of the succeeding somites. Owing to the great increase in size of the cephalic ganglia and first pair of ventral organs, the communication of the first somite with the exterior soon becomes obliterated, and the two portions into which the somite is divided become much reduced in size and finally disappear. Fig. 22 *a*, *som.*[1], on Pl. 9 shows the remnants of the first pair of somites as small spaces situated above the brain and in front of the eye.

(3) The Development and Disappearance of the Second Somite (*som.*[2]).

The early stages in the history of the second somite have been noticed in describing the first and second embryos, and are illustrated in figs. 10 *c* and 10 *d* on Pl. 6, in which it is shown that the somite in question passes above the first one, situated in front of it, and below the third, which succeeds it.

Fig. 11 *b* on Pl. 7 shows the somite under consideration much compressed, and displays a tendency on the part of its walls to come together, and consequently to obliterate the cœlom.

Dorso-ventrally, however, the somite presents a considerable extension. The same figure also shows the lateral outgrowth of the cœlom, which extends the whole length of the rudimentary second appendage. The outgrowth in question is a true appendicular cœlom, on the ventral wall of which the myotome, which has already reached a fairly advanced state of development, is placed, as in all the other somites. Fig. 12 *f* on the same plate shows the second somite divided into median and appendicular portions, both of which are much reduced in size and ultimately disappear.

(4) The Development of the Third Somite (*som.*^{3}).

The third somite passes through the early stages of its development in a way similar to a somite from the mid-region of the body, which has been already described. However, some peculiar points in its history should be noticed, and are illustrated in fig. 12 *g* on Pl. 7. In the first place, the distal extension of the appendicular cœlom is much larger than in any of the succeeding appendages, a fact which is in keeping with the great size of what, in the adult, may be designated the salivary cœlom. In the second place, the downward outgrowth from the appendicular cœlom to form the duct is much larger than the same outgrowth is in any other appendage. The later stages in the development of the appendicular cœlom of the third somite so closely agree with the account given by Mr. Sedgwick of the course followed in the development of the salivary gland in P. capensis, as to make any further remarks unnecessary (**5**).

(5) The Development of the Generative Organs.

Before I proceed to describe the development of the generative system in Eoperipatus, it is necessary to summarise von Kennel's and Mr. Sedgwick's accounts of the development in Peripatus edwardsii and Peripatopsis capensis respectively; for the descriptions given by these two embryologists disagree to such an extent as to render the development of the organs under consideration a subject of absorbing interest.

According to von Kennel's account, first, the germinal nuclei arise from the mesoderm; secondly, only one pair of somites takes part in the formation of the generative organs;

and thirdly, the generative ducts develop almost exclusively from the ectoderm by invagination (4).

According to Mr. Sedgwick's description, first, the germinal nuclei arise from the endoderm, and only later acquire a relation to the mesoderm; secondly, several pairs of somites take part in the formation of the generative organs; and thirdly, the generative ducts are derived from the appendicular outgrowths of the somites of the anal papillæ (5).

The Germinal Nuclei and their Place of Origin.—Having made a brief statement of the present position of our knowledge of the development of the generative organs of the Peripatidæ, I shall proceed to give an account of their origin and growth in the genus Eoperipatus. It would seem that the germinal nuclei can be distinguished at an earlier stage in the prospective female than in the male; for this reason the following description applies to the former rather than to the latter. Because the number of metameres present in the body is not constant, it will be necessary to refer to the somites as counted from the posterior end, though in the early stages this method has the disadvantage that the generative nuclei appear before the last two somites are formed. The somite of the generative duct is the third from the posterior end, *som.*$^{n-2}$, the somites in front of it being *som.*$^{n-3}$, *som.*$^{n-4}$, etc.

Each of the embryos, sections of which are represented in figs. 13 and 14 on Pl. 8, possessed twenty-five pairs of somites, that is two pairs fewer than the smaller number that are accounted for in the adult female. Consequently the last actually developed pair of somites in the two embryos under consideration must be labelled *som.*$^{n-2}$, and the pair situated immediately in front of the last one, and shown in section in the two figures above mentioned, as *som.*$^{n-3}$. In the two embryos represented in section in these figures, germinal nuclei occur in the splanchnic walls of four pairs of somites situated immediately in front of the last actually developed pair (*som.*$^{n-2}$), but they are more numerous in the twenty-third and twenty-fourth pairs than they are in the twenty-first and twenty-second. They are present in all stages of transformation, from the unmodified nucleus of the mesoderm to that of somewhat enlarged germinal nuclei. At first they are very slightly modified, and situated among the single row of nuclei found in the splanchnic walls of the somites. As they grow in size they become pushed towards either side, chiefly to the endodermal; that is, away from the cavity of the somite, the cells of which arrange themselves in a layer round them (Pl. 8, figs. 15 *a* and 15 *b*). There seems to be no doubt that they originate in the mesoderm; and, in conclusion, I must state that I have no hesitation whatever in saying that von Kennel has made an error of observation in deriving the genital organs from one pair of somites, and that Mr. Sedgwick appears to be wrong in concluding that the germinal nuclei are endodermal, unless in these respects the species in question radically differ from the genus Eoperipatus.

The Formation of the Ovary.—The cœlom of the median portion of the four pairs of somites which take part in the formation of the ovary, is not obliterated as in the somites situated in front. From either side the somites approach one another dorsally, and then fuse to form an ovary which, at first, possesses two absolutely independent cavities, and adheres to the ventral wall of the pericardium (Pl. 8, figs. 15 *a* and 15 *b*, and 16 *b* and 16 *c*). Later on the septum which separates the two cavities of the ovary becomes broken down near the anterior and posterior ends, but is retained in the middle (Pl. 8, figs. 17 *a* and 17 *b*). As development proceeds the germinal nuclei, which at first were few, increase in number, and give rise to two germinal bands, which occupy the ventral wall of the ovary and almost fill its cavity. The developing ova are surrounded by follicle cells, and are suspended in the body-cavity, in which for want of space they are wedged against one another (Pl. 8, fig. 17 *b*), an arrangement which should be contrasted with that described by Gaffron in P. edwardsii (**3**, pl. xxi, figs. 9 and 10).

The Development of the Genital Ducts.—In one of two embryos slightly older than those of which sections are shown in figs. 13 and 14, there were twenty-six pairs of somites actually formed, and in the other twenty-seven. At the posterior end, the former had two pairs of somites possessing no germinal nuclei, while the latter had three pairs devoid of them. Of these three pairs of somites which develop no germinal nuclei, the anterior one (*som.*$^{n-2}$) gives rise to the genital ducts, the middle one (*som.*$^{n-1}$) produces the last renal organ, while the hindermost disappears in the female, and gives rise to the accessory glands in the male. It is not quite correct to say that the entire somite becomes the genital duct, for the ventral portion becomes obliterated by the coming together of its walls, of which the cells form at a later period the lining of the blood-spaces which develop in that region. An appendicular outgrowth, which is never separated from the median cœlom, forms in the genital somite, as in any other; but instead of opening to the exterior at the base of the legs, the two tubes debouch together in the median line. The inner ends of the two ducts thus formed come together in the female and unite, subsequently opening by a common pore into the cavity of the ovary. In the male they do not communicate with each other at any time, but each duct acquires a separate opening into the testis of its own side.

Further Modifications of the Oviducts.—As regards the external ends of the oviducts, the stage already described almost corresponds to the structure in the adult. The ectodermal ingrowth, such as it is, forms the extremely short vagina of the adult, and no more. In one of my embryos there is a distinct line of demarcation between the ectodermal and mesodermal constituents. The vagina lies almost horizontally, and the ectodermal portion of its dorsal wall, derived from the posterior lip of the external opening, is decidedly shorter than that of the ventral wall, which pushes its way forward as a tongue-shaped structure, situated in the median line. There seems to be no doubt that von Kennel is in error in deriving almost the whole of the oviducts from the ectoderm; for all the convolutions, which appear later on in the development, are the result of growth in the inner part of the oviducts and not in the outer.

The Receptaculum Ovorum.—The receptaculum ovorum arises as a simple evagination on one side—usually the dorsal side—of the oviducal wall (Pl. 8, fig. 17 *c*, *re. o.*). The evagination in question elongates, and the wall at its free end becomes thinner, so as to form a membrane, which closes its distal end (Pl. 9, figs. 26 *a*, 26 *b*, 26 *c*, 26 *d*, and 26 *e*). The whole organ is merely a local growth which appears relatively late, and for these reasons I am inclined to reject the suggestion made by Mr. Sedgwick, and adopted in the first part of my account of Eoperipatus, that the receptaculum ovorum is homologous with the renal end-sac (**2**).

The Receptaculum Seminis.—The development of the receptaculum seminis has been described by Gaffron (**3**), whose account is essentially correct. In Eoperipatus each oviduct forms a loop (Pl. 9, fig. 26 *a*, *re. s.*). The canal, at the free end of the loop, begins to expand (Pl. 9, fig. 26 *b*, *re. s.*), and the cavity of the receptaculum seminis forms by the continued enlargement of this part (Pl. 9, figs. 26 *c*, 26 *d*, and 26 *e*, *re. s.*). The lateral portions of the loop become the narrow ducts of the receptaculum seminis and always remain embedded in its wall, which is much thinner than was represented by Gaffron, who described in the genus Peripatus a thick middle layer, a layer which in Eoperipatus is extremely thin. Gaffron also figures the openings of the ducts into the receptaculum seminis as situated close together, while in Eoperipatus they are placed on opposite sides (Pl. 9, fig. 26 *e*). At first there is no communication between the two portions of the main canal, save by way of the loop, which gives rise to the receptaculum seminis and its ducts; but later on the septum, at first thick (Pl. 9, fig. 26 *b*), becomes thinner (Pl. 9, figs. 26 *c* and 26 *d*) and ultimately disappears (Pl. 9, fig. 26 *e*). At first the lining of the canals, situated on either side of the loop, is not differentiated, but when the secondary communication has been formed the canals in question are lined respectively by cells which are quite different in character. The portion situated between the receptaculum seminis and the ovary is lined by short cells with no definite cell outlines, and with their nuclei placed either in the centre or near their free end; but the portion situated on the other side of the receptaculum seminis is lined with columnar cells, which possess sharp cell outlines and nuclei placed at their base (Pl. 9, fig. 26 *e*). This difference is probably prophetic of the different functions which these lining cells have to perform later on in life; the columnar cells of the uterine part having to provide the developing young with the enormous amount of food material necessary to enable them to grow to the unusual length of twenty-seven millimetres.

The Male Genital Ducts.—The male genital ducts develop in the same way as the oviducts, up to the stage at which they acquire an opening to the exterior, except that their inner ends do not unite with each other (Pl. 8, figs. 19 *a* and 19 *b*). After the formation of the external pore, the short median portion, which alone is ectodermal, elongates and forms a loop, which is usually placed on the left side of the rectum, in the middle chamber of the body-cavity. Occasionally, however, the loop in question may pass under the left nerve-cord. In the former case the point of union of the vasa deferentia to the common duct is placed in the median chamber, and the right vas deferens does not pass under the left nerve-cord; but in the latter case the point of union of the two ducts is drawn to the left side of the corresponding nerve-cord, and the right vas deferens passes under both cords, just in front of the external pore. It seems from Balfour's description of P. capensis (**1**) and von Kennel's account of P. edwardsii (**4**) that the condition least prevalent in the genus Eoperipatus is almost universal in these species. It would seem that there is no doubt that the condition described by Balfour and von Kennel is the derived one; the primitive condition being the one found in the majority of individuals of the genus Eoperipatus, in which the common duct is placed in the median chamber and does not pass under the nerve-cord.

The Second Somite from the Posterior End (som^{n-1}).—In both male and female, the modifications which this pair of somites undergo are similar to those passed through by any pair of somites situated further forward, except that the renal duct does not become elongated and coiled, and that in the adult male it tends to disappear (Pl. 8, figs. 20 *b*, *ren. or.*, and 21 *b*, *ren. or.*).

(6) The Development of the Male Accessory Glands.

The Last Pair of Somites (som^{n}).—In the female the last pair of somites disappears almost immediately after their formation; but in the male they are destined to become the accessory glands. In an embryo slightly older than the one shown in fig. 4 on Pl. 5 they are fully formed and crescent-shaped. In a somewhat older embryo, oblique sections of which are shown in figs. 20 *a* and 20 *b* on Pl. 8, they are situated close to the posterior ends of the nerve-cords, and curve round it in such a way that they come in contact with the ectoderm of the ventral surface just in front of the anal slit, though they do not yet open to the exterior. In an embryo slightly older than the one shown in fig. 5 on Pl. 5 the last pair of somites open into the exterior, and have already assumed a tubular form, though they are still short (Pl. 8, figs. 21 *a* and 21 *b*, *m. a. g.*).

The above account proves that the male accessory glands of Eoperipatus are in part mesodermal, and that the cavity of their inner moiety is cœlomic. From this conclusion it follows that the male accessory glands are homologous with the renal organs. Therefore in Eoperipatus the salivary glands, the renal organs, the genital ducts, and the male accessory glands are all homologous organs, derived from the mesoblastic somites, and put in communication with the exterior by means of a short invagination of the ectoderm.

VI. The Development of the Nervous System and Ventral Organs.

The development of these two systems has been traced up to a certain stage in describing the four embryos considered in an earlier part of this paper. The common rudiment of the nervous system and ventral organs was found to consist of a thickening of the ectoderm which, developing from before backwards, became continuous from the anterior to the posterior end. The internal layer of the ectodermal thickening becomes separated off as the rudiment of the nervous system, while the outer layer, at first continuous, gives rise to the ventral organs. It is not until the embryo has nearly reached the stage of development shown in fig. 5 on Pl. 5 that any signs of breaking up of the rudiment in question appear. The nervous system does not become divided into separate ganglia, even in the adult, except in so far as the slight swellings occurring between each pair of appendages indicate such a division. This undifferentiated condition of the nervous system renders metameric comparison with the mesoblastic somites a matter of no small difficulty. The rudiment of the brain and first pair of ventral organs is, at first, an undivided mass; but in an embryo which has reached the state of development shown in fig. 5 on Pl. 5 the lobes of the brain are making their appearance, and the first pair of ventral organs have been invaginated, though on the inner side they are continuous with the brain ganglia lying above them. Fig. 23 *a* on Pl. 9 shows a section of the brain which passes near the mid-dorsal line and above both the base of the antennæ and the eyes. The upper side of the figure corresponds to the dorsal aspect, and passes through the archicerebral lobes of the brain (*a. lo.*), while the ventral side shows the lateral lobes (*lo.*^{1}, *lo.*^{2}, and *lo.*^{3}). Fig. 24 on Pl. 9 represents a somewhat oblique section of the frontal part of the brain, and it will be noticed that, on the antero-frontal aspect, the archicerebral lobes project forward as small prominences, which seem to correspond to the cephalic processes discovered by von Kennel, and interpreted as the primitive cephalic antennæ. The lateral lobes of the brain, collectively, correspond to the first somite, and there seems to be no reason whatever for regarding them as separate ganglia representing metameres which have disappeared. They are situated in front of the ganglion which supplies the jaws, and which does not, properly speaking, form a part of the brain. The connection between the ganglia of the jaws and the brain is a ventral one (Pl. 9, figs. 22 *b* and 22 *c.*, *lo.*^{4}), similar to that occurring between any two pairs of ventral swellings of the nerve-cords. The nerves to the jaws are given off from points situated near the dorsal ends of the fourth lobes, one of which is shown on the left side in fig. 22 *c*, just below the line marked *lo.*^{4}. As far as the structure of the brain can be relied upon, it gives no indication of any metameres having disappeared. The dorsal lobes seem to represent the archicerebrum; the three lateral ones are merely differentiations in the portions corresponding to the first somite, while the fourth lobe supplies the jaws, and consequently belongs to the region of the second somite.

The ventral organs arise in a manner which has been fully described by von Kennel and by Sedgwick, and there is no object in further describing them here; but it seems necessary to discuss their relation to the nervous ganglia and the mesoblastic somites. It would seem that the anterior one corresponds to the first pair of somites and to the three-lobed brain, and not to the cerebral somite and archicerebrum. The second pair of ventral organs belong to the metamere which carries the jaws, above which they are immediately situated, though they have acquired a secondary relation to the second and third lobes of the brain (Pl. 9, fig. 23 *b*, *v. o.*^{2}). Their relation to the jaws seems more important than to the brain, for the latter seems to have been brought about by the secondary shifting of the mouth parts. On this view of the second pair, the third pair of ventral organs must be considered as having been divided into two halves, one of which is drawn, during development, into the buccal cavity, while the other is left outside. The position of the intra-buccal half, above the point of union of the salivary glands to form a common duct, tends to prove that it really belongs to the somite of the oral papillæ, to which also the salivary glands are related.

The following tabular form may help to explain the arrangement of the metameres which constitute the head of Eoperipatus:

Mesoblastic Somites.	Nervous ganglia or lobes.	Ventral Organs.	Appendages.
The archicerebral somite is vestigial.	Archicerebral lobe (dorsal lobe).	—	Precephalic processes.
The first somite opens to the exterior and then disappears.	Three lateral lobes of the brain.	First ventral organ.	Antennæ.
The second somite disappears without opening to the exterior.	Fourth lobe of the brain placed on the dorsal end of the para-œsophageal cords.	Second ventral organ placed above and on the inner side of the jaws.	Jaws.
The third somite gives rise to the salivary gland.	First ventral ganglion.	Third ventral organ divided into two halves, one in the buccal cavity and one outside.	Oral papillæ.

From the above table another arrangement of the ventral organs suggests itself, and it must be admitted that there is a good deal to be said in its favour. The view in question is that the first ventral organ corresponds to the cerebral somite, which has become vestigial; the second to the first somite; and that the usually described third one should be considered as forming two complete ventral organs and not two halves. On this view one of these would belong to the somite of the jaws and the other to that of the oral papillæ.

However this may be, it makes no difference in the number of parts which constitute the head of Eoperipatus; for on either view the head is composed of an archicerebral portion, followed by the segment of the antennæ, of the jaws, and of the oral papillæ.

VII. The Development of the Eye.

The first rudiment of the eye appears as a small pit, situated on the dorsal edge of the ectodermal thickening, which in later stages gives rise to the brain (Pl. 7, fig. 11 *a*, *e*.). By degrees the depression in question becomes deeper, and in section presents the appearance of a fold of the ectoderm. The canal putting its cavity in communication with the exterior finally disappears. In fig. 25 *a*, on Pl. 9, the detailed structure of the rudiment of the eye at this stage is shown. The position and arrangement of the nuclei is interesting, those of the outer layer being arranged near the cavity of the depression, while those of the inner layer are separated from the cavity by a layer of cytoplasm, which presents the appearance of being divided into areas. This layer of cytoplasm later on gives rise to the rods existing in the adult eye. Soon after the obliteration of the canal, which puts the cavity of the eye rudiment in communication with the exterior, the outer layer is not in any way distinct from the overlying ectoderm, nor is the inner layer sharply marked from the underlying brain rudiment (Pl. 9, fig. 25 *b*). The cavity of the eye is still small and quite empty, and the nuclei situated on the inner side are beginning to arrange themselves in layers with their long axes radially directed. In the same figure the eye is shown as having been to some extent constricted from the underlying brain rudiment. In fig. 25 *c* on the same plate this constriction has been carried much further, and the eye has been completely separated from the ectoderm. The cavity of the eye is much larger though it is still empty. Pigment is making its appearance in the layer of cytoplasm situated on its inner side, and distinctly marked by radiating lines. Simultaneously with the constriction of the wide stalk shown in Fig. 25 *b* a cord of white matter has developed inside it. The cord in question passes from the white matter of the brain to the eye, and seems to spread itself over the inner half, the nuclei of which are arranged in many layers (Pl. 9, fig. 25 *c*). There seems to be no doubt that this cord, that is the optic nerve, is developed in situ from the wide stalk of earlier stages (Pl. 9, fig. 25 *b*), much in the same way as the nervous strands which connect the ventral organs to the nerve-cords are formed, but with one important difference, namely, that the cells which form the latter are scarcely modified as compared with those of the grey matter of the nerve-cord; while the cells which give rise to the former, that is to the optic nerve, undergo changes similar to those brought about in the elements which produce the white matter of the brain and nerve-cords. The cells which give rise to the white matter are developed from the ordinary cells of the sensory rudiment, that is the common rudiment of the nervous system, eyes, and ventral organs. The cells of the grey matter have small and highly granular nuclei, and a very small amount of cytoplasm; but the cells which give rise to the white matter have large nuclei, with very fine chromatin granules and a large amount of cytoplasm, in which there are no distinct cell outlines. The cells producing the white matter were only observed in embryos. I am not aware of their having been described before.

Conclusion.—There seems to be no doubt as to the correctness of Mr. Sedgwick's account of the development of the eye in P. capensis, as a cerebral eye, and the same statement is equally true of the formation of that of E. weldoni.

VIII. THE ENDODERM.

The history of the younger stages in the development of the endoderm has been given in the early part of this paper (pp. 46—55), but owing to the importance of the question it is necessary to recapitulate, and to add some more facts regarding the changes which take place during the later stages in the development.

The endodermal elements are derived from the lips of the blastopore, and travel inwards along the outer layer of the yolk, which at first is devoid of nuclei (Pl. 6, fig. 9 *c*, *en.*). In the second embryo illustrated in figs. 10 *a*—*j* on Pl. 6 the endoderm forms a complete layer, in which the nuclei, especially towards the dorsal aspect, are placed at a considerable distance from one another. The central yolk is still free of nuclei. In the third embryo, sections of which are represented in figs. 11 *a*—*d* on Pl. 7, the endodermal elements have invaded the central mass, and changed its entire character into one resembling the peripheral layer of the second embryo. In the fourth embryo, which is more advanced than the third, the endodermal elements, leaving behind them a number of yolk masses in the centre, have re-entered the peripheral layer. That such is the case is almost certain, from the irregular disposition of the endodermal nuclei, and from the absence of degenerating nuclei either in the previous or the present embryo. In the next embryo, the seventh in the uterus counted from the ovary, the endoderm has reconstructed itself. Blood-spaces have already appeared, and the intestine is surrounded by a layer of mesoderm. The endodermal nuclei are placed rather far from one another, and close to the mesodermal covering of the intestine. The cytoplasm of the endodermal layer is sparse, vacuolated, and seems to be undivided; and the whole layer is devoid of any kind of food material. In an older embryo, the ninth in the uterus, the general arrangement is the same as in the seventh. The endodermal nuclei are situated at the base, but are closer to one another; and the cytoplasm, which is still undivided, contains a number of small round bodies—presumably food material. In the next embryo, the tenth in the uterus, the general arrangement resembles that of the previous stages in the development. The nuclei are still basal, but the cytoplasm is distinctly divided by cell outlines; and yolk-bodies are much more numerous and larger than they were in the last-mentioned embryo. The endodermal cells are distinctly columnar and rather long, features which are gradually becoming more marked stage by stage. In the eleventh embryo found in the uterus the endoderm possesses the same characteristics as in the last embryo, but all of them are much more highly developed. The cells are longer and possess more marked outlines, and the food-bodies are larger and more numerous. In the twelfth embryo occurring in the uterus all the features which characterised the eleventh are present; but the cells are still longer, and the food-bodies have increased both in size and number. In the last two embryos the cavity of the gut is partially filled with a kind of débris. The globules occurring in the endodermal cells of the older embryos found in the uterus are undoubtedly the same as those found in the same position in the adult.

It will be noticed that there is in the above account of the development of the endoderm in Eoperipatus no mention of a histolytic process, such as has been described by Dr. Willey in P. novæ-britanniæ (7). If such a breaking down of the endoderm took plate in Eoperipatus, it is not likely that it would have been missed, as the nine embryos whose endoderm has been described above represent all stages of development, ranging from an early gastrula to an embryo coloured almost like the mother. As far as P. novæ-britanniæ is concerned Dr. Willey seems very decided; but when the subject is critically examined it does not seem so certain that the process of histolysis described by Dr. Willey does really take place in nature. In the first place, his specimens were preserved in formal, without opening them, consequently the preserving fluid had to penetrate not only the body-wall of the mother, but also that of an embryo almost ready for birth. To say the least it is very doubtful whether formal is capable of doing this. In the second place, the endodermal layer of the older embryo found in the uterus should not be compared, as regards difficulty of preservation, with ordinary tissue, such as the cœlomic end-sac of the renal organs, but with such structures as the ova of Eoperipatus and Peripatoides, cells which are full of food-yolk, and consequently most difficult to preserve in a good condition. How difficult food material of any kind is to preserve is too well known to need any further explanation in the present paper. For these reasons it seems that we are fully justified in questioning the accuracy of Dr. Willey's conclusion. It is much more likely that the older embryos that he took out of the uterus of P. novæ-britanniæ were not well preserved, than that there is a periodic histolysis of the endodermal cells. Dr. Willey's "strands of protoplasm, beset with eosinophile globules of varying sizes," seem to be nothing but the broken cell walls of badly preserved specimens.

Conclusion.

In addition to those whom I mentioned at the close of the first part of my account of the Malayan species of Onychophora, my thanks are due to Mr. P. J. Bayzand, the able artist in the Department of Comparative Anatomy at Oxford, for the trouble he has taken with the drawings on Pl. 5, and especially to Professor Poulton for reading over the proof-sheets.

THE DEPARTMENT OF COMPARATIVE ANATOMY,
THE MUSEUM, OXFORD;
March 19th, 1901.

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EXPLANATION OF PLATES 5—9,

Illustrating Mr. Richard Evans's paper on "The Development of the Malayan Species of Onychophora."

List of Reference Letters.

a. lo. Archicerebral lobe of the brain. *an. gr.* Anal groove. *ant.* Antennæ. *b.p.* Blastopore. *br.* Brain. *c. y.* Central yolk. *e.* Eye. *ec.* Ectoderm. *en.* Endoderm. *en. in.* Endodermal invagination. *en. n.* Endodermal nucleus. *ex. y.* External yolk. *ge. n.* Germinal nucleus. *ge. r.* Germinal ridge. *ht.* Heart. *jaw.* Rudiment of the jaw. *lo.*^{1}, *lo.*^{2}, *lo.*^{3}, and *lo.*^{4}. The first, second, third, and fourth lobes of the brain. *m. a. g.* Male accessory glands. *m. d. t.* Mid-dorsal line. *mesod.* Mesoderm. *myot.* Myotome. *n. c.* Nerve-cord. *ov.* Ovum. *ov. c.* Ovarian cavity. *ovid.* (= *som.*$^{n-2}$). The antepenultimate somite or oviduct. *pa. com.* Para-œsophageal commissure. *po. b. p.* Posterior end of the blastopore. *pc.* Pericardium. *pr. g.* Primitive groove. *proctod.* Proctodæum. *re. o.* Receptaculum ovorum. *re. s.* Receptaculum seminis. *ren. f.* Renal funnel. *ren. o.* Renal outgrowth. *ren. op.* Renal opening. *sa. gl.* Salivary gland. *som.*^{1}, *som.*^{2},......*som.*$^{n-1}$, *som.*^{n}. Mesoblastic somites. *stomod.* Stomodæum. *tes.* Testis. *vas. def.* Vas deferens. *v. o.*^{1}, *v. o.*^{2}, *v. o.*^{3}, etc. Ventral organs. *v. o.*^{3a}. The buccal portion of the third ventral organ. *v. o.*^{3b}. The external portion of the third ventral organ.

All the figures on Plate 5 were carefully drawn by Mr. P. J. Bayzand under the author's supervision. The remaining figures were drawn by the author himself with the aid of the camera lucida.

PLATE 5.

Fig. 1 (× 120).—This figure represents a young embryo of Eoperipatus weldoni. The blastopore is slit-like, and possesses irregular outlines. Externally there is no sign of segmentation. The actual length of the embryo was 1·1 mm.

Fig. 2 (× 120).—This figure represents a young embryo of Eoperipatus weldoni. The blastopore has been divided into two portions by the fusion of the lips. The anterior portion is small and slit-like, and, owing to the external yolk, can only be seen in sections. The posterior portion is a big hole with no very definite anterior lip, but the lateral and posterior lips are considerably thickened and quite definite. The primitive groove and streak have appeared, and two somites of the body are externally visible. The actual length of the embryo was ·9 mm.

Fig. 3 (× 120).—This figure represents a young embryo of Eoperipatus weldoni. The rudiments of nearly all the appendages are externally visible. The antennæ have three rings, but no other appendage is ringed. The actual length of the embryo in its folded condition was 1·4 mm.

Fig. 4 (× 120).—This figure represents an older embryo than the one shown in the preceding figure. The rings on the antennæ have multiplied. The legs as well as the body-wall are already ringed. The lips are appearing, and the oral papillæ present a depression at their outer ends. The actual length of the embryo in its folded condition was 1·3 mm.

Fig. 5 (× 27·5).—This figure represents an embryo which is considerably older than the one shown in the previous figure. The elongation and the increase in the number of rings on the antennæ are well marked. The ring-like markings on the body and the appendages are clearly visible. The posterior end of the embryo exhibits a tendency to pass from the dorsal aspect, a position occupied by it in the embryos shown in Figs. 3 and 4, and to become situated at the side. The actual length of the embryo in its folded condition was 3·1 mm.

Fig. 6 (× 10).—This figure represents an embryo still more advanced than the one shown in the previous figure. The most marked change of form that has taken place consists in the partial straightening of the posterior end after slipping from the position occupied by it in the embryos shown in Figs. 3 and 4, a change which was just commencing in the embryo shown in Fig. 5. The actual length of the embryo in its folded condition was 7 mm.

Fig. 7 (× 5).—This figure represents an embryo in which the body is still more straightened than the one shown in the previous figure is. Not only is the posterior end free of almost any twisting, but the anterior end has so far unfolded itself that only the antennæ and oral papillæ are situated in front of the curvature. The actual length of the embryo in its folded condition was 17 mm.

Fig. 8 (× 3).—This figure represents the oldest embryo in the uterus, an embryo which is coloured almost like the adult. The body is quite straight. The actual length of the embryo was 27 mm.

PLATE 6.

Figs. 9 *a*—9 *d* (× 120).—These figures represent four transverve sections of an embryo slightly older than that shown in Fig. 1, but not as old as the one shown in Fig. 2. There are no nuclei in the yolk, a feature which should be specially noticed.

Fig. 9 *a*.—This figure represents a section passing in front of the anterior end of the blastopore. The ectodermal layer is already thickening to form the rudiments of the brain.

Fig. 9 *b*.—This figure represents a section passing through the anterior end of the blastopore (*b.p.*), which is a wide groove devoid of nuclei and situated on the ventral surface.

Fig. 9 *c*.—This figure represents a section passing through the posterior edge of the blastopore, and shows the thickened lips on either side of it. The blastopore in the region situated between the sections shown in Figs. 9 *b* and 9 *c* is being obliterated by the growing across of cells from the blastoporic lips, which are not well marked in the region in question. The only somite as yet formed is cut across in the present figure, and on its inner side are situated a few endodermal nuclei (*en.*) derived from the lips of the blastopore.

Fig. 9 *d*.—This figure represents a section passing behind the blastopore. The rudiments of the second and third somites are present as groups of nuclei. The endodermal nuclei are more numerous in this region than they are in the front part of the embryo.

Figs. 10 *a*—10 *k* (× 120).—These figures represent a number of sections selected from a series, cut transversely, of an embryo about the same age as the one shown in Fig. 2, in which only the first two somites are visible externally. The blastopore is divided into two parts, an anterior and a posterior. The central cavity of the embryo is occupied by a mass of yolk, which protrudes from the blastoporic openings, and to some extent spreads itself over the ventral surface of the embryo. The ectoderm of the dorsal surface consists of a thin layer of protoplasm with flattened nuclei arranged tangentially to the surface. On the lateral aspects, and on the ventral towards the posterior end, the ectoderm is thickened to form the undifferentiated rudiment of the appendages and nervous system. The endodermal layer is quite distinct from the central mass of yolk, though it contains food material in the form of large round yolk-bodies, as well as numerous small refringent bodies, which stain like the yolk.

Fig. 10 *a*.—This figure represents the twelfth transverse section in the series, counting from the anterior end. It passes through the first pair of somites (*som.*[1]). On the left, above the somite, there is a small cavity which does not exist on the other side, where there are only a few nuclei, which may possibly represent a rudiment in which a cavity similar to the one already existing on the left side will appear later in the development. The centre of the section is occupied by the endoderm (*en.*) of the anterior end of the embryo. The thickened portion of the ectoderm, situated on the latero-ventral aspect, is the rudiment of the brain.

Fig. 10 *b*.—This figure represents the third transverse section behind the one shown in Fig. 10 *a*. It passes through the anterior limit of the central yolk (*c. y.*) and the posterior limit of the endodermal wall of the anterior end of the embryo. The small cavity found in Fig. 6 *a* has disappeared, a fact which proves that the cavity in question does not represent the anterior portion of the second somite.

Fig. 10 *c*.—This figure represents the tenth section behind the one shown in Fig. 10 *b*. It passes through the posterior end of the first somite (*som.*[1]), the middle of the second somite (*som.*[2]), and, on one side, the anterior edge of the third somite (*som.*[3]), which passes forward above the second somite. The central yolk (*c. y.*) is quite distinct from the endodermal layer, and contains no nuclei. At the bottom of the section, at a point which is situated quite close to the anterior edge of the blastopore, the endoderm is being recruited from the undifferentiated cells (*en. in.*).

Fig. 10 *d*.—This figure represents the eighth section behind the one shown in Fig. 10 *c*. It passes through the anterior end of the blastopore (*ant. b.p.*) and the second and third pairs of somites (*som.*[2], *som.*[3]). It shows the yolk (*ex. y.*) protruding from the blastopore and spreading over the lower aspect of the section. The central yolk (*c. y.*) and endoderm (*en.*) have the same appearance as in Fig. 6 *c*, the former being absolutely devoid of nuclei. This section shows the ingrowth at the edge of the blastopore to form the endoderm (*en. in.*). The mesoblastic somites are quite distinct and separate from this ingrowth.

Fig. 10 *e*.—This figure represents the eighth section behind the one shown in Fig. 10 *d*. It passes through the region where the lips of the blastopore have fused (*mid. b.p.*), the third somite (*som.*[3]) on one side and the fourth (*som.*[4]) on the other having been cut.

Fig. 10 *f*.—This figure represents the ninth section behind the one shown in Fig. 10 *e*. It passes through the posterior moiety of the blastopore (*po. b.p.*), the fourth somite (*som.*[4]) on one side and the fifth on the other (*som.*[5]) appearing in it. The yolk protrudes out of the blastopore (*ex. y.*). The central yolk (*c. y.*) is absolutely free of nuclei, while the endoderm (*en.*) can be traced to the edge of the blastopore (*po. b.p.*). The mesoblastic somites have no connection with the invagination, which gives rise to the endoderm.

Fig. 10 *g.*—This figure represents the twentieth segment behind the one shown in Fig. 10 *f.* It passes through the anterior end of the primitive groove. On the left side the rudiments of the seventh (*som.*[7]) and eighth (*som.*[8]) somites are shown; on the other side, owing to the obliquity of the section, the mesoderm band (*mesod.*) is represented. The external yolk spreads in a backward direction along the primitive groove and ventral surface.

Fig. 10 *h.*—This figure represents the fourth section behind the one shown in Fig. 10 *g.* It passes through the primitive groove (*pr. g.*) and the individual mesodermal bands at their thickest part (*mesod.*). The central yolk is still present and devoid of nuclei.

Fig. 10 *k.*—This figure represents the eighth section behind the one shown in Fig. 10 *h.* It passes through the endoderm (*en.*) just at the posterior limit of the central yolk.

PLATE 7.

Figs. 11 *a*—11 *d* (× 120).—These figures represent four transverse sections of the embryo shown in Fig. 3, in which rudiments of all the legs have appeared.

Fig. 11 *a.*—This figure represents the thirty-first section, from the anterior end, of a transverse series. It passes through the first somite (*som.*[1]), the inner wall of which has thickened considerably to form the rudiments of the muscles of the stomodæum (*stomod.*), the anteriorly directed loop of which appears in the section represented. The brain (*br.*) has thickened considerably.

Fig. 11 *b.*—This figure represents the twenty-sixth section behind the one shown in Fig. 11 *a.* It is slightly oblique, consequently it passes through the second somite (*som.*[2]) on the right, and the third (*som.*[3]) on the left. The rudiment of the jaw is shown on the right side, while the anterior edge of the rudiment of the oral papilla appears on the left side. It shows the central yolk divided into masses, each of which possesses a nucleus, a condition which should be compared with that shown in Figs. 10 *a*—10 *k*, in which the central yolk is devoid of nuclei. The endodermal layer is distinct in both cases.

Fig. 11 *c.*—This figure represents the twelfth section behind the one shown in Fig. 11 *b.* It passes through the third somite, that is the somite of the oral papillæ. Even at this early stage the somite in question has been divided into two parts, one of which is situated in the rudiment of the oral papilla; the other, with its cavity almost obliterated, lies in a dorso-lateral position.

Fig. 11 *d.*—This figure represents the twenty-eighth section behind the one shown in Fig. 11 *c.* It shows a somite being constricted through the development of the rudiment of the muscle on its latero-ventral aspect.

Figs. 12 *a*—12 *l* (× 120).—These figures represent a selected number of sections, from a transverse series, of an embryo of the same age as the one shown in Fig. 4. The rudiments of all the appendages, twenty-five in number, are present. The antennæ consist of several rings more than they do in the embryo shown in Fig. 3, sections of which are represented in Figs. 11 *a*—11 *d.*

Fig. 12 *a.*—This figure represents a section across the antennæ, near their base. The brain lobes are cut just in front of their union in the middle line. The most noticeable feature is the divided condition of the first somite (*som.*[1]). The two portions of the somite extend the whole length of the antennæ.

Fig. 12 *b.*—This figure represents a section across the base of the antennæ and through the brain lobes. It cuts the anterior wall of the forwardly directed loop of the stomodæum, and shows the two subdivisions of the first somite.

Fig. 12 *c.*—This figure represents a section across the stomodæal region. It shows the cavity of the first somite divided into two parts (*som.*[1]).

Fig. 12 *d.*—This figure represents a section across the stomodæal region. It shows the first somite divided into two parts, a dorsal and a lateral. The lateral portion opens into the exterior by means of a canal, the external opening of which is situated internally to the rudiment of the lip and in front of the rudiment of the jaw, the former being much enlarged in this region. The Figs. 12 *a*—12 *d* show the brain (*br.*) as an enormous thickening of the ectoderm.

Fig. 12 *e.*—This figure represents a slightly oblique section across the region of the rudiments which develop in the adult into the rings which surround the mouth. The left half of the figure is anterior to the right. It passes also through the canal which puts the first somite in communication with the exterior. The endoderm (*en.*) appears as a ring round the stomodæum, which is developed by an invagination of the ectoderm and which is surrounded by a mesodermal sheath derived from the inner walls of the first pair of somites.

Fig. 12 *f.*—This figure represents a section from the region of the rudiment of the jaws. The section shows the rudimentary mouth-folds (*lip*) as thin ectodermal outgrowths situated above the developing appendages. The second somite (*som.*^{2}) is divided into median and appendicular portions. The appendicular portion grows downwards into the rudiment of the jaws, but is becoming obliterated through the proliferation of its ventral wall to form the muscles of the jaws. The central yolk is devoid of nuclei.

Fig. 12 *g*.—This figure represents a section from the region of the oral papillæ. The section shows the third somite divided into median and appendicular portions. On the left side the appendicular portion grows towards the ventral aspect, and is situated on the outer side of the rudiment of the nerve-cord. On the same side, at the tip of the oral papillæ, is represented the rudiment of the slime-gland.

Fig. 12 *h*.—This figure represents a section from the region of the ninth somite, which is divided into median and appendicular portions. The appendicular portion on the right side grows towards the ventral surface, but it does not yet open to the exterior.

Fig. 12 *j*.—This figure represents a section from the region of the eleventh somite, which is undivided on the left side.

Fig. 12 *k*.—This figure represents a section from the region of the penultimate somite, which is provided with an immense cavity. The section shows the inner end of the proctodæum cut across.

PLATE 8.

Fig. 13 (× 170).—This figure represents a transverse section, passing through the fourth somite (*som.*$^{n-3}$) from the posterior end of the embryo shown in Fig. 3. The last two pairs of somites in the embryo in question are still solid. Note especially the germinal nuclei (*ge. n.*) situated in the splanchnic walls of the somites. The left somite in the figure has been cut through the middle, and shows a group of germinal nuclei which have as yet scarcely assumed the structural and staining characters of the nuclei in question. On the right side of the figure the section does not pass through the middle of the somite, but slightly in front of it, and at the dorsal corner it actually cuts through the wall of the somite situated in front. The outline of the endoderm, which possesses irregularly shaped nuclei, is quite sharp and distinct from that of the mesodermal somite.

Fig. 14 (× 170).—This figure represents a transverse section, passing through the fourth somite from the posterior end (*som.*$^{n-3}$), of an embryo slightly younger than the one shown in Fig. 4. The last two pairs of somites in the embryo in question have not yet developed a cœlomic cavity. Note especially the germ nuclei situated in the splanchnic walls of the somites, and also note that, as regards size and structure, they represent all stages transformation, from the ordinary mesodermal nuclei to that of fairly advance germinal nuclei. The somite shown on the right side of the figure exhibits a rudimentary myotome, and consequently a developing outgrowth, which later on becomes separated off as the appendicular portion of the somite.

FIGS. 15 *a* and 15 *b* (× 170).—These figures represent transverse sections of an embryo about the same age as that shown in Fig. 5. The generative portions of the somites situated on either side have almost come together on the dorsal aspect of the mid-gut. The splanchnic walls, which, owing to a slight change of position, have become ventral, have considerably thickened, and the germinal nuclei are gradually becoming excluded from the cœlomic cavity, that is the ovarian cavity.

Fig. 15 *a*.—This figure shows a section passing through the fourth somite from the posterior end (*som.*$^{n-3}$).

Fig. 15 *b*.—This figure shows a section passing through the fifth somite from the posterior end (*som.*$^{n-4}$).

FIGS. 16 *a*, 16 *b*, and 16 *c* (× 170).—These figures represent transverse sections of an embryo slightly older than that shown in Fig. 5.

Fig. 16 *a*.—This figure shows a section passing through the third pair of somites from the posterior end (*som.*$^{n-2}$), that is the somite of the genital ducts. The somites in question, which are devoid of germinal nuclei, have not yet entered into communication on the dorsal aspect, nor have they at their outer ends fused with the ectoderm of the ventral surface. Note the large blood-spaces situated on either side and ventral to the proctodæum.

Fig. 16 *b*.—This figure shows a section passing through the fourth pair of somites from the posterior end (*som.* $^{n-3}$). Note the germinal ridges (*ge. r.*) placed in the ventral wall of the ovary, and the double ovarian cavity situated above the ridges. The whole structure is fused to—if it does not form a part of—the ventral wall of the pericardium (*p.c.*).

Fig. 16 *c*.—This figure shows a section passing through the fifth pair of somites from the posterior end (*som.*$^{n-4}$). It presents the same characters as the somite shown in the previous figure, except that the germinal ridges are much more strongly developed.

FIGS. 17 *a*, 17 *b*, and 17 *c* (× 170).—These figures represent sections of an embryo which is considerably older than the one sections of which are illustrated in Figs. 16 *a*, *b*, and *c*.

Fig. 17 *a*.—This figure shows a section passing through the third pair of somites from the posterior end (*som.*$^{n-2}$). The somites have fused on the dorsal aspect to form a kind of median chamber, the walls of which are devoid of germinal nuclei.

Fig. 17 *b*.—This figure shows a section passing through the fourth pair of somites from the posterior end (*som.*$^{n-3}$). It illustrates the germinal ridges (*ge. r.*) situated on the ventral wall of the ovary, and separated from the dorsal wall by the slit-like ovarian cavity (*ov. c.*), and the developing ova surrounded by follicle cells derived from the ventral wall of the ovary, and hanging freely in the hæmocœle.

Fig. 17 *c.*—This figure shows a portion of the oviduct in the section succeeding that illustrated in Fig. 17 *a*. Note the rudiment of the receptaculum ovorum (*rec. o.*) developed as a simple outgrowth from the wall of the oviduct.

Figs. 18 *a*, 18 *b*, 18 *c*, and 18 *d* (× 170).—These figures represent four stages in the growth of the ovarian ovum.

Fig. 18 *a.*—This figure shows an ovum in which the cytoplasm possesses a beautifully alveolar structure. The nucleus, placed near the centre and circular in outline, is provided with a nucleolus which is alveolar in character.

Fig. 18 *b.*—This figure shows an ovum very similar in structure to the one shown in the previous figure, but of greater dimensions in all its parts.

Fig. 18 *c.*—This figure shows an ovum in which the cytoplasm is occupied by a large number of globules which are almost uniform in size, and are situated in the alveoli shown in Figs. 18 *a* and 18 *b*.

Fig. 18 *d.*—This figure shows a transverse section of an almost fully grown ovarian ovum. The globules shown in the foregoing figure have fused to form compound systems. The nucleus has wandered from the centre towards the periphery, and consequently has become irregular in outline. Note also the disposition of the yolk-bodies with regard to the nucleus.

Figs. 19 *a*, 19 *b*, and 19 *c* (× 170).—These figures represent sections of an embryo slightly older than that sections of which are illustrated in Figs. 16 *a*, *b*, and *c*.

Fig. 19 *a.*—This figure shows a transverse section through the third pair of somites from the posterior end (*som.*$^{n-2}$). The vasa deferentia open to the exterior by a short common duct, a condition which is permanent in the female (*vas. def.*).

Fig. 19 *b.*—This figure shows a cross-section of the left vas deferens near its inner end, and a section through the funnel of the right vas deferens.

Fig. 19 *c.*—This figure shows a section through the developing testes, showing the germinal nuclei filling the internal cavity, and surrounded by an epithelial layer. Both testes are fused to the ventral wall of the pericardium, and are situated close together, much in the same way as the developing ovaries are in Fig. 16 *c*.

Figs. 20 *a* and 20 *b* (× 170).—These figures represent sections of a male embryo of the same age as the one shown in Fig. 5.

Fig. 20 *a*.—This figure shows an oblique section which passes through the posterior end of the anal groove (*an. gr.*), and on the left cuts the rudiment of the last appendage along its whole length. Note the last somite (*m. a. g.*, *som.*^{n}).

Fig. 20 *b*.—This figure shows a section in a similar direction and parallel to the one illustrated in Fig. 20 *a*. Note the duct of the male accessory gland (*m. a. g.*) and the renal organ (*ren. or.*), derived from the last and penultimate somites respectively.

Figs. 21 *a* and 21 *b* (× 120).—These figures represent sections of a male embryo of the same age as the one illustrated in Fig. 6 on Plate 5.

Fig. 21 *a*.—This figure shows a section of the male accessory gland (*m. a. g.*) and of the last ventral organ (*ven. o.*), which is vestigial in character.

Fig. 21 *b*.—This figure shows a section of the last renal organ (*ren. or.*), the male accessory gland (*m. a. g.*), and the last fully developed ventral organ (*ven. o.*).

PLATE 9.

Figs. 22 *a*, 22 *b*, and 22 *c* (× 50).—These figures represent the thirty-second, the fifty-ninth, and the eighty-first sections respectively of a transverse series of the brain of an embryo which was slightly older than the one shown in Fig. 5, but younger than that illustrated in Fig. 6 on Plate 5.

Fig. 22 *a*.—This figure shows a section passing through the archicerebral (*a. lo.*) and the first (*lo.*^{1}) or antennal lobe of the brain, as well as the first pair of ventral organs (*v. o.*^{1}) near their posterior limit. On the right side the eye is shown; but on the left the section passes in front of that organ. On the ventral aspect the lips situated on either side of the mouth, with the tongue passing down between them, are represented.

Fig. 22 *b*.—This figure shows a section passing through the archicerebral (*a. lo.*) and the third (*lo.*^{3}) lobe of the brain; the second (*v. o.*^{2}) and the divided third (*v. o.*^{3a} and *v. o.*^{3b}) ventral organs. On the right side it passes along the anterior border of the para-œsophageal cord; on the left it passes in front of that cord.

Fig. 22 *c*.—This figure shows a section passing through the third (*lo.*^{3}) and fourth (*lo.*^{4}) lobes of the brain, as well as the fourth ventral organ (*v. o.*^{4}), which corresponds to the anterior pair of walking appendages. On the right side it passes behind the para-œsophageal cords; on the left the para-œsophageal cord is cut along its whole length. Note that on the left side the fourth lobe (*lo.*^{4}) of the brain, which lies on the dorsal half of the para-œsophageal cord, is pierced by the fibres of the mandibular nerve.

Figs. 23 *a* and 23 *b* (× 120).—These figures represent two oblique sections of the head of an embryo of the same age as the one sections of which are shown in Figs. 22 *a*, *b*, and *c*.

Fig. 23 *a*.—This figure shows a section passing dorsally near the median plane, and ventrally above the antenna and the eye. It shows the archicerebral lobe (*a. lo.*) above, and the three anterior brain lobes below ($lo.^1$, $lo.^2$, $lo.^3$). In another section, quite close to the one represented, the continuation of the second and third lobes towards the dorsal aspect, shown in the figure as one lobe, was distinctly divided into two. The fourth lobe of the brain does not appear in the section.

Fig. 23 *b*.—This figure shows a section passing through the head in such a way as to cut the first, second, and third lobes ($lo.^1$, $lo.^2$, $lo.^3$) of the brain on one side, and the fourth ($lo.^4$) on the other. It passes through the first ventral organ ($v.\ o.^1$) of the left side, the second one ($v.\ o.^2$) of the right side, and the anterior portion of the third ($v.\ o.^{3a}$), which is median in position and produced by the fusion of rudiments from either side.

Fig. 24 (× 50).—This figure represents an oblique section of the antero-dorsal aspect of the brain of an embryo of the same age as the two previous ones. It shows the small but distinct archicerebral lobe (*a. lo.*) situated on the left side of the median line; on the right side the section passes nearer to the ventral aspect, and consequently cuts the first or antennal lobe of the brain ($lo.^1$).

Figs. 25 *a*, 25 *b*, and 25 *c* (× 170).—These figures represent three stages in the development of the eye, which is derived from the ectodermal thickening which gives rise to the brain. During all the stages of development the two organs are connected to each other, the optic nerve being formed in situ.

Figs. 26 *a*, 26 *b*, 26 *c*, 26 *d*, and 26 *e*.—The first four of these figures are diagrammatic representations of four stages in the development of the receptaculum ovorum and receptaculum seminis; but the last shows the structure and arrangement of these organs in the adult. The figures were obtained from reconstructions made from series of sections, and have been modified so far as to show the receptaculum ovorum lying in the same plane as the receptaculum seminis, which seems never to be the case in nature.

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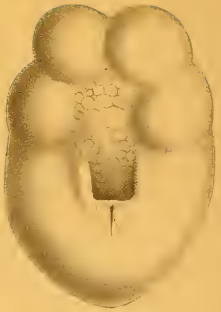

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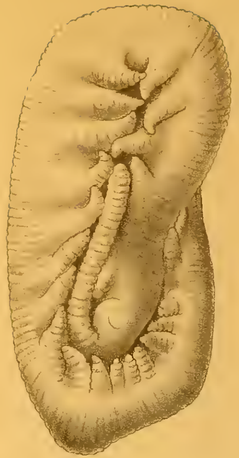

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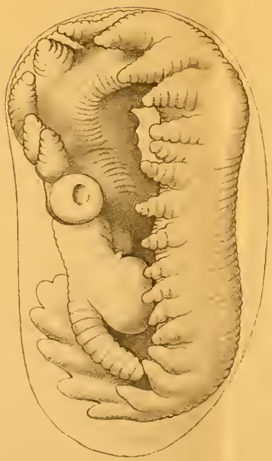

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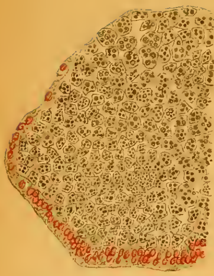

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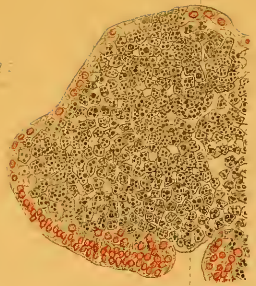
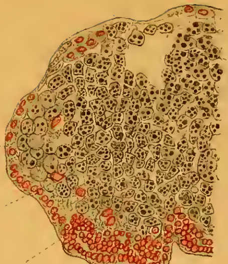


9b.

9c.



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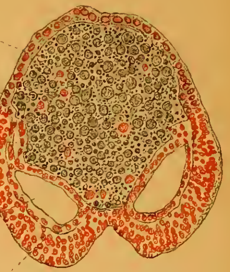

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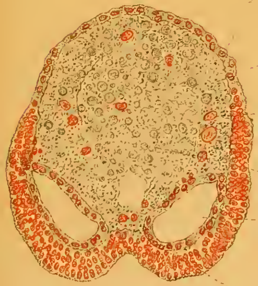

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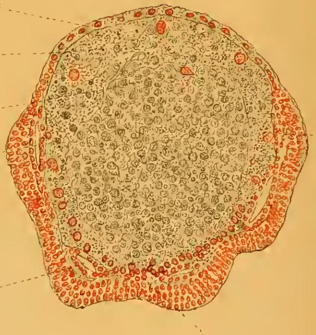

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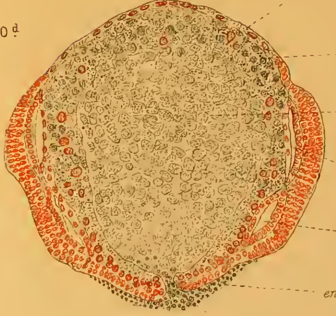

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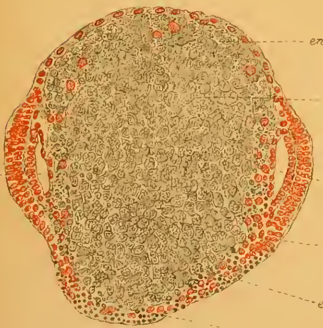

10e.

10f.

10g.

10h.

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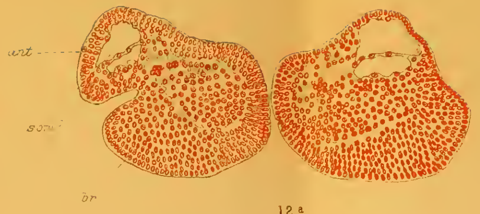
11^{a}.



12^{a}.

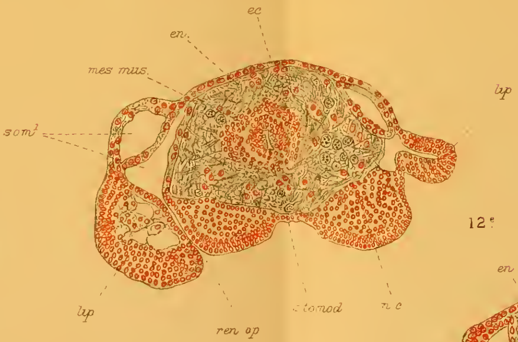
12^{b}.

11^{b}

12^{c}.

12^{d}.

11^{c}



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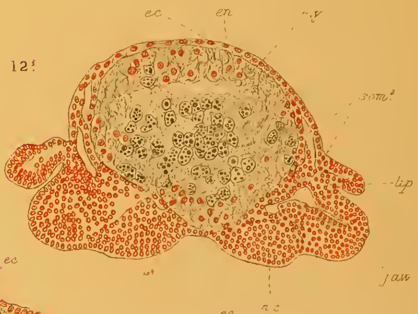

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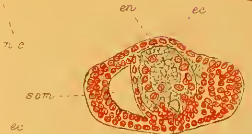

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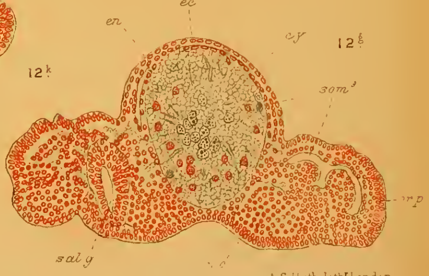

12^{g}

11^{d}

12^{j}.

12^{h}.

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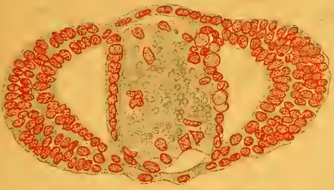

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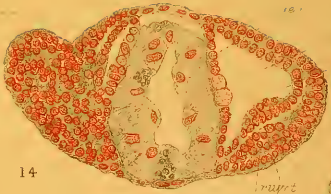

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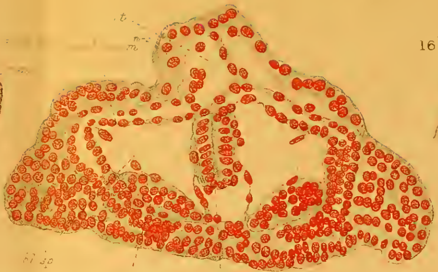

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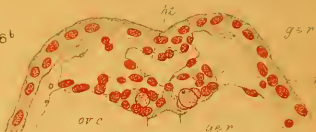

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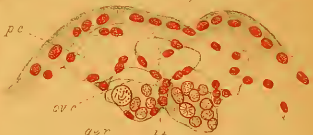

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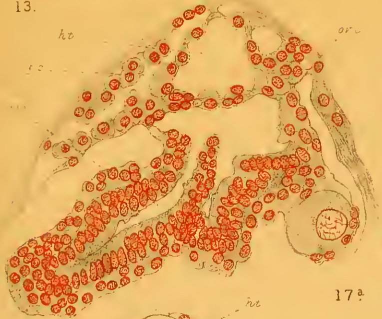

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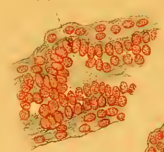

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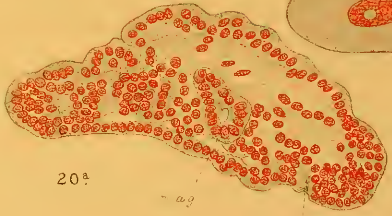

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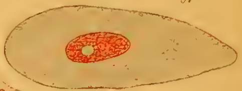

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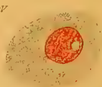

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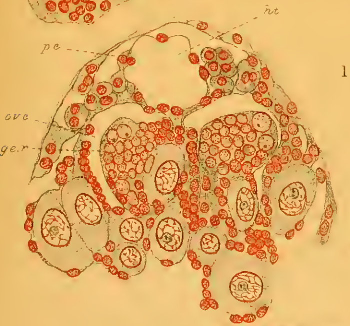

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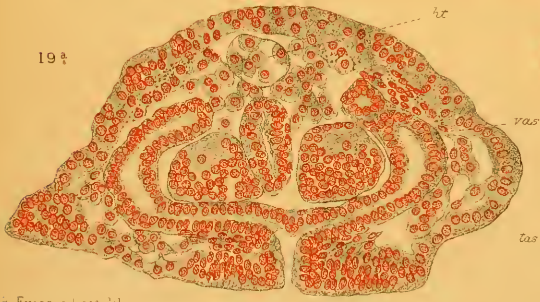

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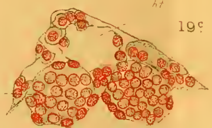

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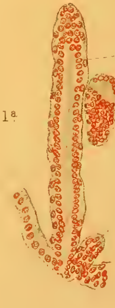

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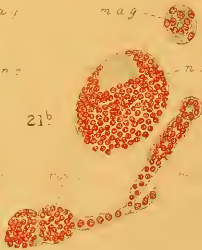

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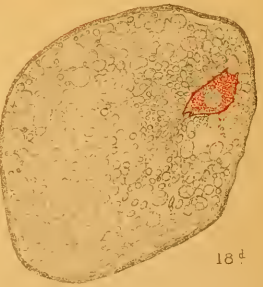

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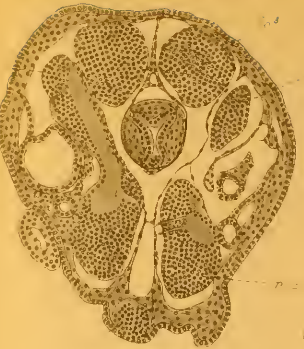

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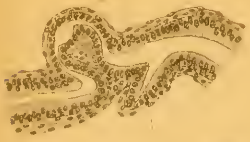

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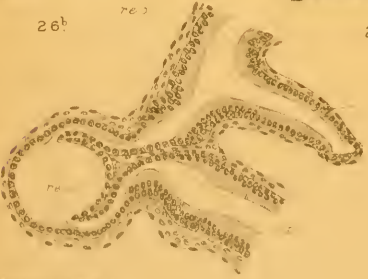

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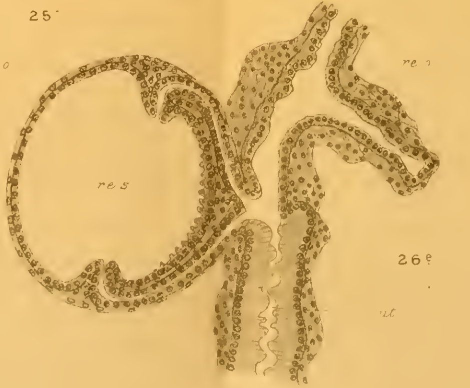

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EDITED BY

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CONTENTS OF No. 178.—New Series.

MEMOIRS:

The Lateral Sensory Canals, the Eye-Muscles, and the Peripheral Distribution of certain of the Cranial Nerves of Mustelus lævis.

By

Edward Phelps Allis, jun.

With Plates 10—12.

I HAVE recently had occasion to examine three series of sections of the head of embryos of Mustelus lævis, one of them being an embryo 12·2 cm. long. It was not my intention, when these sections were prepared, to make any extended study either of the lateral canals or of the cranial nerves of the fish; the investigation I had proposed relating entirely to the innervation of the sensory organs of the ampullæ. I have long had a very decided impression, opposed to that of most workers on the subject, that these ampullary organs must be genetically related to the terminal buds of ganoids and teleosts rather than to the pit organs of those fishes; and I thought that I should easily be able to get some positive evidence of this in the general course and position of the nerves that innervate them in advanced selachian embryos. This positive evidence I have wholly failed to get, for the very simple reason that, in the main nerve trunks, I could not distinguish in my sections the ampullary fibres from the lateral canal ones. Disappointed in this at the very beginning of the investigation, I nevertheless decided to quite carefully trace the lateral canals and the nerves that innervate them and the ampullæ, as far back as my sections went, that is, nearly to the level of the first gill slit. Careful consideration of these observations has fully convinced me, though indirectly, that the ampullary organs do represent the terminal buds of ganoids and teleosts, and not the pit organs. As, in this research, I was also led to trace the other cranial nerves of the region under consideration, and as my observations differ in certain respects from, and complete in others, the results of earlier writers on the subject, I have thought best to fully describe, not only the lateral canals of the head and the ampullary canals, but also the facial, trigeminal, and eye-muscle nerves, notwithstanding the fact that there will necessarily be, in these descriptions, a certain amount of repetition of well-known facts.

The embryos used for the investigation were kindly sent me by the Naples Zoological Station, and varied from 36 mm. to 12·2 cm. in length. As I have no one at present in my laboratory who could properly section these embryos for me, I appealed for help to Prof. G. B. Howes, of the Royal College of Science, London, and he most kindly undertook to have them sectioned, under his personal supervision, by his pupil, Mr. H. H. Swinnerton. Sections of 36 mm. and 55 mm. embryos were first prepared, but these embryos were found to be much too young for the purpose, and one of the largest ones I had—a 12·2 cm. one—was selected. This last size proved an excellent one for the purpose in view, and the following descriptions relate entirely to it unless otherwise stated. Two different specimens of this age were sectioned, one from the anterior end of the snout back nearly to the first gill slit, and the other from the hind edge of the eye back a certain distance beyond the spiracle. This second specimen was sectioned in the hope that I might in it determine the ultimate distribution of the dorsal branch of the glossopharyngeus, which I had been unable to follow in the first specimen. I unfortunately could not follow it in the second specimen either, the tissues being slightly broken at a place where the nerve apparently enters the lateral edge of the cranial extension of the trunk muscles, and the nerve there lost in the displaced muscle fibres.

All of the embryos sectioned were, at Prof. Howes' suggestion, double-stained in Ehrlich's hæmatoxylin and Grüble's orange, the combination which he and Mr. Swinnerton had found so successful in their recent work on Sphenodon (**38**). The two large embryos were cut, the first one 7 μ in thickness, and the other 10 μ in thickness. The first series contained something over 3000 sections.

After the full course of the lateral canals of the head had been first traced in the sections of the 55 mm. embryo, and then in those of the 12·2 cm. one, I had them traced by dissection in two or three others of my larger remaining embryos. This was at first undertaken simply as an aid and guide in the preparation of the simple outline drawings intended for illustration. Mr. Nomura, my assistant, undertook this work, and he soon found that he could, with some care and trouble, trace, not only the main lateral canals, but also the ampullary canals, which latter it had been wholly impracticable to trace in sections. The drawings made from these dissections accordingly show the general course of all the ampullary tubes, and the exact, or closely approximate, number and position of their surface openings. They do not show all the tubules of the lateral canals, and none of the numerous surface openings, or pores, of these canals are even indicated in the general drawings. It was found that these tubules and pores could not be accurately made out without much more work than the subject seemed to warrant. The drawings accordingly only show, accurately, those tubules that project to one side or the other of the canals, but few of the many tubules that run directly outward from the canals to the external surface being even indicated. Fig. 7 shows the exact number and position of the pores and tubules in a part of the suborbital canal where they are particularly numerous, and this, with the general drawings, will give a sufficiently good idea of their arrangement elsewhere.

The methods employed in these dissections were, to examine the undissected head by slanting lamplight, which brought out the pores; to scrape off first the delicate epidermal layer of the ectoderm, and then the entire ectoderm, thus first exposing the tubules and then the canals; and finally to "skin" a head in a single piece, and examine it in glycerine by transmitted light. Fig. 7 is made from such a preparation.

Lateral and Ampullary Sensory Systems.

The manner in which the lateral canals develop in selachians is evidently quite different, in certain respects, from that that pertains in ganoids and teleosts. What it is I cannot make out from my three series of sections, and I do not find in the works at my disposal any description of it that seems complete or satisfactory.

Balfour (**8**) leads one to suppose that there is in selachians simply an abbreviation of the process that gives origin to the canals in ganoids and teleosts. This abbreviation consists in that it is the inner row of cells (Schleimschicht) alone of the epiblast that is concerned in the involution that forms the canal, the epidermis remaining always as a flat and even layer above it. The canal, thus formed, then becomes detached from, and sinks beneath, the epiblast, remaining attached to it at certain points by cords of tissue which represent the primary tubes of the canal. Opposite the outer ends of these primary tubes the epidermis then becomes perforated, thus giving rise to the primary pores.

The ampullary tubules are said by Balfour to arise in exactly the same manner as the lateral canals.

Balfour says that the lateral canal of the body, developed as above set forth, first appears at the hind end of the lateral sensory line, and extends forward from there. Mitrophanow (**44**, pp. 208–9) confirms the latter part of this statement, but the involution of the canal as he describes it seems to involve the entire ectoderm, and not simply its deeper, inner layer. Moreover, it would seem from his figures as if the section of canal said to be thus first formed was nothing more nor less than what Clapp (**10**, p. 239) refers to as "a curious fold of the epidermis, the so-called 'pocket,' which covers the growing end of the line." Whether or not this "pocket" represents the first beginnings of the lateral canal, it is evident that a canal that thus first appeared at the hind end of the lateral sensory line must, appearing as it does before the line reaches the hind end of the body, be continually being pushed bodily backward, following and accompanying the growing end of the line. There is thus here such an important departure from what is found in Amia, that I should hesitate to accept the account as correct.

My own observations, limited to the four series of sections that I possess, tend to confirm Balfour's statement that the lateral canals are formed by an involution of the deeper layer only of the ectoderm. The covered gutter, rather than canal, that is thus first formed then becomes, by a pressing together of its walls, a sharp and apparently solid ridge projecting inward from the inner surface of the ectoderm. This is the condition found nearly everywhere in my 36 mm. embryo. Where the cord is deepest it receives a branch from the underlying and related lateral nerve, but there is as yet no perceptible indication in my sections of a definite sensory organ related to this nerve. Between each two consecutive points where these nerves thus join the cord the cord becomes less deep, and in the regions where it is the flattest there is a small pit-like depression on the outer surface. This depression looks in certain sections like a shallow groove, while in others it has vertical sides, and seems to cut clean through the outer layer of ectoderm down to that deeper layer that is alone directly related to the canal itself. This depression, or pit, quite certainly represents a future pore, the pore thus apparently appearing while the cord that represents the canal is still everywhere attached to the ectoderm.

In my 55 mm. specimen the lateral canals were mostly found as cords of tissue lying in the mesoderm, beneath the ectoderm, and connected with the latter at intervals by smaller cords, which represent the tubules of the adult. In the large main cords there was a small central lumen, either formed or in process of formation, and this lumen was always most fully developed opposite the points from which the cords representing the future tubules arose. In certain places it extended outward a short distance in these latter cords, but in no place did it reach the outer surface of the head. On this outer surface of the head there was, however, almost invariably, opposite the outer ends of the cords that represent the primary tubes, a slight slit-like depression, the appearance being that of a pre-existing opening that had been closed by the pressing together of its walls.

Even at this age, 55 mm., there was no perceptible indication, in my sections, of the sensory organs in the main canals, and the cords that represent the future tubules had already begun to branch, and formed in certain regions a somewhat complicated system. How these branching systems arise could not be traced in my material, but it would seem as if they must arise by the repeated dichotomous subdivision of a single primary cord, exactly as the branching tubules of Amia arise from a single primary tube (2).

The ampullæ in my 55 mm. embryo were nearly all represented by small teat-like processes that arose from the inner surface of the ectoderm, and projected into the underlying tissues. Some of these processes seemed solid, while others contained a small central lumen which sometimes led to the outer surface, the process then appearing as a sharp fold of the entire ectoderm. A small nerve was easily traced to the inner end of each process. While no attempt was made to trace the complete and definite distribution of these little processes, it was easily to be seen that in certain places they had exactly the relations to the lateral canals that the surface pores of the ampullary tubes have in the 12·2 cm. embryo. This seemed to me to indicate that it must be the pore in the adult, and not the ampulla, that indicates the place of origin of the structure. Here, then, from the primary distribution of these organs, as indicated by their surface pores, was perhaps a manner of determining whether they arose from pit-organs or from terminal buds.

To confirm my conclusion that the surface ampullary pore represents, approximately, the place of origin of the ampullary organ, I sought in my younger embryos for the lines of organs that should represent certain regular, constant, and well-marked lines of ampullary pores in my larger embryos. It will be sufficient to describe a single one of them.

In my 12·2 cm. embryo there is on each side of the dorsal surface of the head, and slightly anterior to the external opening of the endolymphatic duct, a regular curved line of ampullary pores. The tubes leading from these pores run forward to a sub-group of the superficial ophthalmic group of ampullæ, these ampullæ lying on the dorsal surface of the nasal capsule. In the 55 mm. embryo there was, in exactly the place occupied by these pores in the older embryo, a line of surface sense organs which greatly resemble, in certain respects, the pit-organs in larvæ of Amia, while in others they greatly differ from those organs. My material was not adapted to a histological study of them, but it may be said that the organs were represented by a series of processes arising from the inner surface of the ectoderm, each process enclosing a little space which may or may not be in direct communication with the exterior. The processes all turn anteriorly, parallel to the overlying ectoderm, and a small nerve enters each process at its deeper or anterior end. These short processes of this 55 mm. embryo thus unquestionably represent the complete ampullæ of the 12·2 cm. one. The long ampullary tube that is found in the latter embryo must then be formed by an exceedingly rapid growth of the short process of the younger one, that process being, so to speak, stretched out into a long tube between the fixed point represented by its surface opening and another relatively fixed one, represented by the point where the sensory nerve enters the process. The tube apparently offers less resistance to this stretching process than the nerve does.

Further evidence that the ampullary pore does not usually travel far away from its place of origin is found in the fact that certain lines of these pores are frequently found on the side of a lateral canal opposed to that on which the ampullæ themselves lie, the ampullary tubes passing internal and not external to the lateral canal. As the lateral canals in Mustelus are certainly already present as well-developed cords before the ampullary tubes are developed, it is evident that the latter tubes, in the cases above referred to, would have had to cut through the canal to attain their adult position, if the pore of the tube travelled from its place of origin in anything resembling the manner that the lateral pores of Amia do (2). An extreme case is shown in Garman's (21) figure of Raia, where long ampullary tubes open along the edge of the body lateral to the lateral canals, the tubes passing internal to the canals. The ampullæ related to these tubes and pores must certainly have had their place of origin in the immediate neighbourhood of these pores of the adult, and from there they must have travelled to their adult position by pushing, or being pulled, through the tissues internal to the canals.

The topographical position of a group of ampullæ in the adult selachian is thus not necessarily any indication whatever of the point of origin of the several ampullæ that form the group, the ampullary organs differing radically in this from the organs of the lateral canals. They also apparently differ from the latter organs in that they have a later and relatively much more rapid development. This is shown in the rapid development of the ampullary tubes just above referred to, between the ages represented by the 55 mm. and 12·2 cm. embryos. In my 36 mm. embryo I could not even find any positive indication of this line.

In Amia (2), and probably in all teleosts also (67), the sense organs of the lateral system lie at first below the outer surface of the ectoderm, along a cord of cells that is differentiated in the deeper layer or layers of the ectoderm. Immediately superficial to the central point of each organ there is a large and specialised cell, which later becomes a vacuole. As the sense organ pushes through the overlying cells to its final exposed relation to the outer surface, this vacuole must, at a certain stage, become a small pit-like depression leading to the outer surface of the head. At and immediately before this stage this organ would strongly resemble in general appearance the ampullary pits in the temporal region of my 55 mm. Mustelus. It would also present somewhat the appearance of the pit-like depressions that I have assumed to represent the future pores of the canal lines in 36 mm. embryos of Mustelus, but my material was not suited to the determination of the homologies here involved. All that I could make out was that the canal organs seem never, in Mustelus, to become exposed on the outer surface of the head, as they do in Amia. On the contrary, they seem to always remain in the deeper layer of the ectoderm, where they arise, and then to split off from that layer, enclosed in, and as part of, a long and nearly solid cord, which later becomes a canal. The ampullary organs, in somewhat marked distinction to the canal organs, may become exposed at the bottom of a little pit apparently formed by the bursting, so to speak, of the little vacuole that forms above the central portion of the organ. The general form and appearance of the several organs in my embryos thus give no definite indication as to whether the ampullæ are developed from pit-organs or not. They, however, seem to indicate a difference between ampullary and lateral canal organs.

No organs in any way resembling the terminal buds of ganoids and teleosts were anywhere observed on the outer surface of any of my specimens, but in the large number of sections examined, and especially as I was not particularly looking for these organs at the time, it is certainly possible that there may have been some, and that they escaped my notice. There were, however, in the 12·2 cm. embryo certain other sensory organs found both on the outer surface of the head and on the body. They closely resemble the organs that in my 55 mm. embryo represent certain of the superficial ophthalmic group of ampullæ, but differ from those organs in that their central lumen in every case leads directly to the outer surface by a pit-like depression. The distribution of these organs will be given in describing the ampullæ.

Infra-orbital Canal.

The general course and position of all the lateral canals of the adult Mustelus has been well given by Garman (**21**). That author makes use of a special nomenclature which I shall adopt only when wishing to designate the various sections of the several canals, elsewhere making use of the nomenclature now ordinarily employed by other authors. The term infra-orbital canal will be used to designate that part of the so-called main infra-orbital canal of my earlier works that is innervated by the buccalis and oticus facialis. In Mustelus the section so innervated extends from the anterior end of the canal back to the supratemporal cross-commissure. The point at which this commissure arises from the main line in different fishes is, as will be later explained, apparently not a fixed one.

The infra-orbital canal of Mustelus, in my 12·2 cm. embryo, and also in the adult, begins near the lateral edge of the anterior end of the ventral surface of the snout, and there communicates directly with the supra-orbital canal. From this point the canal first runs mesially a very short distance, and then turns backward in a short curve. It then continues backward and somewhat mesially, and reaches the middle line of the head somewhat in front of the transverse level of the nasal aperture, curving gradually mesially shortly before reaching this point. There it anastomoses completely with its fellow of the opposite side, the two canals united turning sharply backward in the median line. At about the transverse level of the middle of the nasal aperture the two anastomosed canals separate, each canal turning sharply laterally, and then curving slightly forward until it reaches the very edge of the nasal aperture. There it turns backward and slightly laterally at a sharp angle, and, curving gradually more and more laterally, passes posterior to the nasal aperture toward the lateral edge of the snout. Before reaching that edge, and not far from it, it makes a double bend. It first turns laterally and slightly forward, and connects with the distal end of the supra-orbital canal, this bend being short and being apparent in sections, but not in dissections. It then turns sharply backward, in the line of, and apparently as a direct continuation of, the supra-orbital canal, and continues a short distance almost directly backward, parallel to the lateral edge of this part of the head. It then turns laterally and forward in a short rounded angle, the hyomandibular canal arising at this bend almost as a direct continuation backward of the infra-orbital canal anterior to the bend. Running laterally and forward a short distance the infra-orbital canal reaches the lateral edge of the head, where it turns upward and forward on to the lateral surface of the head, and, continuing in this same direction, soon reaches a point approximately ventral to the anterior edge of the eye. There it curves gradually backward in a short bend, and then runs backward below the eye and upward behind it, between it and the spiracular opening, thus encircling about one half the orbit. Dorsal to the spiracular opening the canal turns upward and forward, and, approximately dorsal to the hind edge of the eye, anastomoses with the hind end of the supra-orbital canal. It then turns sharply backward, upward, and mesially, and so continues to the point where it joins the lateral end of the supratemporal commissure. There the canal turns almost directly backward, and continues backward as the lateral line of the body.

Along this infra-orbital section of the main lateral canal, that is, from its anterior end to the point where the supratemporal cross-commissure is given off, there were, in my embryo, 180 tubules of varying size and length, all leading directly and independently from the canal, and opening on the external surface by one or more surface pores. Along this same length of canal there were 110 sense organs, all innervated by branches of the buccalis and oticus facialis. The tubules in certain parts of the canal lay regularly one between each two successive sense organs, this being markedly the arrangement in the anterior portion of the line, that is, in the anterior portion of that part of the line that is called by Garman the prenasal. Following this anterior portion, and extending to the hind end of the short median section, there were groups of two or three tubules between each two successive organs. Posterior to this median section the tubules were less regularly arranged in reference to the organs, and often had no apparent regular relation whatever to them. The tubules vary greatly in length in different parts of the line, being particularly long along the orbito-nasal section of Garman's descriptions, and immediately ventral and dorsal to the spiracle. Opposite the spiracle they are aborted or wholly wanting. Along the orbito-nasal section of canal the tubules branch repeatedly, and open on the outer surface by numerous pores, as shown in fig. 7. The long tubules ventral and dorsal to the spiracle, on the contrary, branch but little, each branch usually having but a single pore at its outer end.

The first or most distal organ of the infra-orbital canal lies near its anterior end, the canal there connecting with the supra-orbital canal between organs 34 and 35 of that line. The 24th organ of the line lies at the point where the canals of opposite sides meet and anastomose in the middle line. Beyond organ 29 the two canals separate again. There are thus 23 organs anterior to the median section of the canal, and 6 organs in that section. These 6 organs lie on the dorsal or latero-dorsal wall of the canal, always lateral to the median line, and opposite, or nearly opposite, an organ belonging to the line of the opposite side of the head. Between each successive pair of these organs there was a single tubule on each side, that is, a pair of tubules, excepting only between organs 26 and 27. The point between these two latter organs is, morphologically, the middle point of the median section of the canal, and there were here two tubules on each side and a single median tubule. This was the only median tubule found in the entire lateral system, but there was, perhaps, such a tubule at the middle point of the supratemporal cross-commissure—a point that could not be definitely determined, the sections there being slightly broken.

From the hind end of the median section of the canal to the point where the canal joins the anterior end of the supra-orbital canal there are 16 sense organs, the two canals anastomosing immediately beyond organ 45 infra-orbital. The organs along the entire line up to this point, that is, organs 1 to 45, are all innervated by branches of a single large branch of the buccalis facialis, but organs 1 to 25 form a sub-group somewhat separate, in their manner of innervation, from organs 26 to 45.

Posterior to the point where the canal anastomoses with the distal end of the supra-orbital canal, and back to the point where the hyomandibular canal is given off, there are nine sense organs, 46 to 54, and their innervation by two separate branches of the buccalis indicates that they form a separate sub-group, or two such groups, of infra-orbital organs. This section of canal and the one that contains organs 30 to 45, together form the nasal canal of Garman's descriptions, that section of canal thus not being a morphological unit. Organs 55 to 69 lie in the two arms of the suborbital bend of the canal, that is, in that part of the canal that lies between the point where the hyomandibular canal is given off, and a point near the anterior end of the ventral edge of the eye. This section of canal thus includes the orbito-nasal of Garman and a part of his sub-orbital, not corresponding exactly to any of his sections. These organs, in their innervation, form a distinct sub-group of the infra-orbital line, as do also organs 70 to 74, organs 75 to 78, organs 79 to 82, and organs 83 to 86, all of which lie in the sub-orbital part of the canal. These 41 organs together, that is, organs 46 to 86 inclusive, form what may be called a large sub-orbital group, in which there are six well-marked sub-groups.

Posterior to organ 86 the remaining organs of the line, back to the point where the supratemporal cross-commissure is given off, are all innervated by three branches that arise close together from a posterior prolongation of the ganglion of the nervus buccalis. This posterior prolongation of the buccalis ganglion lies close against the side wall of the orbital part of the skull, and extends backward a short distance behind the hind edge of the trigemino-facial foramen. The three nerves that arise from it run upward and backward along the side wall of the skull, which here belongs to the interorbital wall, and come into such intimate relations with each other that it is impossible to determine whether there is or is not an interchange of fibres between them. One of the three nerves that again appear after this intimate juxtaposition separates into two branches, both of which pierce the overhanging cartilaginous roof of the orbit, near its hind end, and reach its dorsal surface,the roof of the orbit here being formed by a projecting part of the postorbital process. One of these two branches there innervates organs 103 to 110 infra-orbital, those organs lying in that section of canal that is called by Garman the occipital, and that is included between the points where the supra-orbital canal and the supratemporal cross-commissure anastomose with the main infra-orbital canal. The other branch innervates organs 97 to 102 infra-orbital, which organs are postorbital, or, more properly, as will be later shown, postfrontal in position. A second one of the three principal nerves innervates organs 92 to 96, which are postorbital in position; the third nerve innervating organs 87 to 91, which are also post-orbital in position, organ 87 lying between the third and fourth tubules ventral to the spiracle. Several of the branches of the second nerve pierce the overhanging cartilaginous roof of the hind end of the orbit to reach the organs they innervate. The branches of these two latter nerves all pass outward immediately anterior to the dorsal end of the superior postspiracular ligament, which will be later described, and also immediately anterior to the levator maxillæ superioris muscle.

Organs 87 to 110 infra-orbital thus form a single large group, sub-divided into four sub-groups. Along the canal, between organs 89 to 96, there were no tubules leading to the outer surface. There were, however, four short tubules leading outward from the canal between certain of the organs and ending blindly, these tubules thus being in process of abortion. This plainly indicates that other tubules, related to the other organs, have here wholly aborted. This partial or complete abortion of these seven tubules is most unquestionably due to the near presence of the spiracular canal, though why, for this reason only, they should have become aborted instead of being retained as short tubules opening along the anterior edge of the spiracle, is not evident.

Wright (**70**) describes in the so-called anterior diverticulum of the spiracular cleft of Mustelus what he considers, under some reserve, as a sense organ belonging to the category of lateral sensory organs, but said to be of hypoblastic instead of epiblastic origin. It is said by him to be innervated by fibres derived from the pretrematic branch of the facialis. My observations lead me to believe that the organ here referred to is innervated, on the contrary, by a branch of that one of the three branches above described that innervates organs 87 to 91 infra-orbital. As the observations on which this conclusion is based require some explanation, it will be discussed in a later section after the spiracular cleft and certain related structures have first been described. The fact that the innervation of this spiracular organ shows that it is quite intimately related to, if it does not actually belong to, the infra-orbital line should, however, be mentioned here.

Supratemporal Cross-commissure and Lateral Canal of the Body.

The supratemporal cross-commissure arises, on either side, from the hind end of the otic section of the main infra-orbital canal, and curving slightly forward crosses the middle line of the head, then curves backward, and joins the infra-orbital canal of the opposite side. The commissure passes immediately posterior to the pores of the endolymphatic ducts, those pores lying relatively close together near the middle line of the top of the head. This position of these pores seems a singular one, if each endolymphatic duct represents the persistent, primary communication of the ear capsule with the exterior, and if the ear capsule itself represents a section of the main infra-orbital sensory line that has been cut out between the facialis and glossopharyngeal sections of that line, and enclosed exactly as the short separate sections of the lateral canals are. The position of the pore, and its long tube, would seem to be much more easily explained on the assumption that the ear, if it be developed from an organ of the main infra-orbital lateral line, had been developed after the manner of the ampullæ rather than after the manner of the lateral canals.

There were, in the half of the supratemporal commissure, in the specimen examined in sections, eleven sense organs and twelve primary tubules. Whether these tubules were all arranged one between each two successive organs could not be definitely determined, but such was probably the case. The mesial tubule was not median in position, and there was no sense organ apparent between it and the mesial tubule of the opposite side. In the dissected specimen from which the drawings were made there were but eight tubules in the one half of the entire commissure, the mesial one not being median in position. The tubules all run directly backward from the commissure.

The organs of the commissure are all innervated by branches of a large nerve that arises from the nervus lineæ lateralis while that nerve is still traversing the canal by which it issues, with the nervus vagus, from the cranial cavity. This supratemporal branch of the nervus lineæ lateralis runs upward from the nervus, through a special canal in the cartilage of the skull, and issues on the dorsal surface of the skull posterior to the commissure and internal to the cranial extension of the trunk muscles. There it turns forward, and passing internal to and beyond the commissure reaches the anterior edge of the trunk muscles. There it turns backward superficial to those muscles, and breaking up into several branches innervates the organs of the commissure. The nerve is thus pushed forward, out of a direct course, by the trunk muscles, as they push forward upon the skull.

Posterior to the commissure the lateral canal of the body begins, but the innervation of its sensory organs could not be determined in either of my series of sections, the nerves that innervate them traversing the superficial layers of the adjacent muscles, and being lost owing to slight breaks in the sections. A certain number of the most anterior organs seemed to be innervated by a dorsal branch of the glossopharyngeus. This branch was an important one, and branches from the lateral canal organs ran toward the point where it was broken, and lost, as it passes upward over the dorsolateral corner of the skull. Another nerve, which arises as a branch of the supratemporal branch of the nervus lineæ lateralis, close to its base, is also broken and lost in the muscle-fibres here, and it might be it and not the dorsal branch of the glossopharyngeus that innervates the anterior organs of the lateral canal.

If certain of the anterior organs of the lateral canal are innervated by the dorsal branch of the glossopharyngeus, as seems probable, it is to be noted that they certainly lie posterior to the supratemporal commissure. In Amia the glossopharyngeal organs lie anterior to the commissure, and Ewart assumes (18) that organs so innervated are probably found in a similar position in most elasmobranchs. As Ewart definitely finds, in Læmargus, a section of the main infra-orbital canal that lies immediately anterior to the commissure innervated by branches of the nervus lineæ lateralis, it is evident that the commissure of Læmargus and that of Mustelus do not arise from similar points of the main line. If the commissure can thus, in principle, shift forward and backward in its point of origin from the main canal, it is evident that it must be used with some reserve in seeking to establish the homologies of the related bones in the skulls of teleosts and ganoids.

Supra-orbital Canal.

The supra-orbital canal begins near the lateral edge of the ventral surface of the head, postero-lateral to the nasal aperture, and slightly anterior to the transverse plane of the anterior edge of the mouth cavity. At this morphologically anterior, or distal, end of the canal it is in direct communication with the infra-orbital canal in the region opposite organs 45 to 50 of that line. As the infra-orbital organs including and anterior to organ 45 form a group separate and distinct, in their innervation, from the organs including and following organ 46, it is probable that the anastomosis of the two canals takes place between organs 45 and 46.

Starting from this point the supra-orbital canal runs forward and mesially in a gentle curve, parallel to the lateral edge of the head, and, near the most anterior point of its course, meets and anastomoses with the anterior end of the infra-orbital canal, the two canals meeting, at approximately a right angle, between organs 34 and 35 supra-orbital.

Anterior to this point the supra-orbital canal runs forward, or forward and laterally, for a very short distance, and reaches the edge of the snout, where it turns upward and reaches the lateral surface of the head. There it at first runs upward, backward, and laterally, in a nearly straight line, until it reaches a point somewhat anterior to the anterior edge of the eye. There it turns forward mesially and upward in a short curve, continues in that direction for a short distance, and then turns upward and backward in a second short curve, beyond which it runs backward, dorso-mesial to the eye, in a line approximately parallel to the mid-dorsal line of the head. Dorso-mesial to the hind edge of the eye it anastomoses by its hind end with the infra-orbital canal between organs 102 and 103 of that line, that is, between the otic and postfrontal groups of infra-orbital organs.

The canal at its distal end lies ventro-lateral to the hind end of the cartilaginous nasal capsule, about midway between it and the ectoderm, and the transverse sections that here cut the region where the canal anastomoses with the infra-orbital canal cut also the hind end of the nasal epithelium. The canal at this point lies considerably lateral to the free, ventro-lateral edge of the cartilage of the nasal capsule, but as it runs forward from here it approaches this free edge of the cartilage, and opposite the hind edge of the external nasal aperture lies but slightly lateral to it.

Opposite the nasal aperture the canal passes mesial to the vertical plane of the free ventro-lateral edge of the cartilage of the capsule, and there lies in a depression on the lateral portion of the internal, or dorsal, surface of what I take to be the anterior process of Gegenbaur's (23, p. 99) descriptions of the "nasenflügel" cartilage of the fish. In my specimen this nasal-flap cartilage was wholly separate from and independent of the cartilage of the nasal capsule. It, however, closely approached anteriorly the ventral edge of the mesial wall of the capsule, and posteriorly similarly approached the ventral edge of a part of the lateral wall. The anterior process of the cartilage is strongly curved in transverse section, the back of the curve being presented dorso-laterally, and the cartilage being so placed that its lateral edge, which is directed ventro-laterally, lies ventral to, or even ventro-lateral to the ventral edge of the lateral wall of the capsule. Near this lateral edge of the nasal-flap cartilage there is, on its dorsal surface, a slight longitudinal ridge. The portion lateral to this ridge is slightly concave, is presented dorso-laterally, and lodges the supra-orbital canal as it passes along the region of the cartilage. The canal thus here has a definite relation to the nasal-flap cartilage.

Anterior to the nasal-flap cartilage the canal lies, for a time, ventro-lateral to the rounded, bulging, lateral surface of the anterior end of the cartilage of the nasal capsule. Continuing its course beyond the capsule it there has no relation to any underlying skeletal structure, until it reaches the point where it turns upward on to the dorsal surface of the head. There it lies latero-ventral to the anterior, united ends of the dorso-lateral and ventro-mesial rostral cartilaginous bars of the skull.

At this point the canal turns backward, and here lies lateral to the dorso-lateral rostral bar of cartilage, lying, however, at such a considerable distance from it that the bar would seem to have no direct supporting relation to the canal. The canal, moreover, here lies latero-superficial to the bar, and not directly superficial to it.

When the canal, in its backward course, now reaches the transverse plane of the anterior end of the nasal capsule, it approaches the roof (morphologically floor) of the capsule, and here sinks to such an extent below the external surface of the head that, when it curves forward, in front of the eye, the dorsal arm of the bend lies at first directly dorsal to the ventral one, at a normal distance from the surface. After the canal has again turned backward it soon comes to lie directly superficial to the rounded dorso-lateral surface of the neighbouring part of the skull, and continuing backward passes on to the dorsal surface of the projecting cartilaginous roof of the orbit.

There were in all, in the entire length of the supra-orbital canal, 93 sense organs. The number of tubules leading from the canal was much larger, many of them having undergone subdivision. In certain parts of the line they were, however, still found, one tubule between each two successive organs. Directly on the top of the snout, about midway between the anterior end of the snout and the point where the canal takes its double bend in front of the eye, there was a large and complicated group of tubules. These tubules all issued from the canal on its mesial side, and ran mesially or mesially and backward. At a varying but short distance from their bases they were all connected by short communicating branches, these branches together having somewhat the appearance of a single curved connecting canal. Beyond these communicating branches certain of the tubules branched dichotomously in the plane of the ectoderm. In the plane perpendicular to the ectoderm there were numerous short tubules leading to the outer surface, and there opening by pores. The whole group of tubules formed a large semicircular structure on the mesial edge of the canal. Both anterior and posterior to it, along the entire length of the canal, on both the dorsal and ventral surfaces of the head, there were, excepting at the bend in front of the eye, no tubules projecting mesially from the canal. All the other tubules projected either laterally or directly outward toward the external surface. This restriction of the tubules to the lateral and dorsal aspects of the canal would seem, from Garman's figures, to be a marked characteristic of the canals of the head in the rays, though what its special significance is is not evident.

The 93 sensory organs found in the supra-orbital canal of my embryo were all innervated by branches of the ramus ophthalmicus superficialis, and were subdivided, by the manner of their innervation, into six groups. The first group includes organs 1 to 16, organ 16 lying approximately in the plane of the anterior end of the nasal sac. The second group includes organs 17 to 34, organ 34 lying immediately posterior to the point where the canal anastomoses with the anterior end of the infra-orbital canal. The third group includes organs 35 to 58, organ 58 lying near the point where the canal turns upward in front of the eye. The fourth group includes organs 59 to 64, all of which lie in the bend of the canal as it turns upward in front of the eye. The organs of this group are related to those of the third group more as a sub-group than as a separate and distinct one. The next, or fifth group, includes organs 65 to 86, organ 86 lying in the plane of the foramen of the superficial ophthalmic nerve. The sixth and last group includes organs 87 to 93, the organs of this group all lying posterior to the superficial ophthalmic foramen, and being innervated by a single nerve which leaves the ramus ophthalmicus superficialis shortly after it leaves its foramen, and runs backwards to the organs of the group.

Hyomandibular Canal.

The hyomandibular canal, using the name adopted by Ewart (18) in his descriptions of Læmargus, begins at the point where the infra-orbital canal bends laterally and forward, just before it passes from the ventral to the lateral surface of the head. It is there in direct communication with the infra-orbital canal between organs 54 and 55, that is, between the second and third groups of the organs of the line. From there the canal runs almost directly backward, lying close to and parallel to the lateral edge of the ventral surface of the head. Posteriorly it gradually approaches that edge, and at a certain distance beyond the transverse plane of the spiracle reaches it, and there turns upward and backward around it, and appears on the lateral surface of the head. Continuing in this upward and backward direction a relatively short distance, it reaches a point something more than half the distance backward from the spiracle to the first gill-slit, and there ends.

The exact number of organs in the canal could not be determined, the organs and related nerves in the posterior part of the canal being so slightly developed that they could not be recognised with certainty. The primary tubes, most of which had undergone subdivision, would seem to indicate that there were about forty organs in the canal. The organs are quite unquestionably all innervated by branches of a hyomandibular part or division of the mandibularis externus facialis, but this could be definitely established for the first twenty-four organs only, counting backward from the anastomosis with the infra-orbital canal. The remaining organs and their innervating nerves could not be traced.

Mandibular Canal.

The mandibular canal is relatively short, lies parallel to the hind edge of the mouth, and extends from near the middle line of the head backward and laterally to the level of the outer edge of the upper labial fold. It lies, in the greater part of its course, directly superficial to the mandibular part of the adductor mandibulæ muscle, near, and nearly parallel to, its anterior edge. At its mesial end the canal extends beyond the adductor muscle, and there lies superficial to the cartilage of the mandible. The canal has very closely the length and direction of the anterior edge of the mandibular part of the adductor muscle. The canal does not approach any of the other canals, either anteriorly or posteriorly, and the canals of opposite sides are separated at their anterior ends by a considerable interval.

The number of organs contained in the canal could not be determined, neither the organs nor the nerves innervating them being sufficiently developed to be traced with certainty. There were twenty-two tubules along the line, counting the anterior and posterior terminal ones. As most of these tubules seemed to be primary ones that had not undergone subdivision, there should be about twenty-one organs in the line.

The organs are all innervated by branches of an anterior or mandibular division of the mandibularis externus facialis, a large branch of the nerve innervating also the mandibular group of ampullæ.

Ampullæ and Surface Sensory Organs.

There are in Mustelus four groups of ampullæ on each side of the head. These four groups correspond in general position to the superficial ophthalmic, inner buccal, outer buccal, and mandibular groups of Ewart's (18) descriptions of selachians, but the group that has the position of an inner buccal group is innervated by branches of the ramus ophthalmicus superficialis, instead of by branches of the buccalis facialis, as will be fully described in describing the nerves. The group in Mustelus is accordingly not the homologue of the inner buccal group of Ewart's descriptions, and I shall describe it as the deep ophthalmic group. No group corresponding to Ewart's hyoid group was found, but it may, perhaps, be represented by a line of surface organs.

The superficial ophthalmic group is a long one, lying in the upper part of the snout, and not far from the middle line of the head. The ampullæ of the group all lie mesial to the dorso-lateral rostral bar of cartilage, the posterior ones lying directly superficial to the nasal capsule. The ampullæ are grouped by their tubules in three somewhat separate sub-groups. The tubules leading from the anterior sub-group are relatively short, and radiate forward, laterally and postero-laterally, their external openings all lying on the top of the snout, the anterior ones mesial to the anterior portion of the rostral part of the supra-orbital lateral canal, and the posterior ones lying mesial to the large rostral group of supra-orbital tubules and pores. In the specimen from which the drawings were made there were forty-three ampullæ in this sub-group on one side of the head, and forty-nine on the other, the number of ampullæ being determined by the number of related surface pores, which alone were counted.

The tubules leading from the second sub-group of superficial ophthalmic ampullæ are long, and run at first almost directly laterally, forming a broad band, which lies at first immediately posterior to the rostral group of tubules and pores of the supra-orbital canal. The ampullary tubules then turn backward and laterally, and pass superficially across the supra-orbital canal immediately anterior to the point where that canal bends backward in front of the eye. The ampullary tubules here lie internal to the short mesio-anteriorly directed section of the supra-orbital canal, and internal to the tubules that arise from that section of canal, the appearance being that of a band of ampullary tubules that had here first pressed the supra-orbital canal inward out of its normal relations to the external surface of the head, and then pulled it out of a straight course and given it the antorbital bend which seems otherwise not easily accounted for. The external openings of these ampullary tubules form a group of pores the anterior ones of which lie mesial or directly superficial to the supra-orbital canal, while the posterior ones lie lateral to that canal, extending nearly to the anterior edge of the eye, certain of the tubules here lying superficial to the tubules of a sub-group of the outer buccal ampullæ. There were twenty-five pores in this group on one side of the head, and twenty-one on the other.

The relations of the tubules of this sub-group of ampullæ to the supra-orbital lateral canal is exactly that that would necessarily arise in every place where the ampulla and its pore lie on opposite sides of a lateral canal if the ampullary tubules were formed by the pores travelling from the place where the ampullary organ was first enclosed by involution, after the manner of development of the canals and tubes of the lateral system in Amia (2). I accordingly turned to the sections of my 55 mm. embryo to see if I could determine whether these particular ampullæ lay postero-lateral or antero-mesial to the supra-orbital canal, and I found, as I had expected, a number of the teat-like processes that here represent the ampullæ in exactly the position that the pores of the group in question occupy in the older embryo. These teat-like processes were directed anteriorly, as they should be, and in my opinion unquestionably represent the ampullæ of the older embryo, though this can certainly not be positively asserted until they have been followed through certain of the intermediate stages. Why these particular ampullæ should have pushed forward external instead of internal to the lateral canal is not evident.

The tubules of the posterior sub-group of superficial ophthalmic ampullæ are, in part, still longer than those in the second sub-group. They all at first run postero-laterally from their ampullæ, the longer ones gradually turning directly backward. Most of them have their external openings in a line slightly mesial to that part of the supra-orbital canal that lies directly dorso-mesial to the eye, but some of them lie scattered between that line and the mid-dorsal line of the head, and six of them form a curved line which lies slightly anterior to the supratemporal cross-commissure, and slightly anterior also to the transverse plane of the external openings of the endolymphatic ducts. These last six pores formed, in all my specimens, one of the most distinctly evident lines of pores on the entire head of the fish, and this line would seem to occupy the position ascribed by Garman (21) to the supratemporal commissure of Chlamydoselachus—a position, however, also held by two surface sense organs to be later described. There were twenty-six pores in this sub-group on one side of the head of the specimen used for the drawings, and twenty-nine on the other.

All of the ampullæ of the entire group of superficial ophthalmic ampullæ are innervated by branches of the ramus ophthalmicus superficialis, in a manner that will be related in describing that nerve.

The deep ophthalmic group of ampullæ lies about half way between the nasal aperture and the anterior end of the head, there lying in the region included between the prenasal section of the infra-orbital lateral canal, and the rostral and subrostral sections of the supra-orbital canal. In transverse sections that pass through the posterior portion of this group of ampullæ, they are seen to form a curved line, extending from the internal surface of the prenasal section of the infra-orbital canal dorsally, and laterally toward the rostral section of the supra-orbital canal. This curved line lies slightly ventro-lateral to a line connecting the ventro-mesial and dorso-lateral rostral bars of cartilage, the most lateral ampullæ lying lateral to the dorso-lateral bar. Anteriorly the ampullæ form, in sections, an irregular group that lies in nearly these same relations to the lateral canals and rostral bars. Posteriorly the anterior end of the nasal capsule presses into the group, and separates it, in sections, into two parts, one part lying ventro-mesial to the nasal capsule, and the other lying on its dorsal surface. Most of the tubules of the group radiate downward from the ampullæ, running in every direction toward the ventral surface of the snout; but some of them first extend downward and laterally, then turn upward and backward as they approach the lateral edge of the snout, and thus reach its dorso-lateral surface. These latter tubules form a sub-group somewhat distinct from the others.

Those pores of this group that lie on the ventral surface of the snout all lie anterior or mesial to the nasal aperture, and there is a line of them on each side of the subrostral section of the supra-orbital canal, and on each side of the prenasal section of the infra-orbital canal, certain of the tubules here crossing the lines of each of the two lateral canals, internal to them, to reach their opposite sides. The pores that are thus arranged in line on either side of the two canals are, in certain places, placed markedly one between each two successive primary tubules of the related canal, canal tubules and ampullary pores thus alternating. Certain of the ampullary tubules extend backward into the tissues that cover the cartilages that lie in the ventral wall of the nasal sac, and in sections, but not in the dissections, certain of them even had their openings in the very edge of the nasal aperture. The tubules that reach the dorso-lateral surface of the snout turn backward, and the related pores form a band that extends backward to the anterior edge of that part of the infra-orbital canal that bends forward below the eye. There were in this entire group of ampullæ, on the one side of the head on which they were counted, 194 pores. The ampullæ are all innervated by branches of the ramus ophthalmicus superficialis, as will be fully described in describing that nerve.

The buccal group of ampullæ lies ventral to the anterior edge of the eye, in the region internal to that section of the infra-orbital canal that lies between the suborbital bend in the canal and the point where the hyomandibular canal is given off. The tubules of the group may be separated into five sub-groups. The tubules of one of these five groups run at first forward and upward, then curve gradually forward mesially and downward, and have their external openings on the dorso-lateral surface of the snout, lateral to the rostral part of the supra-orbital lateral canal, between that canal and the pores of that sub-group of the deep ophthalmic ampullæ that form a band along the lateral edge of the dorsal surface of the snout. There were forty-three pores in the sub-group.

The tubules of a second sub-group run upward, forward, and mesially along the anterior edge of the eye, and there spread, some continuing their earlier course, while others turn backward above the eye. The pores of the sub-group all lie between the antero-dorsal edge of the eye and that part of the supra-orbital canal that lies posterior to the point where the canal bends forward in front of the eye. There were thirty-seven pores in the group.

The tubules of a third sub-group all open on the ventral surface of the head, the tubules running in large part mesially, but in part almost directly forward, and in part almost directly backward. The few tubules that run directly forward have their external openings along either side of the extreme distal end of the supra-orbital canal, that is, along both sides of the posterior end of what Garman calls the sub-rostral canal. Those tubules that run posteriorly open in a group of pores that lie mesial to the anterior end of the hyomandibular canal. Those tubules that run mesially spread, and their external openings form a scattered group of pores the larger part of which lie between the nasal section of the infra-orbital canal and the front edge of the mouth, a smaller part lying between the same section of canal and the nasal aperture. Certain of these pores form a line along each edge of the nasal section of the infra-orbital canal, while certain others form a marked line along the very edge of the upper lip. There were 107 pores in this sub-group.

The tubules of a fourth sub-group run backward and, excepting a few scattered ones, form a wide band of tubules which extends backward ventral to the suborbital part of the infra-orbital canal, occupying the entire lateral surface of the head ventral to that canal. The external openings of the few scattered tubules, and those also of certain of the longer ones, lie on the lateral surface of the head posterior to that section of the infra-orbital canal that lies between the suborbital bend in the canal and the point where the hyomandibular canal is given off, the pores being most numerous near the canal, and diminishing irregularly in number from there backward. The long tubules run at first directly backward, all having a nearly parallel course, the longest ones extending beyond the level of the hind edge of the eye, and there, toward their hind ends, turning upward and backward. Their external openings form a regular, curved, and well-marked line which extends from the hind edge of the infra-orbital canal, immediately below the spiracle, at first backward and but slightly downward, then, having nearly reached the level of the hind end of the hyomandibular canal, turns downward and slightly forward, anterior to the hind end of the latter canal, and ends near the ventro-lateral edge of the head. There were forty-six pores in the sub-group.

The tubules of the fifth sub-group form a continuation, on the ventral surface of the head, of the broad band formed by the fourth sub-group. Their external openings form a long curved line, which begins on a level with, and considerably lateral to, the hind edge of the gape of the mouth, and from there runs backward and laterally, on the ventral surface of the head, in a line lying mesial to and somewhat parallel to the hyomandibular canal. There were twenty-seven pores in the sub-group.

The sensory organs of the entire group are all innervated by two branches of the buccalis facialis in a manner that will be fully described in describing that nerve. The innervation of these ampullæ by two branches of the buccalis may perhaps indicate that they represent the united inner and outer buccal groups of Ewart's descriptions of other selachians.

The mandibular group of ampullæ is a small one lying slightly posterior to the lateral third of the mouth opening, between it and the mandibular canal. In my 12·2 cm. specimen these ampullæ were still in an undeveloped condition. They had already sunk beneath the ectoderm and were united in a close group, but none of them had as yet acquired the pocketed form characteristic of the ampullæ in all the other groups. The tubules of the group radiate from the ampullæ, all running forward, forward and mesially, and backward and laterally, in the general direction of the hind edge of the mouth opening. The organs of the ampullæ are all innervated by a single short branch of the ramus mandibularis externus facialis.

The so-called pit organs, or sensory follicles, of other descriptions of Mustelus I did not seriously attempt to fully or carefully trace. Certain of them that are very evident are shown in the drawings, and I doubt there being many others. A very distinct line of them extends in a curved line, as shown in fig. 3, across the entire ventral surface of the head somewhat posterior to the mouth. At each lateral end this line turns upward on to the lateral surface of the head, passes posterior to all the ampullary pores of the region, and posterior also to the hind end of the hyomandibular lateral canal; it then turns forward dorsal to and approximately parallel to the ampullary pores of the region, and reaches the hind edge of the spiracle, where it ends. Its innervation I could not determine, nor could I satisfy myself as to whether the line was a line of sensory pit organs, or simply a line of undeveloped ampullæ similar to those found in my younger embryos. If the organs represent undeveloped ampullæ, it would seem as if they, or at least a part of them, must represent the hyoid group of ampullæ of other fishes, that group not otherwise being represented in Mustelus. If, on the contrary, the organs are pit organs, of a lateral sensory type, the ventral part of this line of organs recalls markedly in its position the gular line of pit organs of Amia, and may represent that line. In Chlamydoselachus the entire line would seem quite certainly represented in the combined gular and spiracular lines of Garman's (**21**) descriptions, these lines being said by him to be open grooves. If they are so represented it would seem almost certain that the angular canal of Chlamydoselachus, which is clearly the hyomandibular canal of Mustelus, must be the horizontal cheek line of pit organs of Amia, and that the other lines on the cheek of Chlamydoselachus, that is, the spiracular, gular, jugal, and oral, represent the preoperculo-mandibular canal and the vertical cheek line, mandibular line, and gular line of pit organs of Amia. The accord is much too evident not to warrant the supposition. The organs of the line of Mustelus may, accordingly, represent a condition of surface sense organs on the border line between terminal buds and ampullary organs on the one side, and pit organs and canal organs on the other.

Four other pit organs were always found in all my larger specimens, two on each side of the top of the head, slightly anterior to, and on either side of, the endolymphatic pore. These organs, on each side, lie in the line produced of the five lateral ones of the curved supratemporal line of six ampullary pores, and they may, perhaps, represent two ampullæ of that line that have retained their embryonic place and condition. The fact that the mesial one of the six ampullary pores does not lie in this same line seems, however, to indicate that we have here to do with a different class or group of organs, and that the two pit organs more probably represent one of the head lines of pit organs of Amia. In Chlamydoselachus, according to Garman, the supratemporal cross-commissure of the lateral canals has the position relative to the endolymphatic pores of these four surface organs, and not that of the cross-commissure of Mustelus and other selachians. This would be easily accounted for on the assumption that the two organs in Mustelus are lateral sensory ones, and became, in Chlamydoselachus, enclosed in a canal.

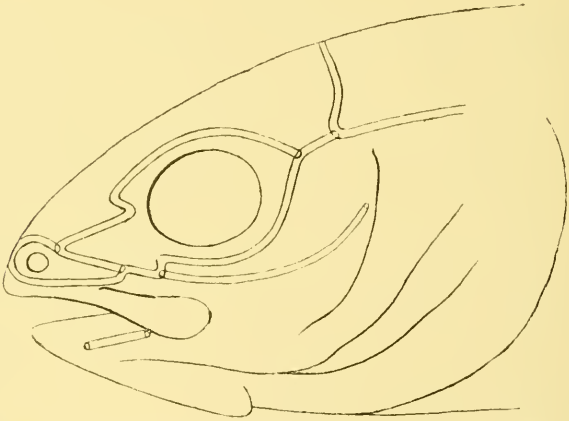
Other pit organs are found in Mustelus, irregularly arranged on the body of the fish posterior to the supratemporal commissure and dorsal to the main lateral line. One line of these organs lies directly superficial to the lateral canal, a position that seems to preclude its being in any way directly related to the organs of that canal. Certain of the organs undoubtedly form the line of "pit organs" that Ewart (**18**, p. 81) describes in Mustelus, and which he says are innervated by a branch of the nervus lineæ lateralis vagi.

Review and Comparison.

The lateral sensory canals of selachians seem, at first sight, to have a distribution that admits of but little detailed comparison with the canals of the bony fishes. This difference in detail is, however, largely in appearance only, and not real.

Imagine the snout of Mustelus pressed backward into and on to the dorso-anterior surface of the head, and the mouth pulled forward until it comes to lie at the anterior end of the snout. What is actually a part of the ventral surface of the snout would then become a part of its dorsal surface, and an arrangement of the lateral canals would arise such as is shown in lateral view in the adjoining cut. This cut represents, in fact, the projection, so to speak, of the canals of Mustelus on to the head of Amia. A front view of such a head would be quite accurately represented in Garman's front view of Mustelus canis (**21**, pl. viii).

Fig. 1.



Side view of an assumed projection of the lateral canals of Mustelus on to the head of Amia.

In this imaginary head the infra-orbital canal begins on the top of the snout, posterior to the single nasal aperture, and is there in direct communication with the supra-orbital canal, at a bend in that canal. It then runs forward and mesially, and, anastomosing with the corresponding canal of the opposite side, forms a median longitudinal section of canal which lies directly between the nasal apertures on the dorsal surface of the anterior end of the snout. The canal then turns laterally and backward, ventral to and around the nasal aperture, and, posterior to the aperture, anastomoses with the distal end of the supra-orbital canal. It then makes a double turn, first upward and then backward, giving off the hyomandibular canal at the first bend, and, having encircled the inferior and posterior edges of the eye, reaches and anastomoses with the hind end of the supra-orbital canal dorso-posterior to the eye. It then turns backward, and reaches and anastomoses with the lateral end of the supratemporal cross-commissure. Posterior to this point it becomes the lateral canal of the body.

The supra-orbital canal begins between the eye and the nasal aperture, there being in direct communication with the infra-orbital canal, at a bend in that canal and at a point that lies between two distinct groups of the organs of the line. The canal first runs forward and mesially on the top of the snout, but, dorso-postero-mesial to the nasal aperture, turns sharply backward, anastomosing at or near this bend with the anterior end of the infra-orbital canal. It then continues backward dorsal to the eye, until it reaches and anastomoses with the infra-orbital canal between its otic and postfrontal sections.

If the canals of this imaginary or projected head of Mustelus be compared with the canals of Amia, it will be seen that that section of the infra-orbital canal of Mustelus that contains the first group of organs of that line, Nos. 1 to 45, and that lies between the two anastomoses of the infra-orbital canal with the supra-orbital one, corresponds, in many respects, with that part of the infra-orbital canal of Amia that encloses the first four infra-orbital organs of that fish (**2**, p. 514). Those four infra-orbital organs form, in Amia, a distinct and separate group, and lie in a part of the canal that I considered as an anterior section or commissure of the line. In Amia there are two nasal apertures on each side of the head. Between these two apertures the backwardly-directed distal end of the supra-orbital canal is directed toward and approaches somewhat the hind end of the so-called anterior, commissural section of the infra-orbital canal. If two separate nasal apertures had been developed in Mustelus, and the posterior one had travelled backward toward the anterior edge of the eye, it would necessarily, since the nose develops earlier than the lateral canals, have passed backward between the growing distal end of the supra-orbital canal and the point where that canal is later to anastomose with the infra-orbital canal. This would thus have here given closely the arrangement found in Amia. It would also probably closely give the arrangement found in Polypterus (**6**), but I have not yet worked out the details of the innervation in that fish. In Batrachus tau a very similar arrangement is also found (**10**), but in this latter fish the anterior organ of the supra-orbital line is not enclosed in, nor does it lie in the line of, the antero-laterally directed distal end of the supra-orbital canal.

In the projection of the canals of Mustelus the anterior end of the infra-orbital canal anastomoses with the supra-orbital canal at or near the point where that canal bends sharply backward, postero-mesial to the nasal aperture. It then joins and anastomoses with its fellow of the opposite side, and here forms a short, median, longitudinal section, which lies on the antero-dorsal surface of the snout, between the nasal apertures of opposite sides of the head. In both Amia and Polypterus the arrangement is here quite different, and there are also differences in the arrangements presented by these two fishes. They can, however, all be easily derived one from the other, and in Conger conger I have lately found exactly the arrangement here shown in the projection of Mustelus. There is thus certainly a full homology in this part of the lateral system of these several fishes. The same is also true of the canals in Scomber and Gadus, but still other differences here exist. In Scomber, that part of the infra-orbital line that corresponds to the anterior, commissural section here in question, has become fused (**4**) with the anterior end of the supra-orbital canal, and forms a direct anterior prolongation of that canal. In Gadus (**12**) the same section of canal forms a short and direct anterior prolongation of the infra-orbital canal, containing, as in Scomber, but a single sensory organ. In both Scomber and Gadus the single nasal aperture of the one, and the two apertures close together of the other, lie relatively close to the eye, posterior to the anterior ends of both the supra-orbital and antorbital canals, and there is no indication of the loop, wholly or partly encircling the nostrils, that is found in Mustelus, Amia, Polypterus, and Batrachus.

In other teleosts and ganoids the descriptions of this part of the lateral canals are either not clear or not sufficiently detailed or complete to warrant an attempt to establish their homologies. This applies even to Herrick's (**32**) careful work on Menidia, in which I am unable to trace the relations of the several surface sensory organs he describes in this region, either to each other or to the lateral canals, or even to decide whether they are lateral sensory pit organs, or terminal buds.

In Læmargus (**18**) the only points in which the canals here differ from those of Mustelus are that the anterior end of the infra-orbital canal does not anastomose with the supra-orbital, and that the distal, turned-back end of the supra-orbital canal anastomoses with the infra-orbital canal at a point that seems to lie morphologically posterior to the one where the anastomosis takes place in Mustelus.

In Raia (**19**) the two anterior sections of Ewart's descriptions of the infra-orbital canal, sections 10^8 and 10^7, each form, at their anterior end, a transverse anastomosis with the corresponding canal of the opposite side of the head. Between these two anastomoses the canals of opposite sides lie parallel to each other, and not far apart. These canals thus differ from the arrangement found in Læmargus in that there is an anterior anastomosis, indicated but not found in Læmargus, and that in this last fish the posterior, internasal anastomosis is formed by the juxtaposition and fusion of longitudinal sections of the canals of opposite sides, as in Mustelus, and not by the fusion, end to end, of transverse sections of canals. Another difference between the two fishes is, that, in Læmargus, the anastomosis of the distal end of the supra-orbital canal with the infra-orbital canal, lies at a point on this latter canal, that is, morphologically, anterior to the one at which the hyomandibular canal is given off, while in Raia it lies morphologically posterior to that point. Mustelus here agrees with Læmargus.

In Chimæra (**11**) the anterior, antorbital section of the infra-orbital canal is probably the one that is innervated by the anterior division of the outer buccal nerve of Cole's descriptions.

In Mustelus, posterior to the anterior section of the infra-orbital canal above discussed, there are three principal groups of infra-orbital organs, each of which is separated into two or more, more or less distinct sub-groups. One of these three principal groups is suborbital in position, and includes organs 46 to 78. The other two together are postorbital and otic in position, and include organs 79 to 110.

Organs 46 to 78, which form the first of these three groups, are innervated by the first three branches that arise from the buccalis beyond its ganglion. They arise consecutively from the nerve, beginning at some little distance beyond its ganglion, and the third and more anterior branch is so large that it may be called a division of the nerve rather than a branch of it. The two posterior branches innervate, the one organs 70 to 74, and the other organs 75 to 78. The anterior branch, or division, of the nerve breaks up into several smaller branches and one large one, the smaller branches being destined to supply organs 46 to 69, and the large one to supply the buccal group of ampullæ.

Organs 79 to 86 form the second one of the three groups, and they are innervated by branches of two nerves that arise separately and independently, but close together, from the ganglion of the buccalis, close to the base of the nerve itself. The most anterior branch innervates organs 79 to 82; the other innervating organs 83 to 86.

Organs 87 to 110 form the third group, and they are separated, by their innervation, into four sub-groups, two of which are postorbital in position, while the other two occupy positions corresponding, in their topographical relations, the one to the postfrontal part of the infra-orbital canal of Amia, and the other to the otic and glossopharyngeal parts together, of the main infra-orbital canal of the same fish. The postorbital organs of Mustelus include organs 87 to 96; the postfrontal ones, organs 97 to 102; and the otic ones organs 103 to 110. The organs of the entire group are innervated by three nerves that arise close together from a posterior prolongation of the buccalis ganglion, and that have already been described. That branch of one of these three nerves that innervates organs 103 to 110 is certainly the homologue of the nerve described by me in Amia as the ramus oticus facialis. What the exact homologues are, in Amia, of the other nerves of Mustelus that are here concerned is not easy to tell. The nerve that, in Mustelus, innervates organs 97 to 102 would seem to be the exact homologue of the nerve that, in Amia, innervates the single postfrontal organ, No. 14 inf., of that fish. The nerve that innervates this latter organ in Amia always arises close to the base of the ramus oticus, if not from the base itself of that nerve, and in one specimen of Amia I found it arising as a branch of the oticus after that nerve had issued from its cranial canal on to the roof of the skull (**2**, p. 515). But it is a branch of the oticus, in Amia, that innervates the spiracular organ, while, in Mustelus, it is a branch of the nerve that innervates organs 87 to 91. It may then be that the three nerves of Mustelus that together innervate organs 87 to 110 and the spiracular organ are the homologue of the otic nerve of Amia plus that branch of the buccalis that innervates the postfrontal organ No. 14 infra-orbital. In that case the two nerves of Mustelus that innervate organs 79 to 86 would be the homologues of the nerves that in Amia innervate organs 11 to 13. It seems to me, however, much more probable that these latter nerves in Amia have their homologues, in Mustelus, in the nerves that innervate organs 87 to 96, the nerve that innervates the spiracular organ in the two fishes not having exactly the same course and possibly not being exactly the same nerve. However this may be, it is evident that either organs 87 to 110, or organs 79 to 110, must represent organs 11 to 16 of Amia, and that the nerves that together innervate the organs in the two fishes must be homologous. These several organs in Mustelus, Nos. 87 to 110, or 79 to 110, as the case may be, and organs 11 to 16 in Amia, thus form, in each fish, a group of organs that is quite distinct and separate, in its innervation, from the remaining more anterior infra-orbital organs. In Amia these organs also develop somewhat separately and independently from the rest of the line (**2**). As this same grouping of these organs is found in Scomber also (**7**), it would seem as if it might be considered as a general rule that there are, posterior to the anterior, antorbital group of organs, two separate and distinct groups of buccal organs in the main infra-orbital line. The anterior one of these two groups, plus the antorbital group of organs, must then correspond to the organs innervated by the outer buccal nerve of Cole's descriptions of Chimæra, and the other group to the organs innervated by his inner buccal nerve. They must also correspond to the two groups innervated by the inner and outer buccal nerves of Cole's descriptions of Gadus (**12**), and to those innervated by the buccalis and oticus facialis of Herrick's (**32**) descriptions of Menidia. But, in Cole's application of these names, inner and outer buccal, to the nerves in Gadus, adopted by Herrick (**33**) in his descriptions of the same fish, it is the outer buccal that innervates the posterior group of organs, and the inner one that innervates the anterior one, the reverse of the conditions described by Cole in Chimæra. That this is due to an error in homologising the nerves in

Gadus with those in Chimæra is evident, and, if perpetuated, it might easily lead to some confusion.

It is, moreover, to be remarked that organs 7 and 8 in Gadus, although innervated by terminal branches of the nerve that innervates organs 9 and 10, are separated from those organs by a considerable interval, and that in this, and also in their general position, they seem to belong more to the anterior group of organs than to the posterior one.

In Batrachus tau Clapp (**10**) shows a line of surface organs lying along the ventral and posterior margins of the eye, the line being continued backward by two similar surface organs that lie in the otic region. This line, or group, of surface organs is unquestionably the homologue of the organs innervated by the so-called inner buccal and otic nerves together of Chimæra, that is, to the postorbital, postfrontal, and otic organs of Amia. The so-called maxillary line of organs in Batrachus would then be the homologue of the suborbital organs of Amia, that is, of organs 5 to 10; and the antorbital line of surface organs in Batrachus would be the homologue of the antorbital commissure of Amia. It is evident that if the anterior ends of the postorbital and maxillary (suborbital) sensory lines of Batrachus were to be continued forward until they met the supra-orbital line, an arrangement almost exactly resembling that found in Chimæra would arise.

Regarding the hyomandibular line of selachians it is impossible to judge whether this line is simply the pre-opercular line of Amia, changed slightly in position at its anterior end, or a line formed by some combination of the pre-opercular canal line and the horizontal cheek pit line of Amia. Amia, in which there is such an abrupt and marked difference of level between the anterior end of the pre-opercular canal and the hind end of the mandibular one, might be considered as representing a stage intermediate between the arrangements found in Gadus or Polypterus (**6**), and the one found in Mustelus, the hyomandibular line in the latter fish being, in that case, the exact homologue of the pre-opercular canal line of Amia.

One feature of this hyomandibular canal of selachians is worthy of notice, though just what its morphological significance may be I cannot tell. The so-called proximal end of the canal, that is, the end at which it anastomoses with the infra-orbital canal, leaves, or joins, that canal anterior to the spiracle, while the nerve that innervates it descends posterior to the spiracular canal. This relation of the canal to the spiracle is much more marked in Polyodon (**13**, figs. 3 and 12), in which fish the branches destined to innervate the organs in the dorsal part of the canal, if there be any, must, to reach the organs, curve forward and upward around the ventral surface of the spiracular cleft. This relation is a singular one, and seems to call for some special explanation, which may, perhaps, be found in the assumption that a part of the line is represented in the horizontal cheek line of pit organs of Amia. In Polypterus (**6**) the dorsal end of the pre-opercular canal lies at the hind end of the spiracle, in what would seem to be its natural relation to that opening.

In Chlamydoselachus (**21**) there is a very close general agreement of nearly all the canal lines with the lines in the projection of Mustelus. The so-called occipital canal of Garman's descriptions of the former fish is the otic canal of my descriptions of the latter. The aural of the former fish is probably represented in Mustelus, as already stated, by the two supratemporal pit organs. The orbital, suborbital, and orbito-nasal canals of Chlamydoselachus are the postorbital and suborbital parts of the infra-orbital canal of Mustelus. The nasal and prenasal of Chlamydoselachus, including between them the region of the non-existent median, are the antorbital section of the infra-orbital of Mustelus. The subrostral, rostral, and cranial of Chlamydoselachus are the supra-orbital of Mustelus. The angular of Chlamydoselachus is the hyomandibular of Mustelus, and the jugal, oral, spiracular, and gular of Chlamydoselachus are, together, represented in Mustelus by the mandibular canal and the long cheek line of surface organs.

From the lateral lines of Chlamydoselachus, thus represented in part by canals and in part by open grooves, Garman derives the canals of the Batoidei.

We thus probably have, on the head of selachians, all the lateral canal and pit lines of Amia excepting the middle and posterior head lines of pit organs of my descriptions of the latter fish, and no others. Both the supra-orbital and the facialis part of the main infra-orbital canal lines of such selachians as Mustelus come to a legitimate termination at both ends by what seems to be an end anastomosis with another canal. One should not, accordingly, expect to find a line of unenclosed canal organs, such as certain of the pit organs of Amia and teleosts certainly are, continuing the line of the canal at either end. There should accordingly be, in Mustelus, no pit organs on the top of the snout, and probably, though not certainly, no anterior head line of pit organs. The middle and posterior dorsal head lines of Amia then alone remain to be accounted for of all the pit lines of the head of the latter fish, the mandibular, gular, and cheek lines of Amia being probably all represented in Mustelus, in the manner just above set forth.

Is it, then, at all probable that the numerous ampullæ of Mustelus can possibly be represented in Amia by the few pit lines on the head of that fish that are not almost definitely and positively otherwise accounted for? And is not the primary distribution of the ampullæ, as indicated by their pores, wholly opposed to any such assumption? The general distribution of these pores, and their particular distribution in certain places, closely resembles that of the terminal buds on the head of larvæ of Amia, and it is noteworthy that, in those places in which certain of the pores of a single group of ampullæ are arranged in line along each side of a lateral canal, the branches of the nerves that innervate the organs of those ampullæ must straddle the lateral canal, and hence its related nerve, exactly as the trigeminal nerves that innervate the terminal buds in Amia, straddle certain of the lateral canals and their associated nerves (**3**).

The ampullæ of Mustelus thus seem, in everything excepting their special form and apparent innervation by the facialis, to correspond much more closely to the terminal buds of Amia than to the pit organs of that fish. As to this apparent innervation of the ampullary organs by branches of the lateral canal nerves, it is quite possible that the fibres destined to the ampullary organs have a different central origin from that of the lateral fibres, as I shall attempt to show, after describing the nerves of Mustelus, by a comparison of the ophthalmic nerves of fishes. The fibres that innervate the ampullary organs would then represent a stage intermediate between the terminal bud, or communis, fibres of Amia, and the lateral canal ones. That such intermediate stages should exist is wholly natural, if all the several forms of special sensory cutaneous organs are derived from a single primitive form, represented most closely by the terminal buds of ganoids and teleosts, as Wiedersheim says (**64**).

In teleosts so-called pit organs, irregularly distributed over the head, are frequently described. These organs, in my opinion, must often be the homologues of the terminal buds of Amia, and not of the pit organs of that fish. In this I differ from Cole and Herrick, but Herrick, it is especially to be noted, says (**32**, p. 37) that the pit organs of Menidia are not situated in pits, being "strictly naked papillæ projecting above the surface of the skin." He further says, in the same work (p. 36), that he inclines to regard the so-called accessory lateral line organs on the trunk of Menidia, "like the buds on the top of the head, as belonging to the communis system."

Nervus Oculomotorius.

The nervus oculomotorius of my 12·2 cm. Mustelus, as it issues from its foramen, lies directly mesial to the rectus internus, and somewhat anterior to the surface of origin of that muscle, as Tiesing (**62**) shows it in his figures. Three branches arising close together, if not as parts of a single branch, are immediately sent to the ventral portion of the rectus internus, and then a fourth branch to the dorsal portion of the same muscle. A fifth and wholly independent branch is then sent upward and backward to the rectus superior. The main nerve, as it gives off these five branches, is here running backward between the skull and the rectus internus, the muscle being so pressed against the nerve that its mesial surface is grooved to receive it. The muscle runs forward immediately dorsal to the eye-stalk. The nerve issues from the skull slightly anterior to the eye-stalk, and dorsal to it, and runs backward above it.

The eye-stalk at this age is of cartilage, but this cartilage is not directly continuous with the cartilage of the skull, an intervening space of procartilaginous tissue separating them. This procartilaginous part of the stalk curves downward, and is continuous with the ventral edge of a defect or perforation in the cartilaginous part of the side wall of the skull, the defect of the cartilage being, however, entirely closed by the perichondrial membranes. The external perichondrial membrane extends outward on to the base of the stalk. The defect lies almost directly anterior to, and not far from, the external opening of the canalis transversus. What the significance of the defect is I could not determine, but it might receive an explanation under the assumption that the eye-stalk is a remnant of a visceral arch, as Gegenbaur has suggested.

As the oculomotorius gives off the five branches above described it passes backward beyond the eye-stalk, and beyond that structure the remaining portion of the nerve, which is now its ventral division only, turns downward between what look like two independent heads of the rectus internus. The ventral and much larger head of this muscle arises from the side wall of the skull posterior to this point, the surface of origin of the muscle lying immediately ventral to the profundus foramen, and extending backward toward the dorsal edge of the trigemino-facial foramen. The surface of origin of the muscle lies immediately dorsal to, and in contact with, the surface of insertion of the ventro-anterior head of the rectus externus, and immediately anterior to the surface of insertion of the dorso-posterior head of the same muscle. The dorsal and smaller head of the internus separates from the ventral head shortly posterior to the point where the latter receives its innervating branches from the oculomotorius. Turning dorsally and backward it comes into contact with the ventral edge and inner surface of the rectus superior, and there, gradually diminishing in size, disappears without ever reaching the cartilage of the skull.

My specimen thus shows a condition of the rectus internus different from any of those described either by Schwalbe (**57**), Tiesing (**62**), or Corning (**14**), and it will be again referred to in describing the eye muscles. The ventral division of the oculomotorius passes outward between these two divisions of the internus muscle, lying dorsal to the one and ventral to the other. It lies wholly in front of, and hence ventro-anterior to, the rectus superior.

The oculomotorius is accompanied in its course between these two heads of the internus muscle by the ramus ophthalmicus profundus, but the latter nerve here runs in the opposite direction to the oculomotorius, that is, forward instead of backward from its foramen. Both nerves lie anterior to the rectus superior, and, as they cross, are closely pressed against each other, as Schwalbe has said, but without any observable interchange of fibres.

After the oculomotorius has passed the profundus, crossing ventral to it, it continues downward and backward, reaches the dorsal surface of the rectus inferior, and then soon passes downward and forward around the hind edge of that muscle. There it continues forward for a time, closely applied to the ventral surface of the inferior muscle, and here sends a large branch to that muscle.

Where the oculomotorius turns downward and forward around the hind edge of the rectus inferior it holds that muscle tightly in a short sharp bend. From the nerve, at this bend, a small and delicate branch is sent outward to the eyeball, near the point where the ophthalmic branch of the anterior carotid artery pierces it, and was there lost. This nerve would seem to be the ciliaris brevis, which must accordingly arise from the ciliary ganglion, and from there run backward along and closely against the oculomotorius to the point where it has its apparent origin from the latter nerve.

Beyond the branch to the rectus inferior the remaining portion of the oculomotorius, now simply the branch destined to innervate the obliquus inferior, comes into intimate relations both with the ciliary ganglion and the ophthalmic branch of the anterior carotid artery. The nerve here passes ventro-lateral to and closely against the artery. The ciliary ganglion is, in transverse sections that cut through about the middle of its length, a crescent-shaped mass that projects downward from the oculomotorius, the hollow of the crescent directed laterally, and the ventral horn of the crescent curving around the mesial edge of the truncus buccalis-maxillo-mandibularis. The anterior end of the ganglion lies mesial to the ophthalmic artery at the point where that artery curves downward to join the anterior carotid. The oculomotorius here lies lateral to the artery, the artery thus here separating the nerve and ganglion. The middle and posterior parts of the ganglion lie mesio-postero-ventral to the artery, and the ganglion is here intimately connected with the oculomotorius. The ganglion lies in the peri-orbital sinus, which the artery and nerve both traverse.

What the character of the cells of the ciliary ganglion is I could not determine, the several tissues here passing one into the other without distinctly apparent limits. Certain of the ganglion cells are, however, small, while others are large and resemble the ganglion cells of the spino-cranial ganglia. There are thus probably both spinal and sympathetic elements in the ganglion.

Near the anterior end of the ganglion two delicate branches are given off, and, running forward and upward, join the ramus ophthalmicus profundus anterior to the point where a first large branch arises from that nerve. They accordingly represent the radix longa, and their point of origin from the profundus would seem to indicate that they cannot be sympathetic nerves, unless they have an intra-cranial sympathetic origin. No extra-cranial sympathetic strand going to the ganglion could be recognised, but it is here too difficult to recognise small nerve strands for me to assert that none existed. The radix brevis is represented by fibres that bind the ciliary ganglion and oculomotorius together.

The two nerves that together represent the radix longa lie, in their forward and upward course, posterior to the nervus opticus, anterior to the rectus inferior, and ventral to the rectus internus. Just before they join the profundus a line of tissue runs from them toward the optic nerve. Whether this line of tissue is wholly fibrous or partly nervous I could not determine, and it will be further referred to in describing the ramus ophthalmicus profundus.

Anterior to the ciliary ganglion the oculomotorious continues forward to the obliquus inferior, here having its well-known relations to the other structures in the orbit.

Nervus Trochlearis.

The nervus trochlearis issues from the skull as two branches, as Tiesing found it, its foramen lying directly internal to the ramus ophthalmicus superficialis. The nerve runs forward and downward around the lower edge of the ophthalmicus superficialis, here being closely pressed against that nerve, but, contrary to Schwalbe's statement (**57**, p. 186), without any apparent interchange of fibres. Lying always dorsal to all the other structures in the orbit, it goes to the obliquus superior muscle which it, and it alone, innervates.

Nervus Abducens.

The nervus abducens issues through the large trigemino-facial foramen, lying along the ventral surface of the trigemino-facial ganglion, and separated from it by membrane only. Running forward and laterally in this position to the anterior edge of the foramen, it there turns upward, mesial to the truncus buccalis-maxillo-mandibularis, and immediately enters the rectus externus.

Tiesing shows the abducens in the adult issuing by a separate and independent foramen, the foramen lying dorsal to the trigemino-facial foramen, which seems a singular position for it.

Eye-Muscles.

The rectus superior arose in my large embryo mainly from the dorsal edge of the trigemino-facial foramen, but apparently also in part from the tough membrane that closes the foramen around the nerves that issue through it. A part of the muscle here lies between the dorsal edge of the foramen and the dorsal surface of the issuing nerves. Its surface of origin thus lies posterior to the profundus foramen, and the latter nerve lies, as it issues from its foramen, anterior, or even slightly antero-dorsal, to the muscle; but it is evident that this relation of muscle and nerve is not morphologically different from that said by Tiesing to exist in the adult, the nerve there lying antero-ventral to the muscle. The muscle of the embryo would simply have to travel at its origin slightly dorsally to produce the conditions found by Tiesing in the adult.

The rectus inferior arises from the side wall of the skull immediately posterior to the profundus foramen, and partly surrounding the hind edge of that foramen. The surface of origin of the muscle lies dorso-posterior to that of the rectus internus, and as the muscle runs outward, downward, and forward, it passes between the two heads or bundles of the latter muscle.

The rectus internus is represented by two bundles of fibres, the ventral and larger one of which arises from the side wall of the skull between the profundus and trigemino-facial foramina, lying ventral to the one and anterior to the dorsal edge of the other. This bundle lies ventral to both the oculomotorius and ophthalmicus profundus nerves, near their exits from the cranium, and also ventral to the proximal end of the rectus inferior muscle. The other, smaller and dorsal bundle of the muscle separates, proximally, from the ventral bundle, and running backward and dorsally, dorsal to the inferior division of the oculomotorius, to the ophthalmicus profundus, and also to the proximal end of the rectus inferior, comes into contact with the ventral edge and inner surface of the rectus superior. There it gradually diminishes in size, and disappears without ever having reached the cartilage of the skull. The dorsal bundle thus lies always dorsal to the inferior division of the oculomotorius and to the profundus nerve, while the ventral bundle lies ventral to both those nerves at and near their exits from the skull. Farther forward this ventral bundle of the muscle lies dorsal to the profundus, the profundus passing downward along the lateral surface, and then forward across the ventral edge of the muscle.

The only part of the internus of my embryo that has an origin on the skull thus differs from the muscle as shown by Tiesing in the adult (**62**, figs. 1 and 5) in that it has a different origin, markedly different relations to the oculomotorius, and somewhat different relations to the ophthalmicus profundus. The muscle of the adult is shown by Tiesing arising from the skull dorso-anterior to the profundus foramen, and from there running forward dorsal to both the inferior division of the oculomotorius and to the profundus. In Tiesing's figure the ocumolotorius is not shown perforating the rectus superior, although it is said in the text to perforate that muscle.

Corning (**14**) finds the inferior division of the oculomotorius of the adult Mustelus perforating the rectus internus, as Schwalbe did before him, but he does not give the relations of the profundus nerve to the muscle. Schwalbe says that this latter nerve also perforates the muscle, near its hind edge, and then runs forward below it.

The relations of the muscle to the oculomotorius, as given by Schwalbe and confirmed by Corning, would arise if the dorsal head of the muscle of my embryo should acquire an origin on the skull. The relations of the muscle to the profundus nerve, as given in Tiesing's figure, would arise if the muscle of my embryo should simply shift forward somewhat, and then upward, at its origin. Its relations to the oculomotorius, as given by Tiesing, are so different from what I find that his results would seem abnormal, if not in part incorrect. The arrangement shown by him would arise if the ventral bundle of my embryo should entirely disappear, the adult muscle being represented by the dorsal bundle only; or by supposing that the entire muscle of my embryo had travelled forward at its origin beyond the oculomotorius, and then backward above it.

My embryo thus probably shows a nerve in the so-called process of traversing one of the eye-muscles, and it is especially to be noted that this takes place in the manner I assumed in my work on Amia (**3**, p. 522), across the ends of the muscle-fibres, and not by cutting through them midway of their length. The nerve, however, here traverses the muscle, or more properly becomes surrounded by the muscle, before the muscle has entirely acquired its origin on the skull, instead of afterwards, as I assumed, the fibres of the muscle growing inward, from their embryonic anlage, toward the skull on both sides of the nerve, the nerve evidently barring their passage, and rendering a part of the muscle wholly functionless for a considerable length of time. That the condition shown in my embryo is not abnormal or unusual is shown by its being found on both sides of the head in both my other embryos.

The rectus externus arises by two wholly separate heads. The ventro-anterior head arises from the side wall of the skull immediately anterior to the trigemino-facial foramen, immediately dorsal to the orbital opening of the canalis transversus, and immediately ventral to, and in contact with, the surface of origin of the ventral head of the rectus internus. The dorso-posterior head arises from the side wall of the skull immediately dorsal to, and contiguous with, the dorsal edge of the trigemino-facial foramen. It there lies ventral to the surface of origin of the rectus inferior, and anterior to that of the rectus superior. The muscle did not have a straight course in my sections, but this may have been due to the action of reagents. When near the eyeball it turned forward, then directly outward to the eyeball, and then backward around it.

The obliqui superior and inferior arise close together, at the anterior end of the orbit. The superior muscle arises from the orbital wall immediately dorsal to the orbital opening of a canal by which the ophthalmicus profundus traverses the antorbital process. The inferior muscle arises immediately posterior to that opening. The latter muscle here lies immediately internal to the anterior end of the muscle Addβ of Vetter's nomenclature, and immediately dorsal or dorso-anterior to the orbital opening of a large canal that extends from the front end of the orbit into the hind end of the nasal capsule.

This latter canal transmits a large branch of what Gegenbaur (**23**, p. 77) considered, in adult selachians, as a peri-orbital lymph sinus. Parker (**47**) has, however, since described, in the adult Mustelus antarcticus, a large venous orbital sinus that would seem to be the same vessel that Gegenbaur described as a lymph sinus. In my embryos this sinus is certainly a part of the venous system, and if both lymph and venous sinuses are here found in the adult, they must both have been cut off from this blood sinus of embryos. That this is what probably takes place seems shown by the fact that, in Amia, the peri-orbital sinus is certainly a lymph one, and that it has the same position and relations to the other orbital structures that the blood-sinus of my embryo of Mustelus has. From the anterior end of this sinus, in Mustelus, the large branch above referred to arises, and, traversing the canal in question, enters the hind end of the nasal capsule. From there it sends a branch downward through the ventral opening of the capsule, the branch then turning mesially along the ventral surface of the skull, and, at the middle line of the head, anastomosing with its fellow of the opposite side. This large branch of the peri-orbital sinus is thus certainly the anterior facial vein of Parker's descriptions of the adult. As it traverses its canal in my embryos it is not accompanied by any other structure, so far as I could find, certainly not by any branch of the ramus ophthalmicus profundus. The canal is thus not the exact equivalent of the orbito-nasal canal of Gegenbaur's descriptions. But if it should, in the adult, become fused with the profundus canal, to be later described, and that canal should become wholly shut off, by cartilage, from the cranial cavity, a canal would arise which would seem to be the equivalent of Gegenbaur's canal. The canal, in my embryo, is quite certainly the homologue of the orbito-nasal canal of my descriptions of Amia (**3**, p. 514), and that canal is thus probably not the exact homologue of the orbito-nasal canal of Gegenbaur's descriptions of selachians. The name orbito-nasal is, however, properly applicable to it. It is evidently, in origin, wholly separate from and independent of the profundus canal.

Another branch of the peri-orbital sinus of my embryos traverses the canalis transversus, in exactly the manner that Gegenbaur says that a branch of his lymph sinus traverses the same canal in the adult (**23**, p. 77). This branch is not described by Parker in his descriptions of the blood-vessels of Mustelus antarcticus. If, nevertheless, it be venous in the adult Mustelus lævis, as it certainly is in embryos, or even if it is simply derived from a sinus that is venous in embryos of the age of my oldest ones, the canal it traverses must be quite differently judged, in any comparison with teleosts, from what it would be if the vessel were a lymph one of independent origin. The homology proposed by Gegenbaur and Sagemehl (**56**) of this canalis transversus of selachians with the eye-muscle canal of teleosts and ganoids is, in fact, wholly based on the supposition that the canal in teleosts and ganoids lodges or transmits, as the canal in selachians was asserted to, a lymph vessel which arises as a branch of a peri-orbital lymph sinus. This assumption I found to be incorrect in so far as Amia is concerned (**3**), the eye-muscle canal of that fish being traversed by a vein, and not by a lymph sinus, and a separate and wholly distinct transverse canal transmitting a lymph vessel from orbit to orbit. I hence concluded that the eye-muscle canal of Amia and teleosts was not derived from the canalis transversus of selachians. This opinion must certainly now be altered, for if the canal in selachians transmits a vessel that is primarily venous, it is evident that it must form a part of the eye-muscle canal of Amia, which canal also transmits a venous vessel.

One other foramen in the orbital region of Mustelus is to be noted. It lies near the anterior end of the orbit, dorso-posterior to the orbital opening of the orbito-nasal canal, and anterior to all the foramina of the nerves, the nervus opticus included. It is, in all probability, traversed by a branch of the peri-orbital sinus, though I could not positively establish this. A branch of the sinus penetrates the membranes that line the outer surface of the cartilage, and is seen, for a certain number of sections, as a vessel lying between the outer and inner lining membranes of the skull. The two edges of the foramen had then been pressed toward each other by contraction or displacement in manipulation, and I could not see that the vessel entered the cranial cavity. In this latter cavity two blood-vessels approached the membrane that lined the inner surface of the opening in the cartilage, and there united. These two vessels seemed to be simply two parts of a single vessel that approached the foramen and then bent sharply away from it, without having any connection whatever with the external vessel. If, however, such a connection existed, the intra-cranial vessels would be branches of the branch of the peri-orbital sinus, and the vessel would probably be the anterior cerebral vein of Parker's descriptions of the adult Mustelus antarcticus (**47**).

In my 55 mm. embryo this cerebral branch of the periorbital sinus traverses the skull and then runs forward, as a large vessel, along the lateral surface of the brain, between it and the skull. Mr. Nomura here found a foramen in the embryo he dissected.

Review and Comparison of Eye Muscles.

Corning (**14**), in his recently published and excellent work on the eye-muscles and their innervation in the several classes of vertebrates, to which reference has already several times been made, comes to the conclusion expressed in the following sentence:—"Ich halte also an der Homologie der vom Oculomotorius innervirten Muskeln fest." This is directly opposed to my own published opinion regarding these muscles (**3**), and I cannot see that Corning in any way satisfactorily explains the rather troublesome facts that I brought forward in support of it. He is obliged, in fact, in order to establish his proposition, to make certain assumptions that have less support in fact than my assumptions had. To explain the unusual innervation of the rectus inferior in Petromyzon, by a branch of the abducens, he assumes that the fibres destined to that muscle become detached from the oculomotorius and attached to the abducens, intra-cranially. And yet, although this interchange of fibres must surely be extra- and not intra-cerebral, he did not establish it in the specimen he examined, and it is in no way indicated in any of the numerous works on the fish. To explain the important differences in the innervation of the rectus internus, by a branch of the superior division of the oculomotorius in certain classes of vertebrates, and by a branch of the inferior division of the same nerve in others, Corning assumes that it would be sufficient, in order to produce the arrangement found in the ones, for the opticus and oculomotorius of the others to change slightly, at their exits from the cranium, their relations to the recti muscles. Here he wholly overlooks the very important fact that, in any such shifting about of the points of exit of the two nerves in question, that branch of the oculomotorius that innervates the rectus internus would still necessarily always remain on the same side of the opticus, ventral or dorsal as the case may be. He chooses Esox to represent one of the two manners of innervation, and Carcharias to represent the other. Take his figure 4, which shows the muscles and nerves of Esox, and imagine the rectus internus to shift, at its origin, forward in front of the opticus and then backward above it. This is simply what Corning proposes, but in the reverse direction, and it is the only way in which the muscle can be brought dorsal to the opticus without assuming that the nerve cuts through the muscle or the muscle through the nerve. The muscle itself, in thus shifting at its origin, would evidently acquire the selachian position, as Corning asserts, but the nerve that innervates the muscle would most certainly not. It would still remain ventral to the opticus.

In Esox the internal and inferior recti are not innervated, as I assumed, from earlier descriptions, that they were in all teleosts, and as they are in Amia. Corning calls attention to this, and Herrick (32), before him, had called attention to a similar difference in Menidia. I myself had already found this to be true of Scomber and certain other teleosts, and had called attention to it in a work on Scomber sent to press now nearly three years ago. In all these fishes the arrangement seems practically to be that the superior division of the oculomotorius innervates the rectus superior alone. A branch is then given off which separates into two parts, one for the rectus internus and the other for the rectus inferior, both branches lying morphologically ventral to the optic nerve, but the branch to the rectus internus passing dorsal to the rectus inferior, instead of postero-ventral to it as it does in Amia. The remainder of the oculomotorius then runs downward and forward around the hind edge of the rectus inferior, and supplies the obliquus inferior. Herrick considers this latter part of the nerve as the first branch of the oculomotorius, the remainder of that nerve later separating into dorsal and ventral portions, the former for the rectus superior and the latter for the recti internus and inferior. This latter portion, which Herrick considers as the continuation of the main nerve itself, runs forward dorsal to both the muscles it innervates, and it is to it that the ciliary ganglion is said to be related in Menidia, as I also find it in Scomber.

Herrick says (**32**, p. 237) that the "deviations" in the innervation of the internal and inferior recti in Menidia, from that given by me in Amia, "can be easily explained mechanically by the great size of the eyes, and the consequent crowding of the recti muscles far backward." Corning explains the differences between Esox and the chick, the chick agreeing practically with Amia, by assuming (p. 136) that the rectus inferior of Esox acquires an origin dorsal to that branch of the oculomotorius that innervates the rectus internus. He does not say that the muscle traverses or is traversed by the nerve in this process, but it is evident that one of these two things must happen, for no simple shifting of the muscles at their origins could derive one arrangement from the other. This applies to Menidia as well as to Esox, and Herrick doubtless recognised it, for although he would explain the change in the relations of nerve and muscle by a different principle, as explained below, he assumes that it could be easily accounted for by a principle said to have been invoked by me; his words being (p. 237) that "he (Allis) invokes a principle to account for the diverse relations of nerve and muscle in elasmobranchs, which, if applied more broadly, might weaken the phylogenetic value of some of his other cases." This statement of Herrick's is, however, clearly based on a misconception of the principle referred to as invoked by me, which principle was contained in the statement that the muscles I was discussing in elasmobranchs "at their origins, either traverse or are traversed by the issuing nerve." I expressly eliminated the probability of a nerve cutting through a muscle or a muscle through a nerve "midway in its length" (**3**, p. 522).

This is, in fact, the vital point of the whole discussion. Does a nerve ever cut through one of the eye-muscles "midway in its length"? Or does one of the muscles, either at its origin or elsewhere, ever traverse a nerve "midway in its length"? I assumed, in my discussion of the subject, that neither of these things occur, and I know of no single fact that proves the contrary. I also assumed, in my discussion of these nerves and muscles, and it was definitely implied though not definitely stated, that an eye-muscle nerve once laid down on one side of any of the eye-muscles, or on one side of any of the nerves that innervate those muscles, or that traverse the orbit, would always be laid down in the same relation to that structure. I then further assumed that the nerve once laid down never changed this embryonic relation to another nerve, but that it might and did change its relation to a muscle in the manner set forth in the principle above referred to as invoked by me. In this assumption that the nerves are always laid down in the same relations to the eye-muscles I was quite unquestionably in error, as my present work on Mustelus shows. For it is evident that since the nerves that innervate the eye-muscles or that traverse the orbit are relatively well developed before the eye-muscles have acquired their attachments on the skull, they might be so placed, because of correlation to other parts, as to obstruct a muscle as it sought its cranial attachment, and hence deflect it, or even split it, as the obstructing nerves split the rectus internus in Mustelus. This is, however, in reality simply an application, in embryonic stages, of the principle I invoked for adults; that is, the muscle here, in principle, traverses, at the end that is to become its end of origin on the skull, a nerve that it encounters. This, it will be readily seen, is a totally different thing from the assumption that the nerve cuts through the muscle fibres; and also totally different from another principle frequently invoked in this connection, and which is very definitely expressed by Herrick (**32**, p. 237) in the following sentence:—"If this be true (that the eye-muscle nerves grow directly out from the brain), I see no reason why a given motor nerve should not grow out either above or below some other structure depending upon the peripheral relations of its end organ with reference to that structure." This seems to me too dangerous a principle to be applied without definite facts to support it in each particular case, and such facts do not here exist. Pushed to a legitimate extreme, a nerve might even be assumed to change its relations to such an obstacle as a visceral cleft. In any event a pure assumption is here invoked by Herrick to explain certain facts that I had sought to explain by what was, at the time, an equally pure assumption; that is, that the internal recti muscles of vertebrates are not all homologous structures. Recent work relating to this especial subject supports, however, my assumption. For both Hoffmann (**34**) and Sewertzoff (**58**) say that the rectus superior and rectus internus of Acanthius and Torpedo respectively arise from the dorsal wall of the head cavity from which all the muscles innervated by the oculomotorius arise; while Rex says (**53**, p. 235) that in the duck the rectus internus and the rectus inferior arise from a single embryonic muscle-mass that has its origin from the ventral wall of the same cavity, the rectus superior alone arising from the dorsal wall of the cavity (p. 238). The bundle of fibres that I found in one specimen of Amia hanging festoon-like between the rectus internus and rectus inferior muscles thus receives an evident explanation, and, inversely, tends to confirm for Amia the origin ascribed by Rex to the corresponding muscles in the duck. This thus seeming to be established, the conditions presented in Mustelus seem to be such as might have necessitated or led to the development of another and different internus. The internus in this fish is so obstructed in its effort to obtain an attachment on the skull, that a considerable part of it remains for a long time wholly functionless. Had it been still more obstructed the muscle might not have been able to maintain its separate and independent existence, and a new and wholly different internus would have been developed.

Herrick calls attention (**32**, pp. 234—236) to two apparent errors in my diagrammatic representation of the eye-muscles and nerves of vertebrates, and he considers them of sufficient importance to "suggest that his (my) entire phylogenetic scheme should be received with some reserve." One of these apparent errors is that I have shown the ophthalmic nerves in all my figures arising "from a common stem which lies ventrally of the III nerve." The nerves in my diagrams are all intended to be shown cut some distance after they issue from their foramina, and I purposely avoided attempting to show their relations at their exits. The data on which my diagram was based were too meagre and too conflicting to warrant my attempting to show anything that could possibly be omitted. The other apparent error relates to the position of that branch of the oculomotorius that innervates the rectus superior in Petromyzon. I showed this branch in my figure lying over instead of under the ramus ophthalmicus. In the text (p. 523) I called attention to the fact that Fürbringer says that it runs under the ramus ophthalmicus, but I assumed this to be an error. As Corning says (**14**, p. 129) that he has confirmed the correctness of Fürbringer's statements, this simply adds another and important variation to be accounted for in the innervation of the eye-muscles.

In my work on Scomber, still in press, I suggested that the differences in the innervation of the rectus internus and rectus inferior in that fish, and in Amia, might be explained by the assumption that the internus of the one was the inferior muscle of the other, ganoids and teleosts thus representing different lines of descent from my proto-urodele type. As, however, Workman (**68**) has recently shown that the eye-muscles of Amiurus melas are innervated much as they are in Amia, while in Pomatomus they are innervated exactly as they are in Menidia, it is evident that it is useless to speculate on the subject until further facts have been accumulated.

Trigemino-facial Complex.

The trigemino-facial ganglion is partly intra-cranial and partly extra-cranial in position. The apparent roots by which it arises from the brain could not be satisfactorily determined in my 12·2 cm. embryo, because of the crowding together of the parts here concerned, and the different bundles of fibres that compose the several roots could not be separately traced through the ganglion, my sections not having been prepared for this especial research. In my 55 mm. embryo the apparent roots could, on the contrary, be easily distinguished, and the different components of the several peripheral nerves could be determined in a general, but certainly not in a complete or absolutely accurate way. From a consideration of the two embryos the following approximately correct results were arrived at.

The so-called anterior root of the trigeminus is formed by two somewhat distinct rootlets—a dorsal one, having a deeper origin in the medulla, and a ventral one, having a more superficial origin. The dorsal rootlet is certainly largely formed by a bundle of fibres that have a course corresponding exactly to that ascribed by Haller (28) to the inner motor trigeminus root of his descriptions of Scyllium. The ventral rootlet certainly arises largely from the "dorsolaterale Längsbahn" of Haller's descriptions, that is, from the ascending fifth tract of English authors. Haller says (p. 437) that in Scyllium all the sensory fibres of Trigeminus I are derived from this latter tract, and this, if true of Scyllium, must doubtless also be true of Mustelus. Both rootlets in Mustelus enter the anterior portion of a large intracranial ganglion. Different regions, rather than separate and independent parts of this ganglion, can be distinguished, and a considerable part of the fibres of the ventral rootlet are seen to enter a ventro-lateral part of the ganglion, which, opposite the anterior half of the ganglion, is separate and independent from the rest of the ganglion, but posteriorly is completely fused with it. From this lobe or process of the ganglion the ramus ophthalmicus profundus arises, that nerve hence, very probably, being composed entirely of general cutaneous fibres derived from the ascending fifth tract. The ramus profundus of Mustelus can thus in no way be the homologue of such a nerve as the so-called ramus profundus of Haller's descriptions of Scyllium, in which fish the nerve is said (p. 438) to be exclusively motor, and to be derived entirely from the inner motor trigeminus root and the anterior upper motor trigeminus nucleus. That Haller has here certainly mistaken a superficialis ophthalmic nerve for a profundus one will be later shown. That he has also made some further mistake is evident, for the superficial ophthalmic nerve of Scyllium is certainly in no part a motor one.

From the antero-dorsal corner of the intracranial ganglion of Mustelus a bundle of fibres, which Haller calls in Scyllium the ventral "Wurzelportion" of the ramus ophthalmicus superficialis, is sent forward and outward to join on its ventral aspect what Haller calls the upper portion of the posterior root of the trigeminus. This bundle of fibres, in Mustelus, has its apparent origin from the intracranial ganglion opposite the point where the inner motor trigeminus root of Haller's nomenclature (my dorsal rootlet) joins it. The fibres of the bundle, however, do not come from that rootlet, but come upward along the lateral surface of the ganglion, from that part of the ganglion that has its origin in relation to the dorsal portion of the fibres that arise from the ascending fifth tract. The bundle is thus seen, from its origin alone, to certainly be composed, in large part, of general cutaneous fibres, and its peripheral distribution, to be later given, shows that it is quite unquestionably entirely so composed. Motor fibres certainly do not exist in it.

From the posterior part of the intracranial ganglion formed on this anterior trigeminal root the truncus maxillomandibularis trigemini has its origin. Issuing from the skull by the trigemino-facial foramen, this truncus, or root of the truncus, there becomes more or less confused with the root or stem of the facialis, and also with the hyoidean part of the posterior trigeminal root. A large extracranial ganglion is formed on these several stems.

The so-called posterior root of the trigeminus, or Trigeminus II, is formed in Mustelus, as it is in Scyllium, of two portions,—a dorsal and a ventral one. There is not here, however, a strict agreement with the conditions described by Haller in Scyllium. The dorsal root, which arises in the so-called lobus trigemini, separates into three parts, two of which run downward close against the lateral surface of the brain, while the third one turns outward and forward, enters the ramus ophthalmicus superficialis, and forms the lobus trigemini component of that nerve. The two other portions, running almost directly downward, straddle the nearly horizontal ventral portion of the root, which latter portion arises from the "äussere sensorische Oblongatagebeit" of Haller's descriptions, that is, from the tuberculum acusticum. One portion, or bundle, of the fibres of this ventral root continues directly forward, and, joining that bundle of the dorsal root that goes to form part of the ramus ophthalmicus superficialis, forms the tuberculum acusticum component of that nerve. The remaining portion, or bundle, of the ventral root turns sharply downward with the two descending bundles of the dorsal root, the three bundles becoming confused in the sections, and together forming a large stem, which issues from the skull through the trigemino-facial foramen, a part of it going to form the ramus buccalis and ramus oticus facialis, and a part becoming lost in the facial, or hyoidean, part of the extracranial trigemino-facial ganglionic complex.

On this so-called posterior trigeminal root, thus formed of two rootlets, there is no intracranial ganglion whatever, and not even any ganglion cells, excepting just as the roots issue from the skull. Externally to the skull, on both the ophthalmic and buccal parts of the root, there is a large, separate, and independent ganglion; but no separate ganglion is found related to the hyoidean branch of the root. The two rootlets together form the so-called lateral sensory root or roots of all those authors that do not treat them as a part of the trigeminus. It is, however, to be especially noted that both the ophthalmic and buccalis-hyoidean parts of the root receive fibres from two quite distinct regions of the brain—the lobus trigemini, and the tuberculum acusticum. The assertion that the lobus trigemini is a part of the tuberculum acusticum, somewhat differentiated as a separate lobus, does not seem sufficient in itself to account for this origin in Selachians, and also in Acipenser (**39**), of the so-called lateral fibres from two distinct centres, while in ganoids and teleosts they arise from a single centre, the tuberculum acusticum (**40**). While I have wholly failed in my attempt to trace in Mustelus the fibres from the lateral canal organs to one of these two centres, and those from the ampullary organs to the other, it is evidently a legitimate supposition that such may perhaps be their central origin, and this has already been suggested by Strong (**60**, p. 194). If it be admitted, the natural conclusion must be, as Strong has said, that the ampullary organs represent the terminal buds of Amia and other fishes, and not organs similar to the pit organs found on the head of Amia. That the ampullæ may be derived from, or be directly related to, certain of the so-called pit-organs of current descriptions of teleosts is, however, quite probable, and will be again referred to.

The facial root of the trigemino-facial complex of Mustelus arises in my 55 mm. embryo by two rootlets, one of which has its central origin in the lobus vagi, while the other contains motor fibres, Mustelus thus apparently fully agreeing with Scyllium. On this facial root there is no important intra-cranial ganglion, though ganglion cells begin on its dorsal surface just before it leaves the skull. It issues through the postero-ventral part of the large trigemino-facial foramen, and a large extra-cranial ganglion immediately forms on it, this ganglion being somewhat separate from the extra-cranial ganglion on the truncus maxillo-mandibularis, and lying postero-ventral to it.

The trigemino-facial nerves of my embryos of Mustelus thus issue from the skull by the three well-known trunks or stems, and each stem has its own special foramen. All three of these foramina pierce the cranial wall in the orbital region, one lying near the roof of the orbit, one near its floor, and the other intermediate between the two. Schwalbe (**57**, p. 183) says that the ophthalmicus superficialis and ophthalmicus profundus issued by a single foramen in the adult specimen of Mustelus lævis that he examined, the trigemino-facial nerves thus issuing from the cranial cavity by two instead of by three foramina. Tiesing (**62**), on the contrary, shows, in the adult, three separate foramina exactly as I find them in embryos.

The dorsal one of the three trigemino-facial foramina of my embryos is the most anterior one of the three, and it transmits the so-called ramus ophthalmicus superficialis, this nerve containing a large component derived from the tuberculum acusticum, another large component derived from the lobus trigemini, and a third and smaller one derived from the so-called anterior or first root of the nervus trigemini. The first two of these three components together form what is now usually described as the ramus ophthalmicus superficialis facialis, the third one being the ramus ophthalmicus superficialis trigemini. The latter nerve is certainly largely composed of general cutaneous fibres, though it may perhaps also contain a certain number of communis fibres, for although Haller says (p. 437) that in Scyllium the sensory part of Trigemini I is formed entirely of fibres derived from the ascending trigeminus tract, this tract is said to have previously received a bundle of fibres coming from the lobus vagi (p. 431). If, then, the ampullæ of selachians represent the terminal buds of Amia and teleosts, these fibres from the lobus vagi must be so-called visceral-sensory communis fibres, which have naturally not suffered the modification that I assume that the terminal bud fibres are undergoing.

The middle foramen is the next anterior one of the three, and it transmits the ramus ophthalmicus profundus, derived from a ventro-lateral and somewhat separate and independent part of the intra-cranial trigeminus ganglion.

The third trigemino-facial foramen is much the larger one of the three. It lies ventral and posterior to the other two, and transmits the united stems of the hyoideo-mandibularis facialis, maxillo-mandibularis trigemini, and buccalis facialis.

In one of my embryos, dissected by Mr. Nomura, a fourth trigemino-facial foramen was found. It lay slightly in front of the ophthalmicus superficialis foramen, was small, and transmitted a small bundle of fibres which immediately joined the ramus ophthalmicus superficialis. The relative size of the two foramina by which the ophthalmicus superficialis thus issued from the skull in this specimen would lead one to suppose that the smaller foramen transmitted the general cutaneous component of the nerve, the larger one transmitting the united lobus trigemini and tuberculum acusticum components.

Ramus Ophthalmicus Superficialis.

The ramus ophthalmicus superficialis, after it issues from its foramen, immediately becomes ganglionic, as already stated, and is a broad, flattened nerve, which lies against and runs forward along the side wall of the skull, immediately ventral to the projecting and overhanging roof of the orbit. The nerve is here formed of two perfectly distinct parts—a large ganglionated dorsal portion, and a small non-ganglionated ventral one. The dorsal portion contains the fibres destined to supply the sensory organs of the lateral canals and those of the ampullæ, and may be referred to as the special sensory portion. The ventral portion contains the general sensory fibres of the nerve.

The descriptions of this nerve and of the others that follow are based entirely on the conditions found in the 12·2 cm. embryo examined by sections, and hence do not agree exactly with the figures.

Immediately outside its foramen the ophthalmicus superficialis gives off two branches, one arising from the dorsal, ganglionic portion of the nerve, and the other from its ventral, non-ganglionated portion, this latter branch running upward, as a flat nerve, along the mesial surface of the special sensory portion of the nerve. Dorsal to the main nerve the two branches anastomose to a greater or less extent, and together perforate the overhanging orbital roof. There they turn backward along the dorsal surface of the roof and separate, the special sensory nerve, which is purely a lateral sensory one, innervating the posterior sub-group of the supra-orbital organs,—that is, organs 87 to 93 of that line, while the general sensory branch goes to the general tissues. This pair of nerves together form the first one of the so-called frontal branches of the main nerve, the portiominor of the nerve thus, contrary to Schwalbe's statement (**57**, p. 184), taking part in the formation of these frontal nerves. Schwalbe says that the portiominor only gives off one branch during its passage through the orbit, that branch being the communicating branch to the trochlearis—a branch that I do not find.

Slightly anterior to this first pair of frontal branches a second pair is given off, one a general sensory branch, and the other a lateral sensory one destined to innervate supra-orbital organ 86. Both of these branches have a forward instead of a backward course. Anterior to them two or three general sensory branches and five lateral sensory ones are successively given off, the latter branches subdividing and innervating organs 76 to 85 supra-orbital. These five lateral sensory branches all pierce the orbital roof by separate foramina, the general sensory branches either accompanying them or traversing separate foramina of their own. All these branches have a forward and upward course.

Beyond the root of the most anterior one of the five lateral sensory branches above referred to, that is, anterior to the branch that innervates supra-orbital organs 76 and 77, and near the front end of the orbit, the ophthalmicus superficialis itself pierces the orbital roof, and reaches its dorsal surface. In the slightly younger specimens examined by dissection the nerve here traversed a notch in the orbital roof, as shown in fig. 4, instead of piercing it. Shortly before leaving the orbit it passes dorsal to the nervus trochlearis, and there comes into intimate juxtaposition with that nerve, but, as already stated, without any indication whatever, that I could observe, of any interchange of fibres.

As, or shortly after, the ophthalmicus passes upward out of the orbit a lateral sensory branch is sent to organs 74 and 75, and two others to organs 65 to 73, organ 65 being the middle one of three organs that lie in that short section of the supra-orbital canal that lies between the two bends in the canal, slightly in front of the eye. At the same time that these three lateral branches are given off the larger part of the general sensory component of the nerve passes gradually upward, as two nerve strands, along the mesial surface of the remainder of the nerve. These two nerve strands leave the main nerve separately, and then, farther forward, unite to form a single nerve, which here lies immediately dorsal to the remaining and much larger part of the nerve. This latter, deeper part of the nerve now consists almost entirely of special sensory fibres, but there is still a small bundle of general sensory fibres in its ventral portion.

Having issued from the orbit the two strands now formed of the originally single nerve lie at first along the sloping surface of the lateral wall of the brain case, immediately dorsal to the anterior end of the roof of the orbit, and then pass dorsal to the antorbital process. Anterior to that process a large general sensory branch is given off from the ventral aspect of the main nerve. Running forward slightly below the main nerve it soon turns outward toward that part of the supra-orbital canal that lies anterior to the double bend in front of the eye, and accompanies it in its forward course. Slightly anterior to the point where this general sensory branch is given off a large lateral canal branch is sent downward and backward, at first along the lateral surface of the brain case, and then along the lateral surface of the nasal capsule. From it numerous branches, some of them quite long, run forward and downward along the side wall of the brain case and nasal capsule, and innervate organs 1 to 16 supra-orbital, the section of canal thus innervated lying on the ventral surface of the head, in the region lateral to the nasal aperture. This large lateral branch leaves the main nerve directly dorsal to the foramen by which the ophthalmicus profundus issues from the brain case, after having re-entered it near the anterior end of the orbit. It is evidently the homologue of the branch s. of.[2] of Ewart's (18) descriptions of other selachians.

Slightly anterior to the large lateral branch to organs 1 to 16, a lateral branch is given off to supply organs 59 to 64 supra-orbital, which organs lie in or near the distal one of the two bends of the supra-orbital canal immediately in front of the eye.

Anterior to this point the main nerve, running forward, comes to lie in the angle between the side wall of the brain case and the dorsal surface of the bulging side wall of the nasal capsule. The ramus ophthalmicus profundus, having issued a second time from the cranium, here lies slightly ventro-lateral to the main ophthalmicus superficialis, the large general sensory branch of the latter nerve lying slightly dorso-mesial to it. As the main nerve continues forward, in this position, it soon reaches a point where the cartilaginous side wall of the brain case is entirely replaced by membrane, this perforation of the cartilaginous skull being the much enlarged prefrontal opening of Gegenbaur's descriptions of the adult. The nerve here lies lateral to the now membranous side wall of the brain case, on the dorsal surface of the cartilaginous nasal capsule, slightly lateral to its highest point. In this position it runs forward, and soon gives off, from its dorsal aspect, two large ampullary sensory branches which run at first forward, and somewhat dorsally and mesially. The more superficial of these two branches here soon breaks up and supplies the organs of that sub-group of the superficial ophthalmic group of ampullæ that has its surface pores on the dorsal surface of the head mesial to the orbit. The ampullæ themselves, of this group, lie, in 12·2cm. embryos, along the lateral surface of the membranous anterior end of the brain case, and immediately dorsal to the nasal capsule. The tubules of the lateral ampullæ of this subgroup lie internal to, and separated by membrane from, the tubules of that sub-group of the ophthalmic ampullæ that has its surface pores in, and posterior to, the ventral one of the two bends of the supra-orbital canal immediately in front of the eye. The organs of this latter sub-group of ampullæ, and also those of the other, more anterior sub-group of the superficial ophthalmic ampullæ, are innervated by the deeper one of the two ampullary branches above referred to. This branch, running forward dorsally and mesially, reaches a position dorso-mesial to the base of the dorso-lateral rostral bar of cartilage, and then, sinking deeper, comes to lie mesial to the bar, where it breaks up and supplies the organs of its two sub-groups of ampullæ.

In that part of the course of the main ophthalmic nerve where these two ampullary branches are given off the lateral canal fibres of the nerve have been gradually collecting in two regions—a dorsal and a ventral one. The dorsal fibres soon separate as a separate branch, and from it ten or more branches are given off, some of them arising from the main nerve, from the bundle of fibres destined to form the branch, but before these fibres have entirely separated as a separate branch from the main nerve. Branching, these several lateral sensory branches supply organs 35 to 58 supra-orbital, all of which lie proximal to the point where the canal anastomoses with the anterior end of the infra-orbital canal, the main branch ending in two branches which supply, the one organs 37 and 38, and the other organs 39 and 40. Organs 38 and 39 lie one directly dorsal to the other in the anterior bend of the canal, where it passes upward from the ventral to the dorsal surface of the snout. A general sensory nerve, derived from the main nerve, accompanies this lateral nerve, and beyond its anterior end breaks up into a number of terminal, general sensory branches.

The remaining, ventral, and larger part of the main ophthalmic nerve contains the lateral sensory fibres destined to organs 17 to 34 supra-orbital, the ampullary fibres destined to the deep ophthalmic group of ampullæ, and certain general sensory fibres destined mainly to supply the prenasal parts of the snout. Organs 17 to 34 all lie in the subrostral part of the supra-orbital canal, distal to the point where the canal anastomoses with the anterior end of the infra-orbital canal. The fibres destined to supply the organs leave the main nerve in several branches, all of which run forward to their destination, neither any of them, nor the main nerve itself, having a recurrent course, such as Ewart shows in his fig. 2. Ewart has here, I think, combined the profundus and certain of the terminal branches of the ophthalmicus superficialis, for the profundus turns backward in the manner shown by him for the superficialis, and Mr. Nomura, in his first dissection, considered it as the distal end of the latter nerve.

This ventral part of the main ophthalmic nerve, in the region where the lateral sensory branch to organs 35 to 58 is given off, comes into intimate juxtaposition with the ramus ophthalmicus profundus, and so remains through about 100 sections. There was here, apparently, no interchange of fibres, but the relations of the two nerves are much too intimate for me to assert that it does not take place. One lateral sensory branch, the one to organs 55 and 56 supra-orbital, also here comes into such close relations with the profundus that it is impossible to say that it does not join it, instead of joining the ophthalmicus superficialis. Nevertheless, I should certainly have decided that it did not join the profundus were it not that Cole finds, in Chimæra, a lateral branch that has its apparent origin from the profundus, and that supplies two supra-orbital organs lying in a part of the canal that is strikingly similar to that in which my organs 55 and 56 are found. The exact innervation of these two organs is morphologically too important not to demand further investigation.

Near the anterior end of the nasal capsule the profundus nerve separates from the superficial ophthalmic one, turns downward around the anterior end of the nasal capsule, and then backward along its ventral surface. The main superficial ophthalmic nerve now acquires a position close to, and ventral or ventro-lateral to, the dorso-lateral rostral bar of cartilage, the separate, general sensory branch acquiring position dorsal or dorso-lateral to that bar. The main nerve, continuing forward, here breaks up into many branches, some destined to supply the supra-orbital canal organs 17 to 34, as already stated, certain others being general sensory ones, but much the larger part of the nerve going to supply the deep ophthalmic group of ampullæ.

Ramus Ophthalmicus Profundus.

The ramus ophthalmicus profundus issues from the skull by a special foramen, as already stated, the foramen lying somewhat posterior to, and nearly in line with, the foramen for the nervus oculomotorius. As the nerve issues from its foramen it lies immediately anterior to the surface of insertion of the rectus inferior muscle, immediately dorsal to the ventral head, or bundle, of the rectus internus, at or near its insertion, and ventro-anterior to the rectus superior. Running forward and slightly outward from there it passes dorsal to and then lateral to the inferior branch of the oculomotorius, which latter nerve here runs backward. The profundus here lies posterior and ventral to that branch of the oculomotorius that innervates the rectus superior muscle, and posterior to the point of origin of the several branches to the rectus internus, thus crossing the oculomotorius distal to those branches. The profundus thus here lies in its well-known position—between the superior and inferior divisions of the oculomotorius, ventral to the one and dorsal to the other. Running outward and forward the nerve passes through the interval between the two bundles of the rectus internus, already described, here accompanying the inferior branch of the oculomotorius, but running in the opposite direction to that nerve. While in this interval a branch arises from the lateral surface of the profundus, and there is, at this point, a small group of ganglion cells which lie on the external surface of the profundus and along the base of the branch in question. These cells have the size and general appearance of the ganglion cells of the cerebro-spinal ganglia, and not that of those of the ciliary ganglion. They would seem, accordingly, to represent a detached and extra-cranial portion of the profundus ganglion. That they represent the entire profundus ganglion seems improbable, though they occupy exactly the position in which that ganglion would naturally be looked for. That the cells represent one of the two sympathetic ganglia described by Onodi (**46**) in the adult Mustelus, I greatly doubt; but I find nothing that corresponds to those ganglia, and I cannot even determine, from his descriptions, where they should be looked for.

The branch that arises from the profundus at the place where the small ganglion is found runs at first backward and but slightly outward along the dorsal edge of the inferior branch of the oculomotorius, here passing with the latter nerve across the anterior edge, and then backward along the dorso-lateral surface of the rectus inferior. While the two nerves are in this latter position the branch of the profundus leaves the oculomotorius, and running outward and backward reaches an outer membranous envelope of the eyeball. In or against this membrane it runs backward and separates into two parts, both of which can be traced backward and outward to the posterior surface of the eyeball, where, still in or against the membrane, they lie against the antero-lateral surface of the rectus externus, between that muscle and the sclerotic. The dorsal and smaller branch of the nerve here gradually disappears in the membrane, and quite certainly never pierces the sclerotic. The other and larger branch continues further outward around the eyeball, and quite probably pierces the sclerotic, though this could not be definitely established, the sections here being imperfect. This nerve, in its origin and in its relation to the oculomotorius, corresponds exactly to the posterior ciliary nerve, or ciliaris longus, of Schwalbe's descriptions, and Schwalbe says that his nerve pierced the sclerotic. Tiesing says that the oculomotorius, as it passes over the eye-stalk, gives off a delicate ciliary nerve, which unites with a branch of the profundus and goes to the bulbus. The conditions that I find differ somewhat from those described by either of these authors, in that one branch of my nerve quite certainly does not pierce the sclerotic. This branch is thus quite probably not a ciliary nerve, and would seem to correspond approximately to the lachrymal nerve of human anatomy.

As it gives off this first branch the ophthalmicus profundus issues from the interval between the two bundles of the rectus internus, and then continues its forward course, passing downward and forward across the postero-lateral surface of the internus muscle, and then ventral to that muscle. When it reaches the ventral edge of the muscle it gives off a delicate branch which separates into two parts, and possibly into three, for a line of tissue here continues the course of the branch, and I am unable to tell whether it is partly nervous or wholly of fibrous or connective tissue. The two parts of which I am sure form the radix longa, and run downward and backward to the ciliary ganglion. The other one, if it be a nerve, must be a part of the ciliaris longus, for it runs downward and forward to join the optic nerve.

Anterior to the point where the radix longa is thus given off, the ophthalmicus profundus continues its forward course, lying lateral or ventro-lateral to the ventral edge of the rectus internus. In this position it passes dorsal to the optic nerve, and immediately beyond that nerve gives off a large branch which runs forward and outward to the antero-ventral aspect of the eyeball. There it pierces the outer membranous envelope of the eyeball, and continuing forward between that membrane and the sclerotic diminishes gradually in size, and finally disappears without ever piercing the sclerotic, so far as I could determine. It lies, in this terminal part of its course, slightly lateral to the ventral edge of the rectus internus, this position thus seeming similar to that occupied by the ciliaris brevis of Herrick's descriptions of Menidia (**32**, p. 224), just as, or before, that nerve pierces the sclerotic. If the nerve in Mustelus does not pierce the sclerotic, as my observations would seem to indicate, it cannot be the homologue of Herrick's nerve, for it would not be a ciliary nerve. If it be not such a nerve it would seem to correspond somewhat to the infra-trochlear branch of the nasal nerve of man.

Near the anterior end of the orbit the ophthalmicus profundus passes between the obliquus superior and obliquus inferior muscles, near their insertions, lying in its accustomed relations, ventral to the one and dorsal to the other. Beyond these muscles the nerve passes along the mesial edge of the muscle Addβ, and then, when it reaches the level of the hind end of the nasal chamber, pierces the cartilaginous side wall of the brain case, considerably dorsal to the nasal chamber, and enters the cranial cavity. There it runs forward along the inner surface of the side wall of the brain case, there lying directly internal to the antorbital process. Somewhat anterior to that process it again pierces the cartilaginous side wall of the brain case, and, issuing a second time from the cranial cavity, reaches the position slightly ventro-lateral to the ophthalmicus superficialis already described in describing the latter nerve. In this position it passes on to the dorsal surface of the nasal capsule, and toward the anterior end of that capsule, after giving off a large branch, comes into intimate juxtaposition with the ventral surface of the ophthalmicus superficialis. Leaving that nerve, it gives off a small branch, and then separates into two large branches, each of which again separates into two branches. All five of the terminal branches thus formed of the nerve turn downward over the anterior end of the nasal capsule, and then backward along its ventral surface. Running backward, ventral to the nasal capsule, the branches of the mesial one of the two large branches of the nerve gradually disappear. The largest branch of the other lateral and larger portion of the nerve soon pierces the ventral wall of the nasal capsule, and reaches the inner surface of the capsule. There it continues backward toward the nasal aperture, breaking up into several branches, some of which pierce the cartilage again, passing outward through it to its external surface.

The large branch given off just before the main nerve comes into intimate juxtaposition with the ophthalmicus superficialis, runs forward, laterally and downward, along the lateral surface of the anterior portion of the nasal capsule, and owing to breaks in the sections at this point could not be definitely traced. It ran down toward and seemed to be distributed to the region adjoining the antero-lateral end of the nasal-flap cartilage, where the supra-orbital lateral canal comes into close relation with that cartilage.

The only branches of the profundus nerve that were sufficiently large to be distinguished and traced thus go either to the eyeball or to the nasal capsule. The nerve, however, diminishes in size between these several branches, and certain of its fibres may have a different and general distribution. That the nerve has anything whatever to do with the innervation of the ampullary tubes, as Ewart states is probable in Læmargus (**17**, p. 527), I greatly doubt. Certain of the terminal branches of the nerve would seem to correspond to the branch said by Cole (**11**) to be distributed, in Chimæra, to the "outer surface of the inner wall of the nostril." This nerve Cole considered as the probable homologue of the motor division of the profundus of the Cyclostomes. This will be later further discussed.

Whether the distribution of the only apparent branches of the profundus to the eyeball and the nasal capsule has any morphological significance or not, or what that significance may be, I cannot venture to assert. The nerve is evidently the nasal or naso-ciliary nerve of the higher vertebrates, as is generally asserted and accepted, and the dorsal and proximal one of its two orbital branches would correspond somewhat to the lachrymal nerve of man, the ventral and distal one corresponding somewhat to the infra-trochlear nerve.

Truncus Buccalis-maxillo-mandibularis.

The truncus maxillo-mandibularis or trigeminal part of the large buccalis-maxillo-mandibularis nerve trunk arises from the antero-ventral part of the extra-cranial portion of the trigemino-facial ganglion, the ramus buccalis arising from the antero-dorsal part of the same ganglion. That part of the ganglionic complex from which the buccalis arises forms a distinctly separate ganglion, which lies partly embedded in the underlying antero-ventral part of the entire complex. Both nerves, forming a single trunk, run at first laterally, forward, and downward, the truncus maxillo-mandibularis separating immediately into two strands, one of which is the ramus maxillaris trigemini, and the other the ramus mandibularis trigemini. The ramus mandibularis immediately passes laterally and forward, ventral to the buccalis, and thus soon acquires a position postero-lateral, and in part ventral to the latter nerve. The ramus maxillaris remains along the antero-mesial edge of the buccalis, also lying in part ventral to it, the buccalis forming, in sections, a large blunt wedge between the two trigeminal nerves. The three nerves together here form a single large and flattened trunk, which lies on the dorsal surface of the so-called basal plate of the skull, which plate, projecting laterally and somewhat downward, forms the floor of the orbit. The nerve trunk lies immediately internal to the large peri-orbital sinus, and in its forward course it passes internal, or ventral, to all the structures in the orbit, excepting only to two arteries, the anterior and posterior carotids of Parker's descriptions. It passes dorsal to the anterior carotid, immediately postero-lateral to the point where its ophthalmic branch is given off, and then lies antero-lateral to the artery. The posterior carotid pierces the floor of the orbit, and passes from its ventral to its dorsal surface, ventral to the hind end of the extra-cranial trigemino-facial ganglion. It then reaches the lateral aspect of the ganglion, and as it traverses the orbit, running forward and laterally, lies ventral to the lateral edge of the truncus buccalis-maxillo-mandibularis, the truncus thus lying dorsal to the artery.

In this orbital part of the course of the truncus the buccalis is, as already stated, a somewhat triangular strand wedged in between the mandibularis and maxillaris. Soon after the truncus leaves its ganglion, certain general sensory branches arise from the ramus maxillaris, and run outward and forward, ventral to the buccalis, and then upward along the lateral surface of that nerve. They thus come to lie along the dorso-lateral edge of the buccalis, between it and the mandibularis, and from that position they later run to the regions they innervate. The ramus mandibularis thus here begins to become detached from the remainder of the truncus, and shortly before reaching the point where the palato-quadrate cartilage articulates with the antorbital part of the skull, it runs outward over the dorsal edge of the palato-quadrate cartilage, and then downward and backward, at first lying along the lateral, external surface of the adductor mandibulæ muscle, but gradually becoming imbedded in the fibres of that muscle.

The remaining portion of the truncus now represents the united maxillaris trigemini and buccalis facialis. It turns more directly forward, and passes lateral to the articular process of the palato-quadrate, there lying at first along the dorsal edge of the dorso-anterior corner of the adductor mandibulæ muscle, but soon turning downward and forward to reach the lateral surface of the muscle Addβ of Vetter's descriptions (**63**). Here both of the nerves immediately give off numerous branches, which, united more or less completely, seem to form a large and important outer division of the truncus. This division, however, immediately breaks up into numerous branches, some destined to innervate the sense organs of the infra-orbital canal, others to innervate the general tissues, and still other and more important ones to innervate the sense organs of the buccal group of ampullæ.

The remaining portion of the truncus has now reached the lateral edge of the head, and here turns mesially, forward and downward on to its ventral surface, still lying along the external surface of the muscle Addβ, that surface here being presented ventro-laterally. Continuing its course in this position, it soon passes beyond the level of the anterior end of the palato-quadrate cartilage, and reaches the level of the hind end of the nasal capsule. It there still lies ventro-lateral to, and along the external surface of, the muscle

Addβ, but that muscle here separates into two heads, one of which has its origin from the mesial edge of the ventral opening of the cartilaginous nasal capsule, near its hind end, while the other arises, dorsal to the hind end of the nasal capsule, from the dorsal and ventral surfaces of the projecting ventro-lateral end of the antorbital process.

Anterior to this point the truncus follows the ventral head of the muscle Addβ, lying ventral to its antero-lateral edge, and, with it, crossing the hind end of the ventral opening of the cartilaginous nasal capsule, posterior to the external nasal aperture. Anterior to the muscle Addβ, what is left of each of the two main nerves turns directly forward, and here lies near the lateral edge of the horizontal plate-like extension of the ventral edge of the internasal cartilage. In this position the two nerves pass mesial to the external nasal aperture, and, anterior to that aperture, lie at first along the ventro-mesial aspect of the rounded anterior end of the nasal capsule, in the angle between the capsule and the ventro-median rostral bar of cartilage, and then, anterior to the capsule, continue forward toward the end of the snout, remaining always along the lateral aspect of the ventro-median rostral bar.

The general course of this truncus buccalis-maxillo-mandibularis having now been described, the branches of the three nerves that form it can be given.

Ramus Buccalis Facialis.

The first five branches of the buccalis facialis arise from the ganglion of the nerve, and not from the nerve itself. The first three branches are given off, close together, from a dorso-posterior prolongation of the ganglion of the nerve, and have already been fully described when describing the lateral organs they innervate. They run upward and backward in the orbit, along the side wall of the skull, and separate into four branches, one of which pierces the overhanging orbital roof to innervate organs 103 to 110 infra-orbital, while the other three turn outward and innervate organs 87 to 102 and the sensory organ of the spiracle, in the manner already described. The branch that innervates organs 103 to 110 is the ramus oticus facialis of current descriptions. The three branches that together innervate organs 87 to 102 probably represent the inner buccal of Cole's descriptions of Chimæra, though it may be that that nerve of Chimæra also includes the next two following branches of the buccalis of Mustelus. These next two following branches of the buccalis are given off, close together, from the lateral aspect of the ganglion of the nerve, not far from the three preceding ones, but from a somewhat distinct and different part of the ganglion. Each nerve is joined at once by a general sensory branch, which arises from the base of a large nerve that has its origin from the postero-ventral end of the trigeminal part of the extra-cranial part of the trigemino-facial ganglionic complex. This large nerve is partly motor, and will accordingly be described as a branch of the ramus mandibularis trigemini. Its motor fibres are destined to innervate the levator maxillæ superioris and spiracle muscles. Each of the lateral sensory nerves here under consideration, with its accompanying general sensory branch, runs at first backward and laterally, ventral to the peri-orbital sinus, then turns outward through the sinus, and then forward and outward, the lateral components separating from the general sensory ones and going to innervate, respectively, organs 83 to 86, and 79 to 82, infra-orbital.

The next two branches of the buccalis arise from the buccalis itself, and not from the ganglion of the nerve. They are given off not far apart, from the lateral aspect of the nerve, just as the ramus mandibularis separates from the still united buccalis facialis and maxillaris trigemini. There are thus no branches given off by the buccalis between its point of origin from its ganglion, and the point where the ramus mandibularis definitely separates from it. The two branches given off at the latter point run forward a considerable distance, nearly parallel to, and not far from the buccalis. The proximal one then first turns laterally, then laterally and backward, and separates into two parts—one of which continues backward and innervates organs 77 and 78 infra-orbital, the other turning forward and innervating organs 75 and 76. The distal one of the two branches continues still farther forward, and, branching, innervates organs 70 to 74. Each of these two buccalis branches is closely accompanied, through a part of its course, by a general sensory branch of the ramus maxillaris.

Anterior to these last two branches the buccalis turns downward, with the maxillaris trigemini, on to the lateral surface of the muscle Addβ, and there immediately gives off a large branch which, breaking up into several smaller branches, is distributed entirely to the sensory organs of the large buccal group of ampullæ. The several branches of this large ampullary branch are grouped into two portions, rather than forming parts of two main branches. The branches of the larger one of these two portions go to ampullæ that lie dorsal to a membrane that extends inward from the internal surface of that section of the infra-orbital canal that lies between the suborbital bend in the canal and the point where the hyomandibular canal is given off, the branches of the other portion going to ampullæ that lie ventro-mesial to the same membrane. The membrane and nerves thus here indicate two sub-groups of this large group of ampullæ, and they may, possibly, correspond to the inner and outer buccal groups of Ewart's descriptions. It is, however, to be remembered that neither of the sub-groups of Mustelus occupies the position of Ewart's inner buccal group, that position seeming to correspond exactly to that occupied by my deep group of ophthalmic ampullæ.

As this large ampullary nerve is given off by the buccalis, the remaining fibres of the nerve, which are now entirely lateral sensory ones, separate into two principal portions. One of these portions separates almost immediately into several branches, all of which run outward, forward, and downward, and supply organs 46 to 69 infra-orbital, these organs all lying in the three arms of the double suborbital bend of the canal; that is, organ 69 lies in the circum-orbital part of the canal, shortly posterior to the point where the canal turns downward and backward ventral to the anterior edge of the eye, and organ 46 lies immediately proximal to the point where the infra-orbital canal anastomoses with the distal end of the supra-orbital canal. This large lateral sensory branch, the ampullary branch, and certain general sensory branches, together form a large group of nerves, which have the appearance of being a somewhat separate branch or division of the truncus buccalis-maxillaris.

The second and remaining portion of the buccalis forms an anterior or terminal division of that nerve. It runs forward along the external surface of Addβ with the remaining portion of the ramus maxillaris, the two nerves lying close together, but as two wholly separate strands. The buccalis here lies lateral to the maxillaris, and soon separates into two parts, one destined to innervate organs 26 to 45 infra-orbital, which lie between the point where the canal anastomoses with the distal end of the supra-orbital canal, and the middle point of the short median section of the canal; and the other one destined to innervate organs 1 to 25. The branch destined to supply these latter organs forms the terminal section of the entire nerve, and in its forward course it crosses ventral—that is, superficial to the ramus maxillaris, and reaches its mesial side.

This anterior division of the buccalis thus innervates the organs that lie in that part of the infra-orbital canal that corresponds to the anterior, or antorbital, cross-commissure of my descriptions of Amia. The nerve accordingly corresponds to that somewhat separate and terminal part of the buccalis that in Amia innervates organs 1 to 4 infra-orbital (2, p. 514). In Chimæra, Gadus, and Scomber the corresponding fibres of the buccalis also form a separate branch or division of the nerve, and I have already had occasion to call especial attention to it, not only in the work on Scomber that is still in press, but also in one of my published works (**4**, p. 366). This branch or division of the buccalis, together with certain branches of the maxillaris trigemini, is quite unquestionably the nerve to which Howes has recently made reference (**38**, footnote, p. 51) as a nerve for which the late Professor Huxley intended proposing the name palatonasal, or hyporhinal. Professor Howes has very kindly sent me[1] a full copy of the unpublished manuscript in which this nerve is discussed by Professor Huxley, and I consider the subject so important that I shall quote quite fully what Huxley says about it. I shall also later quote what Huxley has to say, in the same manuscript, about the chorda tympani.

This unpublished memoir of Huxley's was to have been entitled "Vertebrate Head; with Special Reference to Trigeminal and Facial Nerves and Trabeculæ."

Having described the branches of the facial nerve in man and in Amphibia, Professor Huxley then takes up the facial nerve in the common Ray. The posterior division of this nerve in this fish is first described, and I shall quote his description in full in connection with my discussion of the chorda tympani. He then says:—"II. The anterior division runs forward in the dorsal aspect of the oral mucous membrane, on the inner side and in front of the spiracle. From its outer side it gives off numerous branches, some of which are distributed to the muscles of the spiracle, and some to the spiracular branchia; some run outwards and ventrally along the anterior face of the spiracular cartilage and the ligamentous fibres which connect it with the palato-quadrate cartilage, and can be traced as far as the articulation of the mandible, while yet others proceed to the palatine mucous membrane extending to the posterior margin of the palato-quadrate cartilage.

"It is clear that this nerve answers to some extent to the palato-nasal nerve of the amphibia—answers, in fact, to the posterior palatine nerve, but it gives off no fibres having the distribution of those which pass between the nasal sacs on the dorsal side of the vomers, and which I suppose to be the homologue of the nerve of Cotunnius.

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[1] 'Life and Letters of T. H. Huxley,' vol. ii, App. 1.

"But there is a very large nerve, a branch of the trigeminal, which in the Ray arises almost directly from the short common trunk, but is buried up for a short distance with the second division of the fifth, and then passes forwards and inwards along the base of the skull, and on the inner side of the nasal capsule, to the snout, where it divides into a leash of branches for the sensory tubes of that region. From the outer side of this nerve, while it lies in the orbit, branches are given off to the posterior face of the olfactory capsule.

"This nerve is identified by Stannius with what he terms the ramus buccalis of the maxillary nerve in osseous fishes. But it appears to me to have nothing to do with this nerve, which is otherwise represented in the Rays.

"The branch of the trigeminal under discussion appears to exist in all the Plagiostomes, and considering the many embryonic characters retained by these fishes, I am led to believe that it represents in a distinct form a nerve which in most fishes and in the higher vertebrates has coalesced with the anterior palatine division of the seventh, and has in that manner given rise to the Videan nerve." This branch of the trigeminus in the Ray is later always referred to by Professor Huxley as the palato-nasal.

Huxley then states his conclusions:—(1) That the spiracle of the Ray "answers to the tympano-Eustachian passage of the higher Vertebrata," and (2) "that the palato-quadrate cartilage in the Ray and other corresponding structures in the embryo of the higher Vertebrates is a mere appendage of the mandibular arch, and not a distinct visceral arch, as I was formerly inclined to suppose."

He then says:—"But if the pterygoid cartilage is only an outgrowth of the mandibular arch, it follows that the space between the mandibular and the trabecula on each side represents a trabeculo-mandibular visceral cleft, and this ought to be supplied by a nerve dividing into anterior and posterior divisions as the portio dura does. It appears to me that there is no difficulty in finding the posterior division or nerve distributed to the (morphologically) anterior face of the mandibular arch. The second and third divisions of the trigeminal, in fact, fulfil all the requirements of such a nerve, the second being distributed to the outer face of the pterygoid appendage of the mandibular arch, just as the palatine nerves are distributed to its inner face, and the mandibular, or third division of the fifth, running along the outer face of Meckel's cartilage, in correspondence with the distribution of the long descending branches of the palatine in the Ray on its inner face. If this be the posterior nerve of the trabeculo-mandibular visceral cleft, where is its anterior nerve? On this point it may be well to speak cautiously, but certain facts are highly suggestive. The palato-nasal branch of the fifth in the Ray virtually runs along the ventral outer, a morphologically posterior edge of the trabecula—which, as I think, cannot be doubted is the homologue of a visceral arch; on the other hand, the orbito-nasal nerve (first or ophthalmic division of the fifth) runs along the dorsal, a morphologically anterior edge of the trabecula.

"It seems to me highly probable, therefore, that the palato-nasal nerve of the fifth (or nerve of Cotunnius) is the anterior division of the nerve of the trabeculo-mandibular cleft, which should run along the morphologically posterior face of the trabecula, and that the orbito-nasal nerve is the nerve of the anterior face of the trabecula, which found an actual aperture only in the marsipobranchii (and pharyngobranchii ?), where it limits the naso-palatine canal laterally."

It is impossible to recognise in Mustelus exactly what fibres are included in this palato-nasal nerve of the Ray, and it seems to me that Huxley himself did not have a correct or definite idea of exactly how the nerve is composed. That the nerve contains the terminal portion of the buccalis, as that nerve was described by Stannius, and as it has since been described by other authors, is evident, and the lateral sensory component of the nerve is certainly not coalesced with the anterior palatine division of the seventh in osseous fishes, as Huxley supposed. That this terminal part of the buccalis belongs to a premandibular arch is, however, extremely probable, and is later more fully discussed; and it is to Huxley's very definite opinion on this subject that I have wished to call especial attention. The lateralis component of this nerve of fishes would not, according to recent ideas, be retained in the higher Vertebrates; but the ampullary component quite probably would be retained, and, with such general cutaneous fibres as may belong to the nerve in fishes, it would form the nerve in the higher Vertebrates.

Ramus Maxillaris Trigemini.

The first two general sensory branches of the nervus trigeminus arise from the very base of the large ramus ad musc. lev. max. sup., and would accordingly seem to belong to the ramus mandibularis trigemini rather than to the ramus maxillaris. They, however, both accompany branches of the ramus buccalis, and are hence here considered as branches of the maxillaris trigemini. They have both already been referred to in describing the buccalis. One of them accompanies the buccalis branch to organs 83 to 86, and the other the buccalis branch to organs 79 to 82. Both branches run at first backward and outward, near the floor of the orbit, and then forward and outward to the regions they innervate.

Anterior to these two branches a branch is sent out with the buccalis nerve to organs 75 to 78, and another with the buccalis nerve to organs 70 to 74. These two branches both arise from the latero-ventral part of the maxillaris, and both run at first forward, downward, and laterally, closely applied to the ventral surface of the buccalis, and then forward and laterally, passing outward along the lateral surface of the buccalis, between it and the ramus mandibularis. Having thus reached the dorsal surface of the large truncus, between its buccalis and mandibularis components, they there have their apparent origins from the truncus, and join the buccalis nerves they accompany.

Beyond these four branches the maxillaris turns downward on to the lateral surface of the muscle Addβ, and as it acquires this position a large branch becomes detached from the dorsal surface of the nerve, and runs forward and laterally directly internal to that portion of the buccalis that goes to the infra-orbital organs 46 to 69 and to the buccal group of ampullæ. Two small branches arise from this branch before it becomes entirely detached from the main trunk, and running forward, dorsal to the buccalis and ventral to the peri-orbital sinus, reach the ventral surface of the antorbital process of the skull, being closely accompanied in their course by a branch of the posterior carotid artery. The main branch, after it becomes detached from the maxillaris, sends several branches to the tissues antero-ventral to the eye, certain of them accompanying certain of the buccalis branches that go to infra-orbital organs 46 to 69. The remaining portion of the main branch then separates into two parts, both of which run forward along the lateral surface of Addβ, and beyond the anterior edge of the dorsal head of that muscle lie, one along the ventro-lateral corner of the nasal capsule, and the other in the angle between that capsule and the side wall of the brain case. The ventral branch here lies directly internal to and accompanies the subrostral section of the supra-orbital canal, a maxillaris branch of the trigeminus thus here being associated with the ophthalmic lateral canal.

The large branch just above described is given off from the dorsal surface of the maxillaris. At about the same time two branches become detached, one from the ventral surface of each of the two branches into which the buccalis separates after having given off the branches to the buccal group of ampullæ. These two branches, although having their apparent origins from the two branches of the buccalis, are maxillaris and not buccalis nerves, but they become detached from the maxillaris and intimately associated with the buccalis a very considerable distance posterior to this point, while the main nerves are still on the floor of the orbit. Like the other maxillary branches that leave the nerve in that part of its course, they pass along the ventral aspect of the buccalis in their forward and outward course from their real to their apparent points of origin.

The lateral one of these two maxillaris branches has the most posterior origin from the maxillaris. After it has become detached from that portion of the buccalis that it accompanies, it runs laterally and downward until it reaches the inner surface of a membrane that here bounds the inner surface of the region occupied by the buccal ampullæ and ampullary canals, where it turns backward, downward, and mesially along the inner surface of that membrane. In this position, having first sent a small branch forward, it continues backward, downward, and mesially until it reaches the anterior end of the integumental furrow that separates the maxillary labial fold from the under surface of the head. It then continues backward along that edge, lying ventromesial to it, and gradually disappears.

The other one of the two branches also soon turns downward and backward, sending two small branches forward at the bend. It remains at first close to the latero-ventral surface of Addβ, but later passes into the maxillary labial fold, which it innervates. Whether or not it continues backward until it reaches and enters the mandibular labial fold also could not be determined.

One or both of these two branches evidently correspond to the so-called maxillary branch of the superior maxillary nerve of Amia and teleosts.

Anterior to these two branches the main maxillaris nerve acquires a position directly internal to the buccalis, and there gives off a large branch from its ventral edge, and another from its dorsal edge. The ventral branch is joined by the anterior branches of the branch just above described, with which it fuses. The nerve thus formed runs downward, mesially and but slightly forward, passes beyond the ventro-mesial edge of the muscle Addβ, and reaches the ventral surface of the extreme anterior end of the palato-quadrate cartilage. There it crosses the middle line of the head as a stout nerve, and hence doubtless here anastomoses with its fellow of the opposite side, though this could not be definitely established, my sections being of one half of the head only.

The dorsal branch given off by the maxillaris at the same time as the above-described ventral one passes outward and forward dorsal, and hence internal, to the buccalis, and separates into two parts which accompany the two branches of the buccalis sent, the one to organs 44 and 45 infra-orbital, and the other to organs 42 and 43, these four organs lying in the bend of the infra-orbital canal, just distal to the anastomosis with the distal end of the supra-orbital canal. These two branches of the maxillaris continue forward and mesially beyond the distal ends of the two buccal branches they at first accompany, and reach the ventral surface of the nasal capsule, in the region adjoining that part of the infra-orbital canal that lies posterior to the nasal aperture. A branch is here sent, from the mesial one of the two nerves, to accompany the branch of the buccalis that goes to organs 40 and 41 infra-orbital, the remaining portions of both nerves continuing forward, internal to the infra-orbital canal, toward the hind end of the nasal aperture. The branch that at first accompanied the buccal nerve to organs 42 and 43 infra-orbital, here turns dorsally through one of the slit-like foramina or imperfections in the ventral floor of the nasal capsule, and, entering that capsule, sends one branch forward and mesially, and another forward and laterally, along the ventral surface of the nasal sac. How far forward these branches extended could not be determined.

The main ramus maxillaris, after giving off the branches above described, follows the course of the infra-orbital canal, and passes, with it, mesial to the nasal aperture, here lying always dorso-mesial to the canal and mesial to the buccalis. Several branches here arise from the maxillaris, some running forward and mesially, and others forward and laterally, the latter passing internal, that is, dorsal, to the buccalis. One of these latter branches turns upward into the nasal capsule, and could be traced forward a certain distance, ventral to the mesial portion of the nasal sac. It was then lost, but an important branch which would seem to very probably represent its most anterior section was found turning backward around the anterior end of the sac.

The remainder of the maxillaris then continues forward, lying at first ventro-lateral to the median section of the infra-orbital canal, and then directly internal, and hence dorsal, to the more anterior part of the same canal. It is there distributed to the general tissues of the region.

Ramus Mandibularis Trigemini.

The ramus mandibularis or maxillaris inferior trigemini arises from the trigeminal part of the trigemino-facial ganglion as part of a short truncus trigemini which immediately separates into maxillaris and mandibularis portions. The ramus mandibularis immediately runs laterally downward and forward, ventral to the ramus buccalis, and acquires a position postero-lateral to the latter nerve, there forming the postero-lateral portion of the large, flat, truncus buccalis-maxillo-mandibularis.

At or before the ramus mandibularis thus separates from the ramus maxillaris, and while the truncus trigemini is still ganglionic, a large branch is given off from its posterior aspect. Turning laterally upward and backward, it passes dorsal to the posterior carotid artery, immediately anterior (distal) to the orbital branch of the artery, and then passes upward along the lateral aspect of the facial part of the trigemino-facial ganglion, here being partly imbedded in the ganglion. It passes dorsal to the ramus palatinus facialis, accompanied by the orbital branch of the posterior carotid. Dorso-posterior to the trigemino-facial ganglion it lies ventro-lateral, and then lateral or antero-lateral to the truncus hyoideo-mandibularis facialis, accompanying the truncus in its course, and lying, with it, at first along the mesial surface of the hind end of the peri-orbital sinus, and then ventral to that posterior prolongation of the sinus that goes backward to join the jugular vein. This posterior prolongation of the peri-orbital sinus is called by Ridewood (**54**), in Scyllium, the post-orbital blood-sinus. Here the trigeminal nerve leaves the truncus facialis and turns laterally and backward across, and dorsal to, the anterior portion of the anterior diverticulum of Wright's (**70**) descriptions of the spiracular cleft of the fish. It has here already separated into three parts—one larger and two smaller ones,—all of which pass outward anterior to the superior postspiracular ligament of Ridewood's descriptions of Scyllium, and anterior also to the posterior or auditory diverticulum of the spiracular cleft. One of the smaller parts of the nerve was here lost in the sections. The other two parts both reach the internal surface of the levator maxillæ superioris muscle of Vetter's descriptions, which they seem to penetrate and innervate. A part of the fibres of the nerve are, however, quite unquestionably distributed to the general tissues of the region, for that the nerve contains general sensory fibres is clearly shown by the two branches that arise from near its base, and that accompany the two buccalis branches.

The levator maxillæ superioris muscle of my embryo is apparently exactly such a muscle as Tiesing describes in the adult. The muscles of my embryo that represent the three muscles of the adult considered by Tiesing as parts of Csd_1, differ somewhat from those muscles as described by him, but I should state that I am unable to clearly comprehend his descriptions and figure of them. The muscle called by Tiesing the levator palpebræ nictitantis I find exactly as he describes it, excepting that, as this muscle crosses the two other muscles, dorsal to the spiracle, its postero-ventral edge is imbedded in those muscles to such an extent that the ventral half of its outer and inner surfaces is covered by them. In transverse sections the levator muscle is here of oval section, inclining towards the skull, the other two muscles together forming, in sections, a deep gutter which encloses the lower half of the levator. The other two muscles together form a T-shaped muscle, more or less fused with the levator maxillæ superioris. The T is placed upside down, its leg representing a part of the muscle that first runs inward, and then upward and backward along the outer surface of the hind edge of the levator maxillæ superioris, to have its origin with that muscle from the skull, as Tiesing describes for his muscle $Csd_1\gamma$. The posterior arm of the inverted T runs backward above the spiracle, and has its origin on the fascia there as Tiesing describes. The anterior arm of the inverted T is the retractor palpebræ superioris of Tiesing. Nerve fibres could not be definitely traced to these muscles, but they would seem to be most unquestionably innervated by branches of the same nerve that innervates the levator maxillæ superioris, as Tiesing states. The posterior head of the deeper muscle might, however, easily receive fibres from that branch of the facialis that innervates Csd_2.

Beyond this large and largely motor branch no branch is given off by the ramus mandibularis until after it separates, as already described, from the truncus buccalis-maxillaris just before that truncus passes outward from the floor of the orbit on to the lateral surface of the muscle $Add\beta$. Running laterally across the dorsal edge of the palatoquadrate cartilage, the ramus mandibularis reaches the dorsal edge of the antero-dorsal corner of the adductor mandibulæ. There the larger part of the nerve turns downward and backward along the outer surface of the adductor, lying in a groove between that muscle and the muscle $Add\beta$.

As the ramus mandibularis here turns downward and backward it gives off a large branch, which, separating into two parts, sends one branch forward and downward into the anterior portion of the muscle $Add\beta$, and another backward and downward into the posterior portion of the same muscle. This is, accordingly, the motor nerve of the muscle $Add\beta$, and it is certainly in my embryo a branch of the ramus mandibularis, and not a branch of the ramus maxillaris. Both Stannius (**59**) and Tiesing (**62**) find this muscle innervated by a branch of the ramus mandibularis in the selachians examined by them, while Vetter (**63**) and Jackson and Clark (quoted from Tiesing, p. 96) both find it innervated by a branch of the ramus maxillaris. In Galeus I (**3**, p. 573) found the muscle innervated by the terminal portions of a small double nerve that arose from the base of the truncus trigemini, if not even from the ganglion of that nerve. Proximal branches of this double nerve innervated the levator maxillæ superioris and the larger spiracle muscle. While I cannot affirm the accuracy of these statements regarding Galeus, taken from notes and not confirmed, they led me, at the time that I was considering this subject, to conclude that the muscles Csd_1, Lms, and Addβ might, in part, represent parts of the constrictor superficialis dorsalis of one or more pre-oral arches (**3**, p. 574). This conclusion, in so far as it relates to the muscle Addβ, is greatly strengthened by what I now further find in Mustelus.

The muscle Addβ, the levator labii superioris of Tiesing, arises in all my embryos by two perfectly distinct heads, instead of by a single large one, as Tiesing describes it in the adult. The larger one of the two heads arises mainly from the ventral surface of the antorbital process, and from the outer surface of the bulging hind end of the nasal capsule ventral to that process, but a part of the fibres of the muscle pass upward around the hind edge of the ventral projection of the antorbital process, and arise from its dorsal surface. The other head of the muscle arises from the mesial edge of the ventral aperture of the cartilaginous nasal capsule, slightly anterior to its hind end. The fibres of the two parts fuse completely, and when the muscle reaches the level of the antero-dorsal corner of the adductor mandibulæ, it lies ventral to the latter muscle. Posterior to this point a tendon begins to form on the rounded dorsal surface of the mesial portion of the muscle (fig. 8), and then, gradually, as this part of the muscle diminishes in size, acquires a position at its ventromesial edge (fig. 9). There it separates into three parts. One of these three parts retains its position along the ventromesial edge of the united Addβ and adductor mandibulæ muscles, and continues backward to join, or form part of, the aponeurosis that separates the superior and mandibular parts of the adductor. A second part has its insertion on the anterior end of the posterior upper labial cartilage. The third part continues backward parallel to, and slightly dorso-mesial to, the latter cartilage, and has its insertion on the dorso-posterior end of the mandibular labial cartilage. This insertion of these tendons of Addβ on these two labial cartilages certainly indicates that a part, at least, of the muscle belongs to a pre-oral arch, if the labial cartilages do, as I believe is very generally accepted. The nerve that innervates these parts of Addβ must then belong to the same arch, and must be a motor component of the post-trematic nerve of the arch. Hoffmann, it should be noted, says (**34**, p. 266) that the muscle Addβ arises from the upper part of the wall of the "Kieferbogenhöhle," an origin which would seem to preclude its belonging to a pre-oral arch.

After giving off this motor branch to the muscle Addβ the ramus mandibularis sends a relatively small but still important branch downward and backward along the external surface of the adductor. When it reaches, approximately, the level of the anterior end of the posterior upper labial cartilage it turns forward a short distance, then mesially, and then downward, laterally, and backward into the maxillary labial fold, there lying dorsal to the labial cartilage. If the cartilage belongs to a pre-oral arch, this branch of the mandibularis thus has the relations to the mouth, considered as a cleft, of a ramus pre-trematicus, the ramus mandibularis itself being the related ramus post-trematicus. Considering it as such a branch it would be the ramus branchialis posterior of the posterior labial arch, the motor nerve to the muscle Addβ being the motor component of the ramus branchialis anterior of the same arch. Those two branches of the ramus maxillaris superior trigemini that are also distributed to the labial fold of the fish would then either be the sensory components of the ramus branchialis anterior of the same arch, or perhaps be, respectively, the pre- and post-trematic branches of the next preceding or anterior labial arch. It should here be stated that there are in my embryos, contrary to Gegenbaur's statement (**23**, p. 214) for the adult, two separate and distinct upper labial cartilages, both lying in, or in relation to, the labial fold of the fish. The anterior cartilage has no direct relations to any of the muscles of the fish.*

There are thus two pre-oral arches indicated in embryos of Mustelus. In each arch there are what are considered by Gegenbaur as remnants of the cartilages of the arch, and I now further find not only muscles definitely related to one of the arches, but also nerves that certainly might be considered as the pre- and post-trematic branches of each arch. The nervus trigeminus would then be a nerve formed by the fusion of at least three segmental nerves, and the ramus maxillaris superior trigemini would probably contain the pharyngeal elements of all these nerves, in addition to containing, in its proximal portion, certain of their pre- and post-trematic elements.

The ramus mandibularis of Mustelus, after giving off the branch to the labial fold above described, passes downward and backward on to the lateral surface of the adductor mandibulæ, lying at first between that muscle and the posterior portion of the muscle Addβ, and then becoming gradually imbedded in, and entirely enveloped in, the single muscle formed by the fusion of these two muscles. Continuing backward and mesially in this position it separates into two nearly equal portions. One of these two portions is probably wholly motor, and is the ramus ad musculum adductoris mandibulæ. It remains always in the interior of the muscle-mass, and running backward and downward sends branches both to the superior and inferior divisions of the muscle. Two branches were sent through the muscle to its dorso-mesial corner, and

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[1] Gegenbaur in his references to the labial cartilages of Mustelus, and also elsewhere, refers in the text to his fig. 2, Plate XII, as representing Mustelus, but this figure, in the description of the plates, is said to be of Galeus—an evident typographical error, as Marshall and Spencer have already pointed out.

were there lost. Whether or not they issued from the muscle and supplied other tissues could not be definitely determined.

The other portion of the ramus mandibularis runs downward, backward, and mesially, until it passes the transverse level of the hind corner of the gape of the mouth, where it issues on the ventral surface of the adductor muscle, and, turning forward and mesially, immediately passes from the outer surface of the superior division of the muscle on to the outer surface of the inferior, or mandibular division. This nerve, in this part of its course, is certainly shown in the nerve marked V_3 in Tiesing's figure 9, in which figure the nerve would seem to be cut. But how this ventral part of this nerve unites with the dorsal part it is impossible to tell from the figure; and the mandibularis externus facialis is apparently not shown at all, certainly not in its proximal portion. I am accordingly unable to here make any comparison with his work.

When the ramus mandibularis reaches the outer surface of the inferior division of the adductor, it sends one or more small branches along the external surface of the united adductor muscles, and a large branch downward and mesially, internal to the mandibularis externus facialis, along the external surface of the inferior division of the adductor. This last branch sends two branches forward along the external surface of the adductor, and itself, close to the mesial edge of that muscle, pierces a well-differentiated intermandibularis muscle, which Tiesing neither describes nor shows in his figures. As it traverses this intermandibularis muscle, the nerve turns dorsally and backward around the ventro-mesial edge of the mandibular cartilage, and reaches the dorsal, or internal, surface of the intermandibularis muscle, near its lateral edge. There it continues backward, sends certain branches into the muscle, and, for a certain distance, diminishes in size. Then it begins to increase in size again, and becomes the terminal part of the ramus hyoideus facialis. These two nerves thus run directly into each other, and anastomose completely, exactly as the branch r. ghi of the maxillaris inferior trigemini and the ramus hyoideus facialis of Amia do (**3**). The relations of the nerves to the muscles are not exactly the same in Mustelus and Amia, but the differences are probably not of morphological importance.

The mesial one of the two branches sent forward along the external surface of the adductor by this ramus ad musc. intermand. passed beyond the adductor on to the ventral surface of the intermandibularis, and there, at a certain point in my sections, was lost while it still had a relatively large section. Whether it penetrated the intermandibularis muscle, as the main branch did, or not, could not be determined. The other and lateral one of the two branches continues forward beyond the anterior edge of the adductor muscle, approaching and accompanying the main mandibularis nerve in the terminal part of its course.

The main ramus mandibularis, after giving off the large branch above described, continues its forward and mesial course, lying immediately dorso-lateral to the mandibularis externus facialis, both nerves soon passing beyond the anterior edge of the adductor muscle and reaching the ventral surface of the mandibular cartilage, near its lateral edge. The ramus mandibularis here lies directly lateral to the mandibularis externus facialis. Somewhat mesial to the latter nerve, and following an approximately parallel course, is the anterior branch of the ramus ad musc. intermand. just above described.

When the ramus mandibularis reaches the transverse level of the hind end of the mandibular labial cartilage, a branch is sent outward from it into the mandibular labial fold. The main nerve then separates into three or four branches, all of which continue forward, and here, at first, lie along the ventral surface of the mandibular labial cartilage. At the level of the anterior end of that cartilage the nerve passes internal to the mandibular group of ampullæ, those ampullæ here taking up the larger part of the mandibularis externus facialis, a small branch only continuing forward to supply the anterior organs of the mandibular canal. The mandibularis trigemini, beyond this point, continues forward, in two principal branches and other smaller ones, toward the tip of the jaw, lying always superficial to the mandibular cartilage.

Nervus facialis.

The truncus hyoideo-mandibularis facialis and the ramus palatinus facialis arise separately from the facial part of the extra-cranial trigemino-facial ganglion, the one from its dorso-posterior portion, and the other from its ventral portion.

Ramus palatinus facialis.—The ramus palatinus runs at first downward and almost directly laterally, along the shelving but nearly horizontally cartilaginous floor of the orbit. In this part of its course it passes dorso-lateral to the hind end of the orbital part of the posterior carotid artery, posterior (proximal) to its orbital branch, and then mesio-ventral to the anterior carotid artery.

Before reaching the lateral edge of the floor of the orbit it sends three branches backward, two of them arising from it close to its base. The proximal branch separates into two parts. One of these parts runs backward in the angle between the side wall of the skull and the floor of the orbit, and, leaving the orbit at its hind end, turns outward posterior to the anterior diverticulum of Wright's descriptions of the spiracular cleft. There branches are sent to the mucous lining of the cleft, the main branch itself joining and becoming confounded with the superior postspiracular ligament as that ligament passes downward behind the spiracular cleft. There is here, perhaps, an anastomosis with a small branch of the glossopharyngeus. This branch of the palatinus facialis thus seeks, and acquires in its terminal portion, a post-trematic distribution, and is, accordingly, a recurrent branch of the ramus anterior of the nervus facialis, similar to certain branches of the rami anteriores of the vagus nerves shown in my drawing 59 of Amia (**3**).

The other part of the proximal branch of the palatinus runs laterally and backward, and is accompanied by the other two of the three orbital branches of the palatinus just above referred to, these latter two branches soon uniting to form a single nerve. Branches, which form anastomoses among themselves, are then given off by the two nerves, so formed, certain of them accompanying the pseudobranchial artery to the spiracular pseudobranch, while others turn downward and forward to the roof of the pharynx.

These first three branches of the ramus palatinus thus, together, probably represent the nervus prespiracularis of Tiesing's descriptions of the adult Mustelus. In Wright's (**70**) descriptions of embryos smaller than my own they are probably what he refers to in the words, "Behind the orbit a few twigs, which run backward to the filaments of the mandibular pseudobranch." Wright further says that the main truncus facialis, which is said to arise from the facial ganglion separately and independently of these twigs, "forks between the two diverticula of the hyomandibular cleft into the præ- and post-trematic branches." The few twigs that run backward to the pseudobranch do not, accordingly, form, in his interpretation of the nerves, the prespiracular division of the facial nerve, this conclusion being based, I believe, on an error of observation, his prætrematic nerve quite probably being, as is shown below, either a branch of the oticus facialis, or a ligament mistaken for a nerve.

After giving off these first three branches, the ramus palatinus reaches the lateral edge of the cartilaginous floor of the orbit, and there turns forward, lateral to, and close to that edge, giving off at the same time three branches. One of these three branches runs forward, parallel to, and close to, but slightly ventral to, the main nerve itself, the other two branches running backward and downward. The anteriorly directed branch lies near the dorsal corner of the lateral surface of the pharynx, and gives branches to the tissues there. The main nerve lies slightly dorso-mesial to this branch, and sends branches to the tissues of the roof of the pharynx. Both nerves can be traced forward to the transverse level of the anterior end of the palato-quadrate cartilage, where they become small and are lost. The two backwardly directed branches run downward to the dorso-lateral corner of the pharynx. One of them there continues backward, giving branches to the adjacent tissues. The other, larger branch runs downward until it reaches the superior surface of the mandibular cartilage, that surface being here directed dorsally and mesially. There it turns forward and continues in that direction, lying immediately ventro-mesial to the lower edge of the band of mandibular teeth. In that position it gradually diminishes, and finally disappears, being traceable with certainty, only to, approximately, the transverse level of the angle of the mouth. It lies, in this distal part of its course, in the deeper part of a fold of the tissues of the mouth cavity, and its relations to this fold, as well as its general course and position, show, beyond question, that it is the homologue of the nerve identified by Green (27) as the chorda tympani in the several selachians examined by him. This identification of the chorda, by Green, is said by him to be based on the homologies proposed for that nerve by Herrick, in his Menidia paper, and is further discussed below.

In Raia and Spinax, Stannius (59) says that the nervus palatinus is represented by three branches, a delicate posterior one, and two stouter anterior ones. One of the anterior branches is said by Stannius to be the true ramus palatinus. The other is considered by Herrick (32) and Green (27) as the homologue of the chorda tympani. The posterior branch is said by Stannius to arise from the ramus palatinus by two roots, these roots later uniting to form a single nerve, which later receives an anastomosing branch from the nerve above identified as the chorda tympani. The three branches that I find, in Mustelus, arising from the orbital part of the nervus palatinus thus together represent the posterior branch of Stannius' descriptions plus the communicating branch from the so-called chorda tympani, this latter nerve in Mustelus being wholly separate and independent of the other three. The three branches of Mustelus accordingly represent the ramus pretrematicus facialis sensu stricto of Herrick and Green.

Haller says (**28**, p. 414–16) that, in Scyllium, the nervus facialis is represented by two principal branches and a third smaller one. The two principal branches are said to be a ramus facialis and a ramus hyoideus, the third one being said to be, perhaps, a ramus palatinus. All three of the nerves are said to arise independently from the so-called facial ganglion, and a separate, independent, and more distal ganglion is said to be found on the ramus facialis. The ramus facialis becomes juxtaposited to the truncus maxillaris trigemini, and this juxtaposition is said to represent an early stage in that ultimate fusion of the two nerves that is said by this author to be found in ganoids, and still more complete in teleosts. Reference is here made to Goronowitsch's (**25**) work on Lota, and it is evident, from this reference, that Haller considers his ramus facialis, either in whole or in part, as the homologue of Goronowitsch's posterior division of the palatinus facialis. Haller does not say whether his so-called ramus facialis is, in Scyllium, a prespiracular or a post-spiracular nerve, but his reference to Gegenbaur's work on Hexanchus (to which I am unable to refer), and Goronowitsch's reference to the same work (**24**, p. 485), leaves little doubt that it is prespiracular. This pretrematic part of the facialis nerve of Scyllium must then have a quite different course, and quite different relations to the trigeminus, to those found in Mustelus. It would seem as if it must contain the nerve identified by Green as the chorda tympani in the selachians examined by him, that nerve, and its homologue in Mustelus, accordingly being quite certainly represented, in Amia, in the maxillaris internus trigemini of my descriptions (**3**).

In Chimæra Cole (**11**) comes to the conclusion that the so-called ramus pretrematicus facialis of his descriptions is the chorda tympani of the fish, and Herrick (**32**, p. 165) accepts this conclusion as probably correct. Herrick also accepts (p. 167) as probably correct my conclusion (**3**, p. 749) that the chorda is probably represented in Amia by certain branches that I described as the ramus mandibularis internus trigemini. But these nerves of Amia are probably not represented, in Chimæra, by the so-called ramus pretrematicus of Cole's descriptions. It seems to me much more probable that they are represented in one or both of two other nerves described by Cole. One is the so-called pharyngeal, or visceral branch of the maxillary branch of the trigeminus; the other a nerve said to be formed by the fusion of three branches of the mandibular branch of the trigeminus. The maxillary branch is said by Cole to curve "round under a large muscle attached to the angle of the upper jaw." The three mandibular branches are said to "curve round and under a corresponding muscle to that which the similar branch of the maxillary curved round." What the muscles to which these nerves are thus related may be is not stated, but the general course of the nerves, so far as given, resembles strongly that of the mandibularis internus trigemini of Amia. If these two nerves in Chimæra are, one or both, the homologue of the nerve in Amia, they must also be the chorda tympani of the fish if the nerve in Amia is. Cole's so-called prebranchial nerve could not then be the chorda, and it might even be found to be a postbranchial nerve, similar to the mandibularis internus facialis of Amia, with which Cole himself homologises it, maintaining, in order to establish his homologies, that the nerve of Amia is a prespiracular nerve (**12**, p. 205). That this nerve of Amia is not a prespiracular one I have already had occasion to assert (**4**).

In seeking the homologue of the chorda tympani in Amia I concluded (**3**, p. 638), as certain other authors had before me, that it must be a prespiracular nerve. This opinion was said to be based on the course of the "nerve in man through the upper portion of the tympanic cavity, and then downward anterior to that cavity." Cole, however, says (**11**, p. 660) that "the chorda tympani of mammals passes morphologically under the tympanum." Cole then contends that the nerve, though thus topographically a post-branchial one, is morphologically a prebranchial one. Herrick (**32**, p. 160), following me, concludes that the chorda is a prespiracular nerve because of its course "through the tympanic cavity and above and in front of the Eustachian tube." Dixon, however, one of the latest workers on the subject, certainly shows the nerve in a post-Eustachian position in a five weeks' old human embryo (**15**, Fig. 15). The relation of the nerve to the Eustachian tube in this figure cannot be mistaken, for the tube lies between the facialis and the trigeminus nerves, and the chorda arises from the facialis considerably beyond the tube and has not a recurrent course. In an embryo seven weeks old Dixon shows the nerve in what would seem to be a pre-Eustachian position (Fig. 9). Whether this difference in the two figures is due to some error on Dixon's part, to some error in my interpretation of his figures, or to an actual change of position between these ages, I am unable to judge. That Dixon himself considers the nerve as a prespiracular one, in the adult man, is definitely stated in one of his later works (**16**, p. 479) ; and that the chorda changes its relations to the cleft seems indicated in Broman's statement (**9**, p. 568) that in his human embryo No. III, "Die hintere Spitze der ersten inneren Visceralfurche, die sich im vorigen Stadium gleich hinter der Chorda tympani, lateral von dieser bis an die Körperwand hinausstreckte, befindet sich jetzt eben an der medialen Seite der Chorda." This apparent change in the relations of the two structures might be caused simply by a change in the direction of the first visceral cleft, though this seems improbable. In Broman's Fig. 8, Pl. A, I should certainly say that the chorda had a recurrent prebranchial course. In his Fig. 2, Pl. C, the first visceral cleft seems to lie between the recurrent chorda and the trunk of the facialis, the chorda thus here being postbranchial in position. These apparent changes in the relation of the nerve to the cleft may, possibly, be in some way related to the difference in relation of the chorda to the "Ohrcolumella" in Amphibia and Reptilia, noted by Gaupp. According to that author (**22**, p. 159) the nervus hyomandibularis facialis of Amphibia runs backward over the columella and then gives off its ramus mandibularis internus, which Gaupp considers the unquestioned homologue of the chorda, "der ohne jede weitere Beziehung zur Ohrcolumella aussen um das Zungenbeinhorn herum zu seinem Endgebiete am Unterkiefer verlauft." In Reptilia, on the contrary, the mandibularis internus is said to take a recurrent course and to pass forward over the columella again to reach its destination, thus having exactly the opposite relations to that structure that it is said to have in Amphibia.

While I am unable to even properly follow this discussion, in so far as it relates to mammals, it is evident that Dixon's figure 15 shows a striking resemblance to the conditions found in Amia, the chorda tympani being considered as postspiracular in position, and as represented in the mandibularis internus facialis of the fish, and the mandibularis internus trigemini of Amia being considered as the homologue of the lingual nerve of man. It is of course possible that the mandibularis internus trigemini of Amia may contain both facial and trigeminal fibres, and hence represent not only the lingual nerve but also the chorda, if that nerve be a prespiracular one.

In short, if the chorda be a prespiracular nerve I look for its homologue in the mandibularis internus trigemini of my descriptions of Amia. If it is a postspiracular nerve it must be represented in the mandibularis internus facialis of the same fish.

In this connection it seems proper to give quite fully the late Prof. Huxley's opinion of this nerve, as set forth in the unpublished manuscript to which I have already made reference. In this memoir Prof. Huxley first describes the chorda in man as a branch of the posterior division of the portio dura or seventh nerve. He then says that, "In the frog, the portio dura arises in close connection with the auditory nerve from the medulla oblongata, and as it passes outwards becomes so intimately united with the Gasserian ganglion that it has been commonly described as a root of the trigeminal. In the tadpole, however, and in all the Urodela, the portio dura forms a ganglion which lies close to the Gasserian, but perfectly distinct from it, and which answers to the ganglion geniculatum.

"In all the Urodela a commissural trunk connects the portio dura with the Gasserian ganglion; this I apprehend represents the nervus petrosus superficialis minor.

"From the ganglion of the seventh, whether it be closely united with that of the fifth or not, two nerves proceed—a posterior and an anterior.

"1. The posterior nerve is the larger. It passes outwards in front of the auditory capsule in the frog, or beneath its anterior end in the Salamander (but being in each case morphologically anterior to the labyrinth), and then turns outwards. In the frog it enters the tympanic cavity, and keeping close beneath the tegmen tympani and in immediate apposition with the outer wall of the auditory capsule, it passes above the level of the fenestra ovalis and stapes, over the columella auris; and finally turning downwards appears in the region between the hinder edge of the suspensorium and the hyoidean arch. The course of this part of the nerve is therefore precisely similar to that of the trunk of the posterior or facial division of the seventh nerve in man, while it is contained in the Fallopian canal. Moreover, it gives off an anastomotic branch to the glossopharyngeal, and supplies the depressor of the mandible and hyoidean muscles. And it gives off a slender branch which passes directly downwards and forwards to the inner side of the articulation of the mandible with the suspensorium, and runs along it to the symphysis, anastomosing with the parallel mandibular branch of the third division of the trigeminal. It is clear that the nerve is the homologue of the chorda tympani. In all respects there is a complete correspondence between the posterior division of the seventh nerve in the frog and the facial nerve in man. . . . .

"In osseous fishes the portio dura is very generally closely united with the trigeminal, but in the Plagiostomes the nerves are quite distinct as in the Urodela. In a common ray, or skate, for example (Raia clavata, R. batis), the portio dura arises from the medulla oblongata in close contiguity with the trigeminal in front and with the auditory nerve behind. It then turns outwards through a distinct canal, in front of the membranous labyrinth, and reaching the exterior of the auditory capsule divides into two branches, a very stout posterior, and a small anterior division. Stannius (l.c., p. 57) has observed ganglion corpuscles at the bifurcation so that it answers to the ganglion geniculatum.

"I. The posterior division passes outwards and backwards behind and beneath the attachment of the spiracular cartilage, and behind the spiracle, just as, in the frog, it passes behind and beneath the otic process of the suspensorium and behind the tympano-Eustachian canal. It then turns over the hyomandibular cartilage, about the middle of its length, just as, in the frog, the nerve passes over the columella auris, and then divides into branches, the greater part of which are distributed to that aggregation of cutaneous sensory tubes which lies behind the angle of the jaw; others go to the muscles of the vicinity, and two slender branches run forwards in the inner side of the mandibular cartilage and represent the chorda tympani, which, as in the Amphibia, goes direct to its destination."

Huxley thus considered the chorda tympani as a post-spiracular nerve, and he definitely identified it in the ramus mandibularis internus facialis of Amphibia and fishes. The homology of the chorda tympani with the ramus mandibularis internus facialis of the Anura, which is said to have its homologue in the ramus alveolaris facialis of the Urodela, is now very generally accepted (Strong, Gaupp). This branch of the facialis nerve cannot then be the homologue of the similarly named nerve of fishes, unless that nerve also is the homologue of the chorda. This subject thus clearly needs further investigation, and first of all it is absolutely indispensable to know the definite relations of the chorda of mammals to the spiracular cleft.

Spiracular Cleft.

The spiracular cleft of a 5 cm. embryo of Mustelus, with its two diverticula, has been described by Wright (**70**). Ridewood (**54**) has since made short reference to these diverticula in the adult Mustelus, but, although referring to several earlier authors, he apparently was not acquainted with Wright's paper. In my 12·2 cm. embryo I find both of these diverticula, and also what seems to be a third one; and the structures deserve a fuller description than Wright has given.

What Wright describes as the ventral portion of the anterior diverticulum is, in my embryo, a relatively large pocket projecting dorso-mesially from the antero-dorsal surface of the spiracular cleft, near its inner end. From the dorso-antero-mesial portion of this pocket two small apertures, lying one directly posterior to the other, lead, the one forward and the other forward and upward, into wholly separate diverticula.

The anterior aperture leads into a small diverticulum which runs almost directly forward through sixteen sections of my embryo. It is at first of oval section, but before it ends it becomes a simple slit, which inclines mesially and upward toward the skull. The diverticulum has at its extreme anterior end two short but separate and distinct prolongations, or lobes, which extend through two sections only. The diverticulum may be called, because of its position, the ventromesial diverticulum of the fish. It is not described by Wright. It is lined with an epithelium which, near the posterior end of the diverticulum, seems to resemble exactly that of the spiracular cleft. Toward the anterior end of the diverticulum the lining membrane has somewhat the character of the "modified epithelium" that Wright describes in his so-called anterior diverticulum.

The posterior aperture of the spiracular pocket of my embryo leads into what Wright has described as the distal portion of the entire anterior diverticulum of the fish. The aperture represents, in fact, that middle point of the entire diverticulum of Wright's descriptions where, according to that author, the lumen of the diverticulum becomes suddenly constricted. From here the diverticulum in my embryo led upward and forward until it acquired a position slightly dorso-lateral to the ventro-mesial diverticulum. There it continues forward until it reaches the anterior end of the ventro-mesial diverticulum, where it first takes a sharp turn dorso-laterally, then another forward again, and ends. Its dorso-anterior portion, distal to the first sharp bend, is somewhat enlarged, as Wright has said, and is lined with what he describes as a "modified epithelium." The entire diverticulum may be called the dorso-mesial diverticulum of the fish.

The ventral opening of the pocket from which these two mesial diverticula arise lies mesial to the spiracular pseudobranch. Lateral to that pseudobranch, and from the opposite wall of the cleft, the auditory diverticulum of Wright's descriptions has its origin. The pseudobranch, which is, in position, a mandibular hemibranch of the spiracular cleft, thus lies between the regions where these two diverticula have their origins from the cleft.

The auditory diverticulum runs upward and mesially, at first immediately posterior to the levator maxillæ superioris, and then internal to the dorsal portion of that muscle, and reaches the side wall of the skull. There it turns upward and laterally along the sloping side wall of the skull, and, as Ridewood says, broadens in an antero-posterior direction; its upper end thus being ⊤-shaped, and here lying external to and below the external semicircular canal of the ear. This auditory diverticulum has, in sections of Mustelus, most decidedly the appearance of the antero-dorsal end of the first branchial (hyobranchial) cleft of sections of larvæ of Amia. In this latter fish this antero-dorsal end of the first branchial cleft is a dorsal pocket, or cranial extension, of the cleft, and it almost reaches the side wall of the skull in the otic region

The conclusion thus seems inevitable that it has its serial homologue in the auditory diverticulum of Mustelus, that diverticulum then being nothing more nor less than the dorsal end, or dorsal pocket, of the spiracular cleft. The truncus facialis in Mustelus lies always ventro-mesial to this diverticulum, and the diverticulum nowhere presents a modified epithelium such as is found in both the mesial diverticula.

On the dorsal portion of the orbital wall of the skull, ventro-mesial to the foramen by which the ramus oticus facialis pierces the overhanging post-orbital process, and directly external to the external semicircular canal of the ear, a large and strong ligament has its origin. It is the superior postspiracular ligament of Ridewood's descriptions, and has already been several times referred to. Running downward mesially and backward, external to the postorbital blood sinus, it reaches the dorsal surface of the dorso-mesial diverticulum of the spiracular cleft. There it spreads out, and seems to separate into three somewhat separate parts. One part continues ventro-mesially and is lost in a mass of dense connective or fibrous tissue that lies antero-mesial to the dorso-anterior end of the diverticulum. A somewhat separate part of this fibrous tissue directly surrounds the distal end of the diverticulum, and into it a second part of the ligament has its insertion. The third and larger portion of the ligament continues downward, backward and laterally, lateral to the spiracular pocket from which the two mesial diverticula arise, and then posterior to the spiracular cleft itself. At its distal end it separates into two parts, both of which are inserted on the distal end of the hyomandibular, near its anterior edge, or in the articular ligaments that bind the hyomandibular and palato-quadrate cartilages together. It passes, as already stated, between the truncus hyoideo-mandibularis facialis and that trigeminal nerve that innervates the levator maxillæ superioris. The truncus facialis lies between the ligament and the anterior edge of the cartilaginous hyomandibular, and this may give an explanation of the varying and perplexing relations of the facial nerve to the hyomandibular in different fishes. The chondrification of a ligament is of frequent occurrence, or, if the ligament itself does not chondrify, it may determine the direction of a cartilaginous process of an element on which it has its insertion. If the hyomandibular of Mustelus were to acquire a higher articulation on the side wall of the skull it would become parallel to, and lie immediately posterior to, the superior postspiracular ligament. If then this ligament were to chondrify, or if it were simply to determine the direction of growth of a cartilaginous process from the ventral end of the hyomandibular, the truncus facialis would become enclosed in the cartilage, and the relations of element and nerve found in Amia and teleosts would arise. If, furthermore, the anlage of the selachian hyomandibular and that of its related ligament thus lying parallel to each other, the primary chondrification of the region were to take place in the ligament, and the tissues that represent the hyomandibular were to acquire a ligamentous instead of a cartilaginous character, the relations of the nerve to the element shown by Van Wijhe (**65**) in Acipenser, Spatularia, and Polypterus would arise. And in Polypterus I find a ligament extending, posterior to the main facial nerve, from the dorsal to the ventral end of the hyomandibular, enclosing the nerve between itself and the hind edge of the hyomandibular, exactly as might have been expected. The hyomandibulars of these several fishes would then not be strictly homologous structures, and one would not have to assume, in order to explain the facts, that the facial nerve cuts through the hyomandibular, being sometimes found in front of that element, sometimes behind it, and in still others intermediate in position between these two extremes.

Wright says, as already stated, that the truncus hyoideomandibularis facialis of his embryo of Mustelus "forked," between the diverticula of the hyomandibular cleft, into the pre- and post-trematic branches of the nerve. The pretrematic branch is said to "appear" to "end in the mucous membrane of the dorsal and anterior wall of the hyomandibular cleft, without there being any modification of the epithelium at the point in question." The modified epithelium of the anterior diverticulum of his descriptions of the cleft, considered by Wright as a neuro-epithelium, is said to receive some fibres from this pretrematic branch.

In none of my embryos did the truncus facialis here separate into pre- and post-trematic portions, and it seems to me almost beyond question that Wright mistook the superior postspiracular ligament of the fish, together with a nerve described below, for a pre-trematic branch of the facialis, a part of the ligament, together with the nerve, having, in embryos, almost exactly the position and distribution of the so-called nerve described by him. The modified epithelium of Wright's anterior diverticulum, my dorso-mesial one, received, in all my embryos, a nerve which made its first appearance in sections as a large nerve lying in the middle of the postspiracular ligament at the point where that ligament begins to spread and break up into its three parts. The section of the nerve as it here first appeared in following the series of sections backward was large, and lay close to the truncus facialis, but it was distinctly and definitely separated from that truncus by a small slip of the ligament. Traced posteriorly the nerve ran downward and backward to, and ended in, the modified epithelium of the dorso-mesial spiracular diverticulum. Fibres of it here quite certainly also went to the modified epithelium of the closely adjacent ventro-mesial diverticulum, but this could not be definitely traced because of the dense fibrous tissues that here surround both diverticula. In the section next anterior to the one in which this spiracular nerve thus suddenly appears, there was no indication whatever of it, excepting only a slight discoloration of the mesial edge of the postspiracular ligament. I was, therefore, at first inclined to consider the nerve as a branch of the truncus facialis, as Wright had done before me. Later I became convinced that it could not be a branch of the truncus facialis—that I can positively affirm,—and I was then first inclined to consider it as a part of the ligament and not a nerve. Still later I found that the slight discoloration of the mesial edge of the ligament, noticed in the section next anterior to the one in which the nerve so suddenly and distinctly appeared, could be traced upward and forward to a point where the ligament crossed, and lay closely against that branch of the ramus oticus that innervates organs 87 to 91 inf. Here, then, was a rational explanation of it, and as I could not definitely trace the nerve in sections, I had Mr. Nomura try to find it by dissection. He succeeded, in two embryos, in finding the dorsal end of the nerve, where it turned downward along the ligament, but he could not trace it to its termination in the diverticulum of the spiracle. As I readily find its ventral end in sections, I am fully convinced that the nerve is a branch of the oticus facialis that has this course and origin—a conclusion practically confirmed by Hoffmann's (**36**) work on Acanthias. Such being the case, and there being no special sensory tissue in the auditory diverticulum of Mustelus, it is plainly evident that the sensory diverticula of Amia and Lepidosteus cannot be the homologues of the auditory diverticulum alone, of Mustelus, as Wright was inclined to believe, unless it be assumed that the spiracular sensory organs in the three fishes are not homologous. It seems much more reasonable to assume either that the three diverticula of Mustelus have fused to form the single diverticulum of Amia, and of Lepidosteus, or that the auditory diverticulum of Mustelus has entirely disappeared in Amia, but is still represented in Lepidosteus in that dorso-lateral branch of the diverticulum of the fish that Wright considered as the blind outer end of the spiracular cleft itself. In Wright's descriptions of the cleft in Lepidosteus he says, "The cleft itself is directed upwards, outwards, and slightly backwards, but it will be readily observed from fig. 5 that it is separated from the most anterior filaments of the pseudobranch by the whole thickness of the hyomandibular adductor muscles." In my copy of Wright's paper the plates are lacking, so I cannot compare this statement with the figure referred to; but it seems singular that the pseudobranch should have acquired a position posterior to the adductor hyomandibularis instead of lying in front of it, where it would naturally lie, and where it is found in Amia.

The auditory diverticulum of Mustelus being simply the dorsal end or pocket of the spiracular cleft, do the two anterior or mesial diverticula of this fish represent similar pockets of more anterior clefts?

Hoffmann (**36**, pp. 350 and 366) describes, in Acanthias, what he calls the "dorsale Spritzlochanhang." This pocket of the spiracular cleft is said to receive at its summit a ventral branch of what Hoffmann designates as the "Ramus accessorius" of the facial nerve, that ramus being said to be, in all probability, the ramus oticus facialis of other authors. This pocket in Acanthias must therefore be what I have described as the dorso-mesial diverticulum of Mustelus. Hoffmann considers this pocket in Acanthias as a remnant of that branchial cleft that should be found between the mandibular arch and Gegenbaur's second labial arch. He then states that a still more anterior cleft, which must have originally existed between the first and second labial arches, has disappeared entirely, without even leaving a remnant. If Hoffmann's interpretation of these pockets is correct, may not the ventro-mesial diverticulum of Mustelus be such a remnant?

Hoffmann and Wright both consider those tissues of the spiracular diverticula of selachians that are innervated by the so-called ramus accessorius of the one, and the ramus pretrematicus VII of the other, as of undoubted hypoblastic origin. Both authors accordingly consider the nerve that is distributed to these tissues as a ventral branch of a dorsal cranial nerve. If the sensory organs here concerned are of hypoblastic origin, they would seem necessarily to be homologous with the sensory buds described by Alcock (**1**) on the diaphragm of Ammocœtes. These organs of Ammocœtes are, however, only found in the glossopharyngeal and vagus arches, as I understand Alcock, and they are innervated by a nerve that arises from the ventral division of the nerve of the arch, wholly separate and apart from the ramus dorsalis of the segment. The innervation of the organ in Mustelus by a branch of the ramus oticus, usually considered as a ramus dorsalis, and its position in what Hoffmann considers as a remnant of the mandibular cleft, are accordingly both decidedly opposed to the assumption that the organ finds its homologue in the hypoblastic organs of Ammocœtes. Hoffmann avoids this difficulty, in so far as it relates to the innervation, by the very legitimate conclusion that both the ramus oticus and the ramus buccalis, the nerve from which the oticus arises, are ventral and not dorsal nerves.

In my work on Amia (**2**) I was led to suggest that the spiracular organ of that fish was simply an infraorbital lateral canal organ, of ectodermal origin, that had wandered into the spiracular cleft as the external opening of that cleft was closed. If the same assumption be made regarding Mustelus, it is evident that, if Hoffmann's conclusions are correct, the cleft into which the organ wanders must be the mandibular and not the spiracular cleft. It is also probable, under the same assumption, that another infraorbital organ similarly wanders into the next anterior, or labial cleft. That these assumptions are not improbable is evident from Hoffmann's account (**36**, p. 339) of the similar wandering of what he calls rudimentary "Hautsinnesorgane" from the outer surface into the branchial clefts related to the glossopharyngeus and vagus nerves. These rudimentary cutaneous sensory organs are said to be formed in relation to the ganglion of the ramus ventralis of the nerve concerned, and they are said to abort completely soon after entering the related cleft. From Hoffmann's account of them they seem not to be considered by him as organs homologous with the organs of the lateral canals, but it seems probable that they find their exact serial homologues in the so-called spiracular organs of Mustelus, excepting only in their being innervated by a branch of a ramus ventralis instead of by a branch of a so-called ramus dorsalis. This difficulty is, however, wholly overcome if one accepts Hoffmann's conclusion, already stated, that the ramus buccalis facialis is a ramus ventralis and not a ramus dorsalis. While I can express no opinion as to this, it seems to me highly probable that the ramus buccalis may be a serial homologue of the ramus mandibularis externus facialis, and if it be accepted as such it would seem to lead legitimately to the conclusion that the separation of the buccalis lateral canal of fishes, by its innervation, into three somewhat separate sections, is due to the fact that each one of these sections has a descending course, one in relation to the mandibular arch and the other two in similar relations to the next two anterior arches. The preopercular canal of ganoids and teleosts would then be a similar descending line related to the hyoid arch, and the descending line of epithelial pits described by Alcock (**1**, p. 145) in the glossopharyngeal arch of one specimen of Ammocœtes would be a similar line related to that arch. The several ventral pit lines of Ammocœtes would then represent lines corresponding, in the several arches to which they are related, to the mandibular part of the canal line of the hyoid arch of Amia and teleosts, these lines not existing in the premandibular arches.

One of the branches of the ramus pretrematicus facialis of Mustelus runs backward and then outward posterior to the dorso-mesial diverticulum of the spiracular cleft, and there turns downward posterior to the latter cleft. The other two branches, and also the so-called chorda tympani, lie anatomically anterior to the dorso-mesial diverticulum of the spiracular cleft. If, then, that diverticulum represents a remnant of the mandibular cleft, the nerves here concerned must actually lie anterior to that cleft. How they could have acquired that position, if they are regular pretrematic branches of the nerve of the hyoid arch, it seems difficult to imagine, unless it be assumed that the persistent remnants of the mandibular and more anterior clefts represent only the outer, external portions of the clefts concerned, the fusion of the clefts with the hyoid cleft, and with each other, taking place at their external ends only, the internal ends wholly aborting. Hoffmann's description of the development of the diverticulum in Acanthias seems, in fact, to indicate that this is what takes place. That the internal ends of the clefts could have persisted, and that the prebranchial facial nerves could have in any way slipped forward over the aborted top of the cleft, seems excluded by the fact that both a ligament and a branch of the oticus facialis extend downward to the dorsal end of the cleft, directly across the path that the nerves concerned must have taken in so slipping forward.

Truncus hyoideo-mandibularis facialis.

The truncus hyoideo-mandibularis facialis, after its origin from the dorso-posterior surface of the trigemino-facial ganglion, runs backward and upward along the side wall of the skull, immediately anterior to the hind end of the peri-orbital sinus. It is accompanied, in this part of its course, by the r. ad. musc. lev. max. sup., as already fully described. Soon after this trigeminal nerve turns outward, anterior to the superior postspiracular ligament, the truncus facialis turns outward posterior to that ligament, passing, as the trigeminal nerve does, ventral to the postorbital blood-sinus. The truncus facialis here runs dorsal to the posterior portion of the dorso-mesial diverticulum of the spiracular cleft, and antero-mesial to the dorsal end of the auditory diverticulum of the same cleft. Its relations to the spiracular structures are thus exactly those given by Ridewood (**54**) in his descriptions of the corresponding parts of Scyllium. The truncus then turns downward and laterally, passes immediately posterior to the spiracular cleft, and reaches a position lateral to the anterior edge of the distal end of the hyomandibular.

Slightly distal to the point where the truncus thus turns downward and laterally, a small ganglion forms on its hind edge. From, or in connection with, this ganglion four branches arise. Three of them run outward along the anterior edge of the muscle Csd_2, passing posterior to the auditory diverticulum of the spiracular cleft, and postero-ventral to the levator maxillæ superioris. Having reached the outer surface of Csd_2 they there turn backward, and then break up and spread out on the outer surface of the muscle, near its ventral end. They are apparently entirely sensory, but they evidently correspond to the branches described and figured by Vetter in Acanthias, one of which branches is said to penetrate Csd_2 from its outer surface, and innervate it. The fourth branch, in Mustelus, arises from the hind end of the small ganglion, runs outward to the inner surface of the muscle Csd_2, and there separates into two parts, one of which penetrates the muscle, and running backward is lost in it, while the other turns backward along the inner surface of the muscle, and there gradually disappears. This fourth branch thus probably contains all the motor fibres destined to the muscle Csd_2. What the ganglion from which the four branches arise may be I cannot determine, nor do I find any description of anything that seems to correspond to it in any of the works at my disposal. The ganglion cells have the size and general appearance of those of the ciliary ganglion, which may indicate that it is a sympathetic ganglion.

Beyond this ganglion and the branches that arise from or in connection with it no branch is given off by the truncus facialis until it reaches the level of the distal end of the hyomandibular, where the nerve separates into several branches. One of these branches is destined to innervate the sense organs of the hyomandibular lateral canal, and another those of the mandibular lateral canal and the mandibular group of ampullæ. These two branches arise from the truncus close together, if not as two parts of a single branch, and they together constitute the ramus mandibularis externus facialis of the fish. The branch destined to the organs of the hyomandibular canal separates into two parts, both of which run at first laterally and slightly downward, but soon separate, one turning forward and the other backward, both going exclusively to the sense organs of their canal, no related ampullæ being found. The other branch or part of the externus runs downward, forward, and mesially, along the external surface of the adductor mandibulæ muscle, passes into the mandible, lying superficial to the ramus mandibularis trigemini, and ends in the lateral and ampullary sense organs it innervates.

Beyond the point where the ramus mandibularis externus is given off by the truncus hyoideo-mandibularis the remaining portion of the truncus separates into three principal branches, and one or more smaller ones. The smaller ones go to the general tissues of the region. One of the three larger and principal parts runs at first downward and backward, and acquires a position on the external surface of the posterior portion of the adductor mandibulæ. It then turns forward and mesially, and passes from the outer surface of the adductor on to that of the muscle Csv_2, where it gradually disappears. A second one of the three principal parts runs directly backward, immediately lateral to the dorsal end of the ceratohyal, and near the hind edge of that element turns downward, internal to the muscle Csv_2, and around the hind end of the mandibular cartilage. It then runs forward and mesially between the superficial and deeper layers of Csv_2, to both of which it sends branches, apparently innervating them. Anteriorly it lies immediately internal to the intermandibularis muscle, and there anastomoses completely with that branch of the mandibularis trigemini that pierces the intermandibularis from its outer surface. This anastomosis is, as already stated, the undoubted homologue of the one found in Amia of the ramus hyoideus facialis, with the branch r.ghi of the maxillaris inferior trigemini.

These two principal branches of the truncus facialis of Mustelus thus form the ramus hyoideus of Stannius' descriptions (**59**, p. 65).

The third and remaining part of the truncus facialis of Mustelus turns downward, forward, and mesially between the ceratohyal and the mandibular cartilage, and closely accompanies the pseudobranchial artery as far as that artery extends. Continuing forward beyond the artery, internal to the mandibular cartilage, and near its ventro-mesial edge, it there gradually disappears, numerous branches being sent toward the adjacent mucous lining membrane of the mouth cavity. In the terminal part of its course it lies quite close to the terminal portion of that branch of the ramus palatinus that Green considers as the homologue of the chorda tympani. This part of the truncus facialis of Mustelus is thus the ramus mandibularis internus s. profundus of Stannius, and it is the nerve that Ruge (**55**) and many others homologise with the chorda tympani of man. Whether it be or be not that nerve depends on whether the chorda is a post- or pre-spiracular nerve.

Review and Comparison of the Ophthalmic Nerves.

There is, as is only too well known, much confusion in the descriptions of, and more particularly in the nomenclature relating to, the ophthalmic nerves of fishes. This is often so misleading that I venture to give, before discussing the nerves, an explanation of the manner in which it seems to have arisen.

Stannius (**59**, p. 34) included all the ophthalmic nerves of fishes under the name ramus primus n. trigemini s. ophthalmicus, a name which, shortened to Trigeminus I, is even still retained by certain authors. Stannius says that the nerve thus defined by him is always wholly sensory, excepting in the Cyclostomata, and that it is formed by the union of two bundles of fibres, one derived from an anterior trigeminal root and the other from a posterior one. In certain teleosts, he says that the ramus ophthalmicus is found as a single trunk which runs forward, near the roof of the orbit, dorsal to all the muscles of the eyeball. In other teleosts, and in all the Plagiostomata, the nerve is said to be represented by two branches which sooner or later unite, more or less completely, to form a single trunk. In these latter teleosts both branches of the nerve are said to have the course of the single trunk in the first-mentioned ones, while in all the

Plagiostomata one branch only of the nerve has that course, the other running forward across the orbit ventral to the rectus superior and obliquus superior muscles; its relations to the rectus internus not being especially mentioned. This latter branch of the nerve in the Plagiostomata is called by Stannius the ramus ophthalmicus profundus, and as he does not apply this term, profundus, to the deeper one of the two branches in those teleosts in which two ophthalmic branches are said to be found, it seems evident that he intended the term to be limited to a nerve that held a position anatomically different from that of an ophthalmicus superficialis. It seems, however, equally evident that he considered the two strands of the superficial nerve in teleosts as the homologues of the two more completely separated branches in the Plagiostomata. He says that the superficial strand in teleosts, and the ramus superficialis in the Plagiostomata, are both derived from a posterior, broad-fibred root, while the deeper strand in the former, and the ramus profundus in the latter, arise from the anterior trigeminal root.

Schwalbe (**57**, p. 182) concluded that the ophthalmicus superficialis of Stannius's descriptions of selachians was formed of two distinct and different components, the larger one of which always lay superficial to the other. He accordingly called the two components the portio major and portio minor of the superficialis nerve, and says that they derive their fibres partly from the dorsal part of the posterior root of the trigeminus, and partly from the anterior, more ventral root of that nerve. These two bundles of fibres he calls the "radix dorsalis (posterior) and ventralis (anterior) ophthalmici." The portio major of the ophthalmic nerve is said to receive all the fibres that traverse the radix dorsalis, and to be composed of those fibres alone. The portio minor receives one half of the fibres that traverse the radix ventralis, the other half of those fibres going to form the ramus ophthalmicus profundus. The portio minor and the ramus profundus are thus formed of similar fibres, and those fibres are said to be derived from the anterior root of the trigeminus. The ramus profundus is said to either pierce the rectus superior muscle, or to lie wholly ventral to it, and then to run forward ventral not only to the obliquus superior, as stated by Stannius, but ventral also to the rectus internus. Schwalbe's descriptions and figures also show that the ramus profundus lies between the superior and inferior divisions of the nervus oculomotorius, ventral to the former and dorsal to the latter, but he does not call attention to this important fact. In his references to teleosts and ganoids he makes no application of the terms portio major and portio minor.

Balfour in his well-known work on the development of elasmobranch fishes, to which I am unable to directly refer, and which was published shortly before Schwalbe's work above referred to, described, according to Marshall and Spencer (**43**), the ophthalmic nerves both in the adult and in embryos of Scyllium. In those descriptions he is said to have entirely overlooked the true profundus nerve, giving the name ramus ophthalmicus profundus to what Schwalbe describes as the portio minor of the superficial nerve. Balfour, although he was thus, as Marshall and Spencer state, the first to clearly recognise the double nature of the superficial ophthalmic nerve of elasmobranchs, was also probably the first to make that misapplication of the name profundus that has since caused so much confusion in the descriptions and discussions of these nerves. Balfour evidently did not so apply this term either thoughtlessly or carelessly, for Marshall and Spencer state that he sought to explain the apparently exceptional position of the nerve in Scyllium by the assumption that it had shifted upward from the deeper position in which it is usually found in selachians; this explanation adding, in my opinion, a misconception of the nerves to a misapplication of their names.

Marshall, in his own embryological work on Scyllium (**42**), and also in a second work on the same fish published in connection with Spencer (**43**), concluded that the portio major and portio minor of Schwalbe's descriptions were, respectively, the ophthalmic branches of the facial and trigeminal nerves (p. 89). The ramus ophthalmicus profundus is said by him to be of a totally different nature from either of these superficial ophthalmic nerves, and is said to be definitely characterised by its own particular course and position, from which, in his opinion, it never shifts. This opinion, definitely and succinctly stated, seems to have since been either entirely overlooked, or, perhaps, regarded as not worthy even of consideration.

Van Wijhe (**66**) confirmed Marshall's conclusion that the portio major and portio minor of Schwalbe belonged, respectively, to the facial and trigeminal nerves, and he moreover found in stages K and L of embryos of Scyllium and Pristiurus, what he considers as a third component, or portio, of the superficial ophthalmic nerve. It is said by him to arise from his ciliary (profundus) ganglion, and, because of its origin and distribution, he calls it the portio ophthalmici profundi of the ramus ophthalmicus superficialis. This portio profundi is said (p. 21) to abort in slightly older stages of Scyllium and Pristiurus, but in Polypterus and Lepidosteus it is said to persist throughout life. It is fully described by him, in these latter fishes, in another work (**65**). In this latter work (p. 275) van Wijhe also identifies and describes, in the adult Lepidosteus, the other two portiones (portio trigemini and portio facialis) described by him in the superficial ophthalmic nerves of embryos of Scyllium and Pristiurus. In the adult Polypterus, his descriptions, in the same work, lead one to infer that he found all three portiones in that fish also, but the reference is not clear, and Pollard (**51**, p. 395), somewhat later, could not definitely establish the existence of a portio trigemini. In Polypterus both van Wijhe and Pollard describe a ramus ophthalmicus profundus which is said to have the usual selachian relations to the rectus superior and obliquus superior muscles, but not to the rectus internus, the nerve lying dorsal, instead of ventral, to that muscle, the internus of Polypterus, like that of Amia and teleosts, hence perhaps not being the homologue of the similarly named muscle in selachians.

In the same work in which van Wijhe describes the nerves in Polypterus and Lepidosteus, he also describes the nerves in Acipenser. In this latter fish, doubtless misled by Balfour, he first describes an ophthalmicus superficialis trigemini and an ophthalmicus profundus trigemini which have the mutual relations of the superficialis and profundus nerves of Balfour's descriptions of Scyllium. Later, but in the same work (p. 230), van Wijhe says, in a footnote, that the anatomical position of this so-called profundus nerve precludes its being a ramus profundus, in the sense in which that term is applied in selachians, and he accordingly concludes that the two ophthalmic nerves of his descriptions of Acipenser are very probably simply the portio major and portio minor of Schwalbe's nomenclature, and hence both integral parts of the ramus ophthalmicus superficialis. There is accordingly, according to his descriptions, no true ramus ophthalmicus profundus in Acipenser, and there is, moreover, no portio ophthalmici profundi described as such. In here first giving to the two ophthalmic nerves of Acipenser the names superficialis and profundus, van Wijhe had probably a more direct influence than Balfour on that misapplication of the name profundus that has since been so frequently repeated, and that is so confusing and misleading if one is not continually on one's guard.

Instances of this misapplication that I am sure of are found in Goronowitsch's descriptions of Acipenser (**24**), Lota (**25**), and Salmo (**26**), and in Wright's descriptions of Amiurus (**69**); and it is exceedingly probable that the same error occurs also in Pollard's descriptions of Siluroids (**52**). The misapplications relating to Lota and Amiurus have already been recognised and signalled by Herrick and Workmann respectively.

This use of the term ophthalmicus profundus for a nerve that has the anatomical position of an ophthalmicus superficialis always implies, whether intentionally or not, that a nerve having the position of a selachian profundus has moved upward, from that position, to the position of a selachian superficialis, and there fused completely with the portio minor of the ramus superficialis. Such an ascent of the profundus nerve is, I believe, very generally assumed to have taken place in all teleosts and in most ganoids. In Amphibia and the higher animals it is, on the contrary, as generally assumed that the portio minor of the superficial nerve has moved downward and fused with the ramus profundus. Wiedersheim (**64**, p. 285) so definitely asserts, and Strong (**60**, p. 193) accepts as probably correct, a similar statement attributed to Wilder in a work I have not at my disposal. Balfour also definitely accepted this principle in his statement, already referred to, that the profundus nerve of Scyllium had shifted upward to the position of a portio minor of the ophthalmicus superficialis.

The assumed ascent of one, or descent of the other, of these two ophthalmic nerves seems usually to be made in the sense of a simple juxtaposition and subsequent fusion of the two already developed nerves, but it is evident that this could not take place without the enclosing of the trochlearis and the superior division of the oculomotorius in the single nerve so formed. While this might be assumed, from existing descriptions, to have taken place in certain fishes and other animals, my work leads me to believe that in every such instance it will be found that the motor nerves are simply juxtaposited to one or the other of the two ophthalmic nerves, and not enclosed between the two nerves united. An apparent exception to this might be considered as being presented in a single specimen of Carcharias that I examined (**5**). In that specimen a part of the trochlearis certainly perforated and traversed the ophthalmicus superficialis. An important and apparently normal ophthalmicus profundus was, however, found, in this same specimen, in its typical place and relations to the other nerves and structures of the orbit. It might, nevertheless, be said that this perforation of the superficial nerve by a part of the trochlearis here represented some intermediate stage in the fusion of the superficialis and profundus nerves. This I do not believe, and while the condition presented by Carcharias certainly needs further investigation, its explanation may perhaps be found in the frequent assertion that the trochlearis is a branch of the ophthalmicus trigemini.

That in the ascent or descent of one or the other of the ophthalmic nerves one of them could cut through the trochlearis and oculomotorius, temporarily severing their fibres, or that it could cut through the intervening eye muscles distal to the point of attachment of the associated nerve, is not I think assumed by anyone.

If then a simple juxtaposition of the two nerves, already developed in their typical positions, be eliminated from the discussion, it is evident that any assumed fusion of them presupposes, either that one or the other of the two nerves is not primarily developed in its typical position, or that the two nerves develop before the structures that typically separate them have been sufficiently developed to interfere with their juxtaposition and subsequent fusion. The whole question of the development of nerves is thus here involved, and it is not my intention to in any way discuss it. Certain statements regarding the development of the nerves here especially under consideration, and bearing directly upon their relations to other structures in the orbit, deserve however to be given.

Dixon (**15**) believes, with His, that the permanent fibrous nerve grows outward, either directly from the brain, or from the related ganglion. Of the ophthalmic nerve in man, he says (p. 33) that the first-formed fibres of the nerve are deflected from their primary direction by reason of some correlation to other growing tissues, and that they become the nasal branch of the ophthalmic nerve of the adult. Later fibres, not similarly obstructed, continue in the primary direction of the ophthalmic nerve and form the frontal branch of the nerve of the adult. We thus have, under this theory of the development of nerves, a statement which certainly involves, in principle, the change of a nerve from the position of a superficialis to that of a profundus. Because of its position Dixon considers the frontal nerve as the probable homologue of the portio trigemini of the ophthalmicus superficialis of selachians, the nasal branch being quite unquestionably considered as the homologue of the ophthalmicus profundus, though I do not find this statement definitely made. With equal, or even greater reason, the frontal branch of the nerve in man might be considered as the homologue of the portio ophthalmici profundi of ganoids, and hence more probably the homologue of branch I of the ramus ophthalmicus profundus of Ewart's descriptions of Læmargus (**17**) than of the ramus ophthalmicus superficialis trigemini of that fish. Under either assumption, Dixon's facts and conclusions are opposed to the assumption that the superficialis and profundus trigemini of selachians are both represented in the nasalis, or naso-ciliaris, of higher animals.

Platt (**49**) says that, in Necturus, the ramus ophthalmicus profundus is split off, as a line of cells, from the under surface of the same line of thickened epidermis that later gives similar origin to the ophthalmicus superficialis facialis. In my work on Amia I assumed (**3**, p. 635), in referring to an earlier work by Platt (**48**), that the two nerves thus described by her were the portio minor and portio major of the ophthalmicus superficialis, and that they retained, throughout life, the positions of those nerves. Platt's later work shows conclusively that the profundus of her descriptions is the ramus nasalis of Schwalbe's descriptions of other Urodela, in which animals it is said by the latter author to have exactly the relations, to other orbital structures, of the ramus ophthalmicus profundus of selachians. We thus have, under a theory of the development of nerves opposed to that of His, a nerve that can be followed, if Platt is correct, from the position of an ophthalmicus superficialis to that of an ophthalmicus profundus. This profundus nerve is said to differ from all the other sensory nerves of the animal in that it "is formed from the ectoderm in the same manner as are the cranial ganglia" (p. 488), and that neural crest cells participate in its formation throughout its entire length (p. 535). This, it will be seen below, would seem to exclude the possibility of the nerve containing any of the elements of the portio minor of selachians, a descent of the latter nerve thus not here taking place.

Goronowitsch (**26**) says that, in Salmo fario, the two nerves called by him the nervus ophthalmicus superficialis trigemini and nervus ophthalmicus profundus trigemini are both developed from ectoderm cells proliferated from the sam supra-orbital region of the ectoderm. As the profundus nerve of these descriptions holds the position, throughout life, of a ramus ophthalmicus superficialis, it might be here assumed that this nerve contained the elements of the similarly named nerve in Platt's descriptions of Necturus, and that in Salmo its descent to the typical profundus position had been simply arrested, the nerve remaining where originally laid down. The profundus nerve, as first laid down in Salmo, is, however, said to be directly developed from ectoderm cells, and not from cells that could in any way be attributed to the neural crest, thus differing so markedly in this from the ophthalmicus profundus of Necturus, as described by Platt, that the two nerves cannot be considered as homologous. A marked difference in the manner of development of this nerve in Salmo and that of the ophthalmicus profundus of the chick is also noted by Goronowitsch, who says (p. 31): "Bei den Vögeln zeigt die Entwicklung des Ophthalmicus Stammes eine Abweichung, inden der Nervenstamm primär im Mesoderme angelegt wird. Der Ophthalmicus der Vögel bekommt auch, wie von mir beschrieben, ectodermales Bildungsmaterial durch eine Reihe von Zellenvermehrungs-Heerden welche längs der Verlaufsrichtung des Nerven zerstrent sind." What the exact anatomical position of this ophthalmic nerve of the chick may be I cannot find, but I presume it holds the position of a ramus naso-ciliaris, which is I believe always that of a true profundus. Marshall, however, says (**41**, p. 29), that it "passes under the rectus superior but dorsal of the other eye muscles and of the optic nerve,"—a somewhat anomalous position.

Neal (**45**), in Squalus, finds the ramus ophthalmicus profundus developed from two processes formed at the ventral end of a descending line of neural crest cells. One of these processes grows posteriorly, unites with the anlage of the ganglion of the nervus trigeminus, and forms the basal portion of the future profundus nerve. The other process grows anteriorly and forms the distal portion of the same nerve. The descending line of neural crest cells is said to be Platt's thalamicus nerve, and it is said to later entirely disappear. The processes that form the profundus nerve do not begin to develop until the descending line of cells that represents the thalamicus has reached the dorsal surface of the optic vesicle, the profundus nerve thus being first laid down in its adult position. The oculomotorius and trochlearis are later developed as fibrillar processes from neuromasts in the medulla, and take at once their adult relations to the profundus. The nerve that Neal identifies as the ramus ophthalmicus superficialis trigemini develops later than the profundus, and is first described in 17mm. embryos, where it "appears as a fibrillar nerve with peripheral nuclei extending from the Gasserian ganglion just dorsal to the point of exit of the fibres of the r. ophth. profundus V, and passing anteriorly close to the ectoderm below the r. ophthalmicus superficialis VII" (p. 233). The two trigeminal ophthalmic nerves are thus first laid down in their adult positions, and there is no question whatever of the profundus cutting through the oculomotorius or trochlearis, or of its cutting through the as yet undeveloped eye muscles. The late development of the ophthalmicus superficialis corresponds with Dixon's account of the late development of the frontal branch of the ophthalmic nerve in man, and strongly suggests their being homologous nerves. The ramus ophthalmicus superficialis facialis is said by Neal to develop "in close connection with the skin along what in the head corresponds with the dorso-lateral line of the trunk."

There is thus nothing in the development of the ophthalmic nerves, so far as known, to definitely indicate either that the portio trigemini of the ophthalmicus superficialis of selachians ever descends, in other verebrates, to the position of a profundus, or that the latter nerve ever ascends to, or simply remains in, the position of a superficialis.

Leaving aside, now, all question of the possibility of a simple juxtaposition and subsequent fusion of the profundus and superficialis nerves, the central origin and composition of these nerves can be considered.

In Acipenser, Goronowitsch (**24**) says that the nerve called by him the ophthalmicus profundus trigemini, and which is, as stated above, simply the ramus ophthalmicus superficialis trigemini in the nomenclature of most other authors, arises from the ventro-anterior trigeminal root of the fish, which root is called by him the root of the nerve Trigeminus I. The ramus ophthalmicus superficialis trigemini, or ophthalmicus superficialis facialis of other authors, is said to arise from Trigeminus II, and this latter nerve is said to arise from the medulla by two roots, one dorsal and the other ventral. The ventral root is said (p. 477) to be a thick-fibred, motor one, arising from a so-called dorso-lateral tract of the medulla. The dorsal one is said to be a fine-fibred, sensory one, arising from the lobus trigemini. Strong (**60**, p. 168) concluded that the ventral root of Trigeminus II, thus described by Goronowitsch, could not be motor, and he ascribed to it a lateral sensory character, the dorso-lateral tract of Goronowitsch being homologised with the tuberculum acusticum of his own and certain earlier descriptions of the medulla. The dorsal root of Trigeminus II, Strong considers as a part of the fasciculus communis system, and not as a lateral line nerve (p. 192). Kingsbury (40) agrees with Strong that the ventral root of Goronowitsch's descriptions must be a lateral sensory one, and he homologises it with a root called by him VIIb in Amia; that is, with the entire lateral sensory root of the latter fish. He considers the lobus trigemini of Goronowitsch's descriptions as simply a somewhat separate part of the tuberculum acusticum, and says that both it and the root that arises from it, Trigeminus II dorsalis, are "absent as such" in Amia, Lepidosteus and teleosts. The fasciculus communis component of the V—VII complex is, according to him, represented entirely in the dorsal root of the facialis of Goronowitsch's descriptions, he thus differing from Strong in the root to which this component is assigned. Goronowitsch, in a later work (**25**, p. 12), refers to Strong's conclusion that the ventral root of Trigeminus II could not be a motor one, but, after renewed investigation, he reaffirms his belief that it is such. Johnston (**39**) follows Strong and Kingsbury in assigning this ventral root to the lateral sensory system, the dorsal root of Trigeminus II being said by him to also belong to the same system, he thus here agreeing with Kingsbury as against Strong. Herrick (**32**), still later, also asserts that the ventral root is sensory, and not motor, and such is unquestionably the case.

Goronowitsch does not give, in Acipenser, the separate peripheral distribution of the fibres arising by each of the two roots of Trigeminus II, but Strong assumes that the fibres of the two roots are completely mingled, and that they must accordingly be found in all the so-called lateral sensory branches that have their origin from this root (**60**, p. 179). This would seem to be practically established by what I find in Mustelus. Strong says that the branches said by Goronowitsch to be derived from the nerve Trigeminus II, his (Strong's) facialis, have, in Acipenser, the same course and position as the lateral sensory branches of the facialis in the tadpole. They also have the same course and position as the lateral sensory facialis branches in Amia and Scomber (**3** and **7**), excepting only the branch said by Goronowitsch to join and accompany the ramus hyoideus facialis. This lateral branch of Acipenser seems to be represented in Amia by that part only of the mandibularis externus facialis that goes to the preopercular lateral canal, or perhaps even to the dorsal part alone of that canal. These latter fibres of the mandibularis externus of Amia arise directly from the truncus hyoideo-mandibularis, as apparent branches of that nerve, while the remaining, more distal, branches all arise from the ramus mandibularis externus after it separates from the ramus hyoideus, to which nerve the mandibularis externus has, in its further course, no relations whatever. The absence, in Acipenser, of this distal and independent part of the mandibularis externus nerve of other fishes was noticed by van Wijhe, who says (**65**, p. 237) that his failure to find it was probably due to its being so small that it was overlooked, or missed, in dissection. It is, however, to be noticed that neither he nor Collinge (**13**) describe, in Acipenser, either a preopercular or mandibular section of the lateral canals. This thus certainly calls for further investigation.

According to Goronowitsch (p. 481) neither the ophthalmicus superficialis nor the ophthalmicus profundus of his descriptions of Acipenser receives a communicating branch from the facialis roots. If, then, Kingsbury is correct in his assertion that the communis component of the V—VII complex of Acipenser is derived entirely from the dorsal root of the facialis of Goronowitsch, it is evident that the communis fibres, if they exist as such in either of the two ophthalmic nerves of the fish, must be derived from those fibres that are said by Goronowitsch (p. 479) to connect the ganglion of Trigeminus II with the nervus facialis. As the communis elements that could possibly enter into the ophthalmic nerves by this route would necessarily be limited, they certainly cannot represent the nervous supply of the nerve-sacs of the snout of the animal, those organs thus quite certainly being innervated by fibres derived from one of the two roots that Kingsbury and Johnston both consider as lateral sensory ones; that is, the nerve-sacs of Acipenser and the ampullæ of selachians are quite unquestionably innervated in the same manner, and are hence homologous organs.

In Amia, both Kingsbury (**40**) and myself (**3**), in works published at nearly the same time, find two of the trigemino-facial roots arising close to the root of the nervus acusticus. Kingsbury calls them VIIb and VIIaa, and says that VIIb enters the tuberculum acusticum, and is composed of coarse fibres identical with those of the lateral line nerve; while VIIaa arises "from the fasciculus communis system which disappears with the exit of this root" (p. 7). The spinal Vth tract of the fish is said by Kingsbury (p. 23) to probably furnish all the general sensory elements of the trigeminal nerve. The root here called VIIaa by Kingsbury was considered by me (l. c., p. 596) as the antero-dorsal root of the facialis, and was said to have its central origin "at a high level in the brain, probably from the fasciculus communis of Osborne and Strong." The ramus ophthalmicus superficialis trigemini of my description of Amia is certainly largely, and perhaps entirely, composed of fibres derived from this communis root. The ramus ophthalmicus superficialis facialis is certainly largely, and probably entirely, composed of fibres derived from the tuberculum acusticum. The portio ophthalmici profundi is probably exclusively composed of spinal fifth fibres. Compared with Acipenser the ramus ophthalmicus superficialis of Amia thus contains a large communis component, not found as such in Acipenser, while the nerve of Acipenser contains a large lobus trigemini component not found as such in Amia. The inference is evident that the two components are homologous, and as the communis component of the nerve of Amia is largely, and perhaps exclusively, destined to the innervation of terminal buds, and as there are neither nerve-sacs nor ampullæ in Amia, these latter organs of Acipenser and selachians must be the homologues of the terminal buds of Amia. That the ampullæ of selachians are derived from the terminal buds of ganoids and teleosts was Strong's impression, rather than opinion, for he says (**60**, p. 202), in discussing selachians, that "it would seem likely that those fibres in the lateral line nerves of the head derived from the lobus trigemini are devoted to the innervation of the ampullæ. If this were true, as further research is necessary to show, the ampullæ would represent the end buds of other fishes."

The descriptions of other fishes do not throw much further light upon this subject, but they are certainly in accord with, rather than opposed to, my conclusions. The varying use and misuse of descriptive terms, and certain probable errors in the descriptions, make most of the comparisons very difficult and of but little value. The probable homologies can, however, be indicated.

In Lota Goronowitsch (**25**) says that Trigeminus II arises by two stems, a dorso-median and a ventro-lateral one. The dorso-median stem is said to arise mainly from a special centre of grey substance, which Goronowitsch says (pp. 25-27) is peculiar to teleosts, and which he considers as the homologue of the lobus trigemini of Acipenser. Certain fibres found in the dorsal root of Trigeminus II of Acipenser, which root arises from the lobus trigemini of the fish, are, however, said by Goronowitsch not to be found in the dorso-median stem of Lota. What they are is not evident. The ventrolateral stem of Lota is said to be formed largely of motor fibres, but partly of fibres derived from the same centre as the dorso-median stem. The motor fibres here referred to are, as in Acipenser, unquestionably lateral sensory ones, as Herrick has already pointed out (**32**, p. 210), and it might be assumed that the dorso-median stem was composed of communis fibres, because of Goronowitsch's conclusion that the centre from which the stem arises is the homologue of the lobus trigemini of Acipenser. The composition of the two ophthalmic nerves of the fish are, however, decidedly opposed to this assumption. The dorso-median stem of Trigeminus II, as I understand Goronowitsch, alone sends fibres to his ramus ophthalmicus superficialis, and as that nerve is largely a lateral sensory one, the fibres it receives through this stem must be lateral sensory ones, if there be no error here. The nerve is not exclusively a lateral sensory one, since it is said to send certain branches to the skin, but this is not important in this connection. The ramus ophthalmicus profundus of Goronowitsch's descriptions, which is simply a deeper strand of the superficialis nerve, is said to be formed of two bundles of fibres, one derived from Trigeminus I, and the other from the so-called dorsal root of the facialis. The former bundle is the spinal fifth component of the ophthalmic nerve, the latter being the communis component. The communis component of the ophthalmic nerve thus being accounted for, the special centre of grey substance from which the dorso-median stem of Goronowitsch has its origin, cannot be the homologue of the lobus trigemini of Acipenser if, as I conclude, that lobus is a centre of communis fibres. As the so-called profundus nerve, which receives no fibres from the lateral sensory centres, is said to send a branch to the sensory canal in the antorbital bone of the fish, it is evident that the subject needs further investigation. The spinal fifth component of the so-called profundus nerve is evidently the homologue of the portio ophthalmici profundi of my descriptions of Amia.

In Amiurus the fasciculus communis system, and especially its pre-auditory portion, that is, root VIIaa, is said by Kingsbury (**40**) to be enormously developed, giving origin to the lobus trigemini of the fish (p. 30). From this root and system the deeper ophthalmic nerve of Wright's descriptions is said by Kingsbury to derive most of its fibres (p. 14). By Workmann (**68**) this same nerve is said to receive general cutaneous and communis fibres in approximately equal numbers, and the nerve is said to be, in position, an ophthalmicus superficialis trigemini, and not a profundus nerve. The two components that form the nerve are said to arise, one from the sensory trigeminus root, and the other from the communis root of the facialis, the former thus being the probable homologue of the portio ophthalmici profundi of my descriptions of Amia, and the latter the homologue of the ophthalmicus superficialis trigemini.

In Menidia Herrick (**30**, p. 428) says that the "r. oph. sup. VII and the r. oph. sup. V are fused throughout their entire course, but each can be easily distinguished and separately followed by difference in the calibre of the fibres." The ophthalmicus superficialis facialis is a lateral line nerve, and is said to arise from the dorsal one of two lateral line roots of the V—VII complex, a root which must accordingly be the homologue of the dorso-median stem of Trigeminus II of Goronowitsch's descriptions of Lota. No communis fibres are here said to accompany those nerves.

In a later work (**31**) Herrick says that some fasciculus communis fibres "probably run forward with the ophthalmicus superficialis," while in his still later and complete work (**32**) these communis fibres are said to be so completely united with the ophthalmicus trigemini that it is impossible to separate them. This trigeminal ophthalmic nerve, thus formed, is accordingly quite probably the homologue of the portio ophthalmici of Amia plus the ophthalmicus superficialis trigemini of the same fish. "A very small r. profundus V" is said by Herrick to be found in Menidia, being said to be there represented by certain general cutaneous fibres that accompany the radix ciliaris longa to the ciliary ganglion. While I should certainly consider these general cutaneous fibres as an integral part of the radix longa, and not as representing a ramus ophthalmicus profundus, as will be later more fully discussed, it is important here to notice that the fibres are general cutaneous ones, this thus indirectly supporting my conclusion that the portio ophthalmici profundi of Amia, and that nerve alone, is the general cutaneous component of the ophthalmic nerves of teleosts.

In Polypterus both van Wijhe (**65**) and Pollard (**51**) describe a portio ophthalmici profundi, and also a ramus ophthalmicus profundus that has the position of a selachian profundus; but, in marked distinction with Amia and Lepidosteus, no portio trigemini of the ophthalmicus superficialis is definitely given by van Wijhe, and Pollard says that he wholly failed to find that nerve. There is thus in this fish, as in Acipenser, an apparent absence of a communis component in the superficial ophthalmic nerve. In Acipenser this apparent absence was accounted for under the assumption that the dorsal one of the two so-called lateral sensory roots of the fish, the Trigeminus II dorsalis of Goronowitsch, is a somewhat modified communis root, and that it is concerned in the innervation of the sensory organs of the nerve-sacs, those organs being derived from terminal buds. What the apparent absence of this component in Polypterus is due to is not evident from existing descriptions of that fish.

Turning now to selachians, Haller (**28**) has recently very thoroughly investigated the central origin and composition of the cranial nerves in Scyllium. In this fish this author says that Trigeminus II is mainly, if not exclusively, sensory, and that it arises by two roots, an upper one from the "lobus n. trigemini," and a lower one from the ventral portion of the so-called outer sensory "Oblongatagebiet" (p. 436). The lobus trigemini is said by him to be simply an "Abschnitt" of the outer sensory oblongatagebiet, and that part of the latter "gebiet" from which the ventral root of Trigeminus II arises, is said to be the homologue of the dorso-lateral tract of Goronowitsch (p. 423).

Kingsbury (**40**, p. 27), before the publication of Haller's work, was led to conclude that the lobus trigemini of Acipenser was the probable homologue of the similarly named structure in sharks, and, moreover, that further investigation would probably prove this lobus to be a modified portion of the acusticum system.

According to Haller no fibres from the inner sensory oblongatagebeit (Lobi vagales) enter either of the trigeminal roots of Scyllium, that fish thus agreeing with Acipenser in the total or practical absence of communis fibres, as such, in the so-called trigeminal roots.

The two roots of Trigeminus II of Scyllium thus seem to be the exact homologues, in so far as the central regions from which they take their origins are concerned, of the two roots of the same nerve in Acipenser, and it may be assumed that the several peripheral branches that arise from the two roots in the two fishes have a similar distribution, though this cannot be definitely confirmed from Haller's descriptions. A bundle of fibres from each of the two roots of Scyllium is said by Haller to be sent to the so-called second trigeminus ganglion, from which the ramus ophthalmicus superficialis, and that nerve alone, has its origin. The remaining fibres of the two roots are said to enter the Gasserian ganglion. From the hind edge of the latter ganglion, and even partly as a part of the dorsal root of Trigeminus II, four branches, said to be lateral branches of the Trigeminus, are said to always arise. The three distal ones of these four branches always unite to form the ramus oticus, this last nerve being thus formed of three separate branches, as it is in Mustelus. The other and most proximal branch is the one that has its apparent origin partly from the dorsal root of Trigeminus II. It runs backward, and joins the so-called ramus hyoideus facialis, thus doubtless forming the lateral and ampullary sensory component of the post-trematic branch of the facialis. There thus remains only the ramus buccalis to be accounted for of all the lateral sensory branches of the facialis, and this nerve is, unfortunately, not especially described, and not even indicated in any of Haller's figures. It may form part of the so-called ramus maxillaris superior trigemini, and it would seem as if it must receive fibres from both of the roots of Trigeminus II. That the nerve exists as an important nerve is evident from Marshall and Spencer's descriptions of it in embryos.

The ramus ophthalmicus superficialis of Haller's descriptions of Scyllium is thus formed of two components, a dorsal and a ventral one, both of which arise from what are considered by several authors as lateral sensory tracts of the brain. As in Haller's descriptions, there are but two ophthalmic nerves, a ramus superficialis, and a ramus profundus, the natural conclusion would be that the two components described by him in the ramus superficialis must necessarily be the united portio major and portio minor of the nerve. A comparison with Schwalbe's descriptions of this same fish (**57**, p. 187) lead one, however, to strongly suspect that Haller has simply repeated Balfour's mistake, and given the name profundus to what is in reality the portio minor of the superficial nerve. Haller's fig. 52 practically confirms this. The subject is then still further complicated by Haller's statement (p. 496) that in Salmo the fibres corresponding to those that form the ramus profundus of Scyllium arise from the posterior instead of from the anterior root of the trigeminus, thus belonging to his Trigeminus II instead of to Trigeminus I. Haller attempts to explain this uncomfortable fact in the statement that "bei den Salmoiden und wohl auch anderen älteren Vertretern der Teleostier eine Rostralwärtsverschiebung vom Boden des chordalen Hirnes stattfand und dass damit auch ein grosser

Theil des erster Trigeminus nach rosträlwarts wanderte, während der R. ophthalmicus profundus, fixirt durch seinen gesonderten Austritt aus dem Cranium, zurückblieb und nun mit dem zweiten Trigeminus vom Centralorgan abgeht." It seems much more probable that Haller has made some mistake in homologising his fibre tracts, in addition to wholly overlooking the true ramus profundus.

Scyllium thus probably presents a portio major of the ramus ophthalmicus superficialis, formed by two bundles of fibres derived, the one from the lobus trigemini, and the other from the tuberculum acusticum, and a large portio minor of the same nerve, derived from the anterior root of the trigemino-facial complex. These two nerves issue from the skull by separate foramina (Schwalbe), but soon unite to form a single nerve. The portio minor is evidently the homologue of the general sensory component of my descriptions of Mustelus, and hence is what I am led to consider as the portio ophthalmici profundi of the superficial nerve. It is relatively very large in Scyllium, the true ramus profundus being, according to Schwalbe's descriptions, correspondingly small. The two components of the portio major are, according to my conclusions, destined, the one to innervate the sensory organs of the lateral canals, and the other the sensory organs of the ampullæ. The former is the homologue of the portio facialis of the ophthalmic nerve of Amia, and the other the homologue of the portio trigemini. Haller says that his so-called profundus nerve is exclusively motor. This is too manifestly an error to need discussion, but it well shows how liable one is to error, in the present state of our knowledge of the subject, if one limits one's attention entirely to the central origin of a nerve.

In Læmargus the ramus ophthalmicus superficialis trigemini of Ewart's descriptions is said by him to be found as a separate slender nerve, which springs either from the trunk of the trigeminus, or from its mandibular branch. Of it Ewart says (**18**, p. 76) that it "neither innervates sensory nor ampullary canals. It may, however, supply some of the taste buds found in the roof of the mouth of certain fishes. If these taste buds are modified lateral sense organs, the nerves supplying them are likely to be made up of suprabranchial fibres." Ewart further says (p. 45) of this so-called trigeminal ophthalmic nerve in elasmobranchs in general, "In sharks and rays this nerve supplies the eyelids and the skin over the anterior part of the cranium, but it also sends fibres to the snout. More or less distinct in sharks, the superficial of the ophthalmic of the trigeminal in rays consists of a very few fibres which, on leaving the trigeminal, at once more or less completely unite with the superficial ophthalmic of the facial." Ewart's statement that branches of this trigeminal nerve may innervate taste buds in the roof of the mouth is clearly an error, and the nerve is, in all probability, the homologue of the general sensory component of the ophthalmic nerve of Mustelus; that is, according to my conclusions, the homologue of the portio profundi of the ophthalmicus superficialis of Amia, and not of the portio trigemini of that fish. In Læmargus there is, however, a branch of the ophthalmicus profundus called branch I by Ewart (**17**), which also has the course of an ophthalmicus superficialis, the portio profundi of the superficial ophthalmic nerve of this fish thus apparently being represented by two separate branches.

In Acanthias Hoffmann says (**35**, p. 287) that the portio minor s. trigemini of the ramus ophthalmicus superficialis is a branch of the ramus ophthalmicus profundus, and that it is connected with the nervus trochlearis by a communicating branch. He further says (p. 294), as I understand him, that, after a certain stage of development, that "Stück des Trochlearis, welches den Verbindungsfaden mit dem Ophthalmicus profundus bildet," becomes the portio minor of the ophthalmic nerve. On page 287 he says that the nervus profundus arises as an independent nerve, wholly separate and distinct from a single, large anlage from which the nervus trochlearis, portio minor s. trigemini, ramus maxillo-mandibularis, and communicating branch from the trochlearis to the trigemini all arise. In a later work (**36**, p. 357) he says that "der

Trochlearis und die Portio trigemini rami ophthalmici superficialis ein und derselbe Nerv ist." While it is evidently unfair to Hoffmann to quote these several statements apart from his general discussion of the subject, I must confess to being unable to form a clear idea either of the relationships of the nerves here concerned, or of their manner of development. If the portio minor s. trigemini is a branch of the ramus ophthalmicus profundus, it is evidently the homologue of the portio ophthalmici profundi of Amia, as I am seeking to establish. If it arises as a branch of a nerve complex that is wholly separate and independent of the nervus profundus, it would seem as if it could not be the homologue of the nerve of Amia, and it may be that serially homologous branches of two independent nerves—the trigeminus and profundus—are here concerned, the two branches being found separate and distinct in the two branches of Læmargus just above referred to. The so-called thalamic nerve of Hoffmann's descriptions, the nerve marked X in certain of his figures (**34**, fig. 38), may then be one of these two branches.

In Squalus Acanthias Neal says (**45**, p. 233) that the fibres that form the rami ophthalmicus superficialis and ophthalmicus profundus trigemini arise from the posterior root or portio major of the trigeminus. This so-called posterior trigeminus root (portio major) is simply a part of the anterior trigeminus root of Haller's nomenclature, and as the anterior root (portio minor) of Neal's descriptions is said by him to be largely motor, and destined entirely to the mandibular arch, the posterior root must be the spinal fifth component of the nervus. The ophthalmicus superficialis trigemini of this fish is then evidently the homologue of the portio ophthalmici profundi of Amia, and not of the portio trigemini of that fish. Neal shows the nerve X of Hoffmann's descriptions in one of his figures (fig. K, p. 234), but I do not find that he describes it.

As some slight further evidence of my conclusion that the terminal-bud communis fibres that form the so-called ramus ophthalmicus superficialis trigemini of Amia are represented in Acipenser and selachians by those fibres of the ramus ophthalmicus superficialis of the latter fishes that have their origin in the lobus trigemini, it may be noted that Goronowitsch says (**25**, p. 8) that a few fibres of the dorsal or lobus trigemini root of Trigeminus II of Acipenser can be traced back into the lobi vagales. As no other communis fibres are found, as such, in the ophthalmic nerves of the fish, are these few fibres the remnant of an aborting nerve, or are they a few fibres, still unchanged, of a nerve that is undergoing modification? My impression is decidedly in favour of the latter one of these two suppositions. That communis fibres, as such, once existed in these ophthalmic nerves, and that some of them have actually undergone modification, must be admitted if it be accepted that the sensory organs of the lateral canals of all fishes pass through a stage represented by the terminal bud (**64**, p. 298).

It should here be noted that Herrick concludes (**32**, p. 169) that his own work, and Johnston's also, favours the belief that the acustico-lateral has been differentiated from the general cutaneous system, and hence not from the communis system.

The ramus ophthalmicus profundus now remains to be considered. This nerve is almost invariably said to be a purely sensory one, excepting only in the Myxinoids, where it is said to have motor branches. Haller's assertion that the profundus of Scyllium is entirely motor (**28**, p. 438) has already been referred to; but apart from the fact that this statement is probably an error, his profundus nerve is quite unquestionably simply the portio minor of the ophthalmicus superficialis, and has been already discussed.

In Chimæra, Cole says (**11**, p. 645) that one of the branches of the ophthalmicus profundus is possibly motor, and that its origin and distribution make it exceedingly probable that it corresponds to the motor division of the profundus found in the Cyclostomata. The nerve thus referred to in Chimæra lies dorsal to the opticus. The motor nerve with which it is compared lies ventral to the opticus in both Myxine and

Petromyzon (**20**). In Bdellostoma the "Stamm des Ophthalmicus" is said by Fürbringer (p. 31) to run forward over the opticus, and his reference to Müller (a work I have not at my disposal) leads one to suppose that this stem contains motor fibres. This statement, attributed to Müller, certainly deserves to be controlled, and if found to be correct, the homologies of the muscles so innervated well deserve to be carefully established. That they can be the homologues of muscles that are innervated in Myxine by a nerve that lies ventral to the opticus I wholly doubt, and yet this is always assumed to be the case. Pollard even cites this particular case in support of his propositions (**52**, p. 397) that "The topographical position and course of nerves is not of great importance;" and that "the fundamental grounds for determining the homology of nerves are, (1) origin from homologous nerve-cells, (2) terminal distribution to definite structures. The course of the fibres is of less importance." And so impressed is this author with this very easy manner of accounting for the apparently anomalous positions of certain nerves, that he does not even attempt to show either that the cells of origin or the structures innervated are homologous. The reasoning is that the structures innervated must be homologous, because otherwise the nerves would not be. Much more rational assumptions would be, either that there is some error in the descriptions of Bdellostoma, or that the muscles innervated are not homologous. As to Myxine, it would seem as if certain motor and sensory fibres of the truncus maxillaris trigemini were simply juxtaposited to the ramus ophthalmicus, as that nerve issues from the skull, and that they later take their proper course ventral to the opticus, leaving the true ophthalmic fibres to course above that nerve. Such a juxtaposition is shown by Herrick (**29**) in Amblystoma, and is said to occur in Cryptobranchus also. In these two cases there is certainly no question of anything more than a simple juxtaposition of the two nerves concerned, and I believe that a similar explanation will be found to hold in all other similar cases. Pollard himself even says (p. 400) of this motor nerve in Myxine, that although "it is usually considered to be an ophthalmic branch . . . . it is better to consider it as a special branch, and not a portion of the ophthalmic." He then, by the name that he gives it—the premaxillary nerve—definitely homologises it with the similarly named nerve in his descriptions of Siluroids, in which fishes it is said to be a branch of the maxillaris trigemini. He cannot, however, rid himself of the idea that the nerve is the homologue of the ophthalmic nerve of Bdellostoma.

In Chimæra, Cole says (p. 645), as has been already stated, that two sense organs of the supra-orbital lateral canal are innervated by a branch that has its apparent origin from the ramus ophthalmicus profundus. In Mustelus I find one lateral sensory branch so closely associated with the profundus that I could not definitely determine whether it fused with that nerve, or later left it to join the main ophthalmicus lateralis. A possible association of lateral sensory fibres with the profundus nerve is thus here indicated, and if the profundus nerve is actually thrown down from the same line of ectoderm that later gives origin to the superficialis, as Platt states to be the case in Necturus, it would certainly not be wholly improbable that certain lateral fibres might be dragged down with it, and so apparently form part of it. I, however, agree most decidedly with Cole (p. 639) that the subject needs further investigation. A totally different case is presented in Platt's statement that in Necturus four organs of the infra-orbital line "are supplied by nerve twigs composed in equal parts of fibres coming from the buccalis, and from the ophthalmicus profundus" (**49**, p. 530). That profundus fibres could descend to the buccalis or buccalis fibres ascend to the profundus is clearly impossible, the early developed nervus opticus intervening. Platt's explanation is contained in her statement (p. 540) "that the attachment of the superficial receptive cell to one fibre of transmission is not constant. A shorter part when offered is at once accepted." This, as already stated, my work does not lead me to accept, and Goronowitsch seems to hold a similar opinion, for he says (**26**,

p. 48) that "Die Verbindung zwischen dem Nerv und seinem Endorgan ist . . . . in der Ontogenie eine Primäre."

Herrick finds, in Menidia, what he considers as a "ramus ophthalmicus profundus fused for its entire length with the radix longa" (**32**, p. 209). The fibres that represent the ramus profundus, thus identified, are said to be general cutaneous ones. As all the other fibres that enter the radix longa of the fish are said to be sympathetic ones, it seems as if Herrick must arrive at his conclusion by the assumption that the term radix longa should strictly be applied only to a sympathetic nerve. This seems to me an error, for Thane says (**61**, p. 238) that the "long or sensory root" of the ciliary ganglion of man arises from the nasal branch of the ophthalmic trunk, and is wholly separate from the "middle or sympathetic root" of the ganglion. The so-called long root thus here contains no sympathetic fibres. Moreover, Schwalbe says (**57**) that, in the dog, the ramus naso-ciliaris sends a radix longa to the ciliary ganglion, and that ganglion is, according to Holtzmann (**37**), partly spinal and partly sympathetic in character. The radix longa of the animal must, accordingly, very probably contain general cutaneous as well as sympathetic fibres, and yet there is a distinct and separate ramus naso-ciliaris, the homologue of the ramus profundus of fishes. I should accordingly look upon the general cutaneous fibres of the radix longa of Menidia as an integral part of that root, and not as a remnant of the ramus profundus, that ramus being wholly wanting, as it is in other teleosts, so far as known. This is, moreover, practically shown to be the case, by the arrangement found in Scomber, where there is (**7**) a radix longa, which arises from a separate and independent profundus ganglion, and is later joined by sympathetic strands from a large sympathetic ganglion associated with the trigeminal ganglion.

SUMMARY.

There are, in fishes, several ophthalmic nerves between which it is necessary to carefully distinguish. While their exact inter-homologies cannot as yet be definitely affirmed, certain very probable homologies can certainly be arrived at.

The portio ophthalmici profundi of bony ganoids, and the ramus ophthalmicus profundus and ramus ophthalmicus superficialis trigemini of elasmobranchs, are general sensory cutaneous nerves, and probably contain all of those general sensory elements that belong to the ophthalmic nerves of vertebrates.

The portio ophthalmici profundi of ganoids is the homologue either of the ramus ophthalmicus superficialis trigemini of elasmobranchs, or of a frontal branch of the ramus profundus that has, in certain selachians (Læmargus), the position of a superficial ophthalmic nerve; or it is the homologue of both those nerves of elasmobranchs. In the higher animals this portio profundi becomes the frontal branch of the ophthalmic nerve.

The ramus ophthalmicus profundus of elasmobranchs and of Polypterus, and that nerve alone, is the homologue of the ramus nasalis or naso-ciliaris of higher animals. This nerve and the portio ophthalmici profundi vary inversely in importance.

The ramus ophthalmicus superficialis trigemini of Amia is a communis nerve, and is probably the homologue of that part of the ophthalmicus superficialis facialis of Acipenser and elasmobranchs that is derived from the so-called dorsal root of Trigeminus II. This latter root arises from the lobus trigemini of the latter fishes, is considered by certain authors as a lateral sensory root, and is called by them the dorsal root of the ramus opthalmicus superficialis facialis.

The ramus ophthalmicus superficialis facialis of Amia is a lateral sensory nerve, and has its probable homologue in that part only of the ophthalmicus superficialis facialis of Acipenser and elasmobranchs that is derived from the so-called ventral root of Trigeminus II. This root arises, in all fishes, from the tuberculum acusticum.

The so-called ramus ophthalmicus superficialis trigemini of teleosts is the ramus ophthalmicus superficialis trigemini of

Amia plus the portio ophthalmici profundi of that fish, these two components being found in varying proportions.

The ramus ophthalmicus superficialis of selachians probably always contains the same three components, or portiones, that are found in the superficial ophthalmic nerve of Amia, but the portio ophthalmici profundi, called in selachians the portio trigemini, is usually small and may be reduced to a few fibres only (Rays, Ewart). The portio trigemini of Amia is represented in selachians, as stated above, by those fibres of the so-called portio facialis that arise from the lobus trigemini; that is, by the fibres that form the so-called dorsal root of Trigeminus II.

The terminal buds of ganoids and teleosts, the nerve-sacs of Acipenser, and the ampullæ of selachians, are in all probability homologous structures.

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DESCRIPTION OF PLATES 10—12,

Illustrating the paper by Mr. Edward Phelps Allis, jun., on "The Lateral Sensory Canals, the Eye Muscles, and the Peripheral Distribution of the Cranial Nerves of Mustelus lævis."

Fig. 1.—Side view of the head of a 10 cm. embryo of Mustelus lævis, the skin being removed so as to expose the lateral and ampullary canals. The surface pores of the lateral canals are not shown at all; and very few of the tubules of the canals, excepting those that project to one side or the other, are even indicated. × 9.

Fig. 2.—Top view of the same. × 9.

Fig. 3.—Bottom view of the same. × 9.

Fig. 4.—Side view of a deeper dissection of the same head. The lateral and ampullary canals, the eyeball, and the eye muscles have been removed, the other muscles being all left in place. Part of the ampullæ have been removed, others being left in place. × 9.

Fig. 5.—Bottom view of the same. × 9.

Fig. 6.—Side view of the skull of a 10 cm. embryo of Mustelus lævis. × 5.

Fig. 7.—The suborbital section of the infra-orbital canal of a 10 cm. Mustelus lævis, showing the tubules and pores of the canal. × 12.

Fig. 8.—Part of a transverse section of a 12·2 cm. embryo of Mustelus lævis, showing the adductor mandibulæ and Addβ muscles, the mandibular cartilage, and the anterior upper labial cartilage.

Fig. 9.—Part of a more posterior section of the same embryo, showing also the anterior end of the posterior upper labial cartilage, with a part of the tendon of the muscle Addβ inserted on it.

Index Letters.

acafr. Foramen of anterior carotid artery. *acvfr.* Foramen of anterior cerebral vein. *Addβ.* Muscle Addβ of Vetter's descriptions. *Am.* Adductor mandibulæ. *ba.* Buccal group of ampullæ or their pores and tubes. *ba.*$^{1-5}$ Five sub-groups of buccal ampullary pores and tubes. *bf.* Ramus buccalis facialis. *b.mx.md.* Truncus buccalis-maxillo-mandibularis. *ct.* Canalis transversus. *Csd_2.* Muscle Csd_2 of Vetter's descriptions. *Csv_2.* Muscle Csv_2 of

Vetter's descriptions. *end.* Endelymphatic pore. *es.* Eyestalk. *eye.* Eye. *gc.* Ciliary ganglion. *gl.* Nervus glossopharyngeus or its foramen. *hf.* Ramus hyoideus facialis. *hmc.* Hyomandibular lateral canal. *HMD.* Hyomandibular cartilage. *hmf.* Truncus hyoideo-mandibularis facialis. *Im.* Intermandibularis. *ioc.* infra-orbital lateral canal. *llc.* Lateral line canal. *M.* Meckel's cartilage. *m.* Mouth. *mda.* Mandibular group of ampullæ or their tubes and pores. *mdc.* Mandibular lateral canal. *mdt.* Ramus mandibularis trigemini. *mef.* Ramus mandibularis externus facialis. *mlc.* Mandibular labial cartilage. *mxt.* Ramus maxillaris trigemini. *na.* Nasal aperture. *nc.* Nasal capsule. *o.* Nervus opticus or its foramen. *ocm.* Nervus oculomotorius or its foramen. *ocmi.* Inferior branch of nervus oculomotorius. *onc.* Orbito-nasal canal. *opad.* Deep group of ophthalmic ampullæ. *opas.* Superficial group of ophthalmic ampullæ. *opas*$^{1-3}$. Three sub-groups of pores and tubes of superficial ophthalmic ampullæ. *opp.* Ramus ophthalmicus profundus or its foramen. *oppc.* Ophthalmicus profundus canal. *Ops.* Ramus ophthalmicus superficialis or its foramen. *Os.* Obliquus superior. *otf.* Ramus oticus facialis. *pcafr.* Foramen of posterior carotid artery. *pf.* Ramus palatinus facialis. *PQ.* Palato-quadrate cartilage. *soc.* supra-orbital lateral canal. *spr.* Spiracle. *sso.* Surface sense-organs. *stc.* Supra-temporal cross commissure. *tAddβ.* Tendon of muscle Addβ. *tffr.* Trigemino-facial foramen. *tr.* Nervus trochlearis or its foramen. *ulca.* Anterior upper labial cartilage. *ulcp.* Posterior upper labial cartilage. *x.* Foramen which probably transmits the general cutaneous component of the ramus ophthalmicus superficialis.

Fig 1

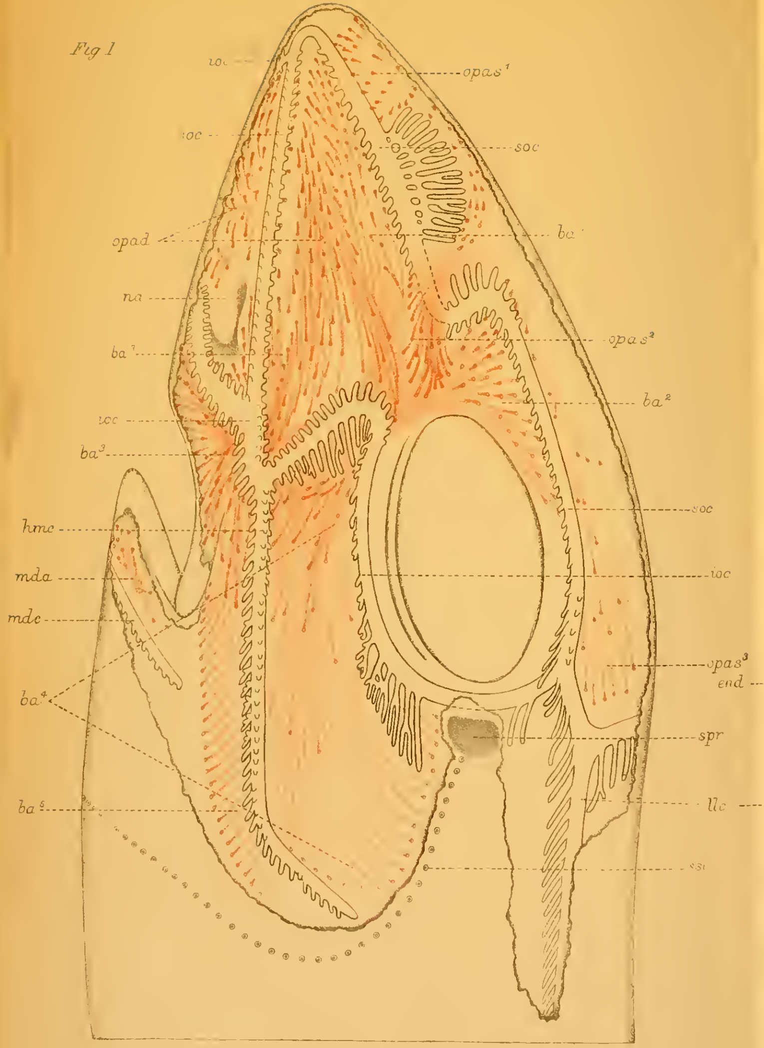
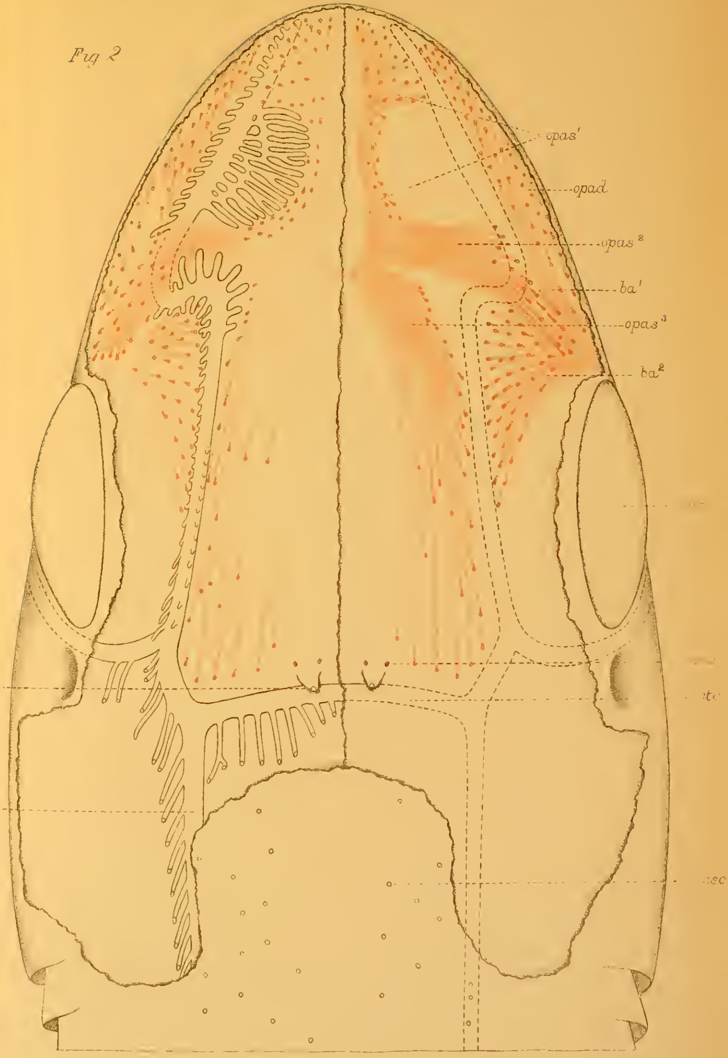


Fig 2



West, Newman chromo.

Fig. 3.

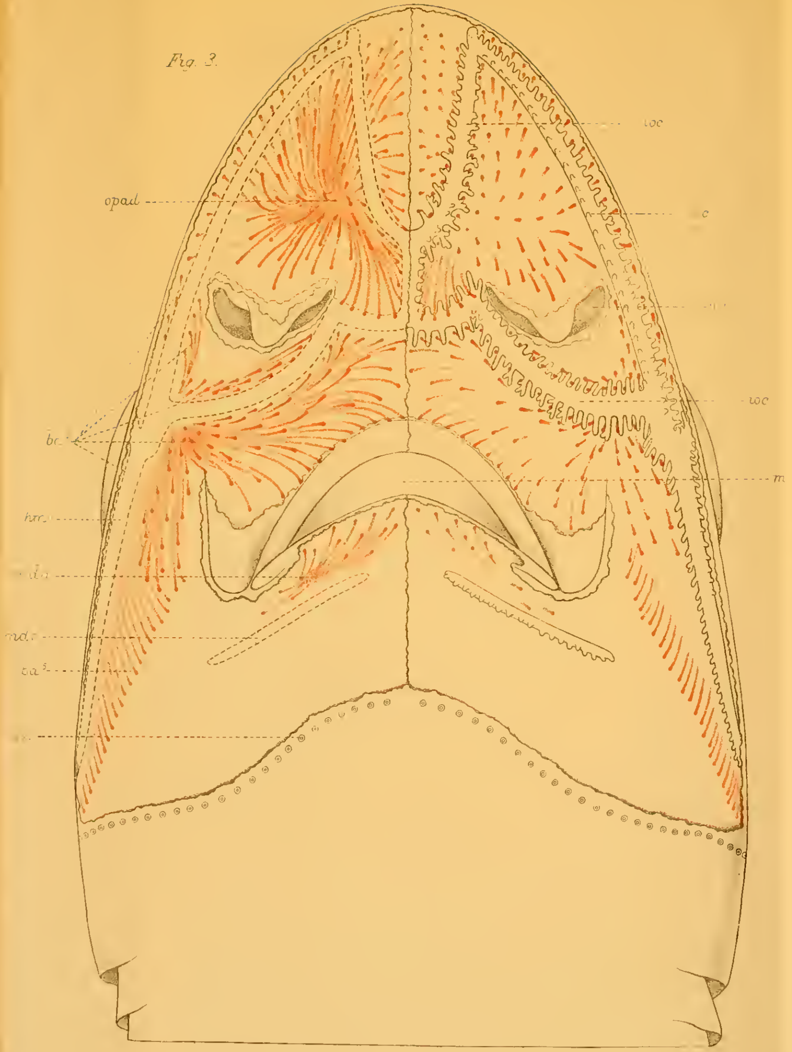
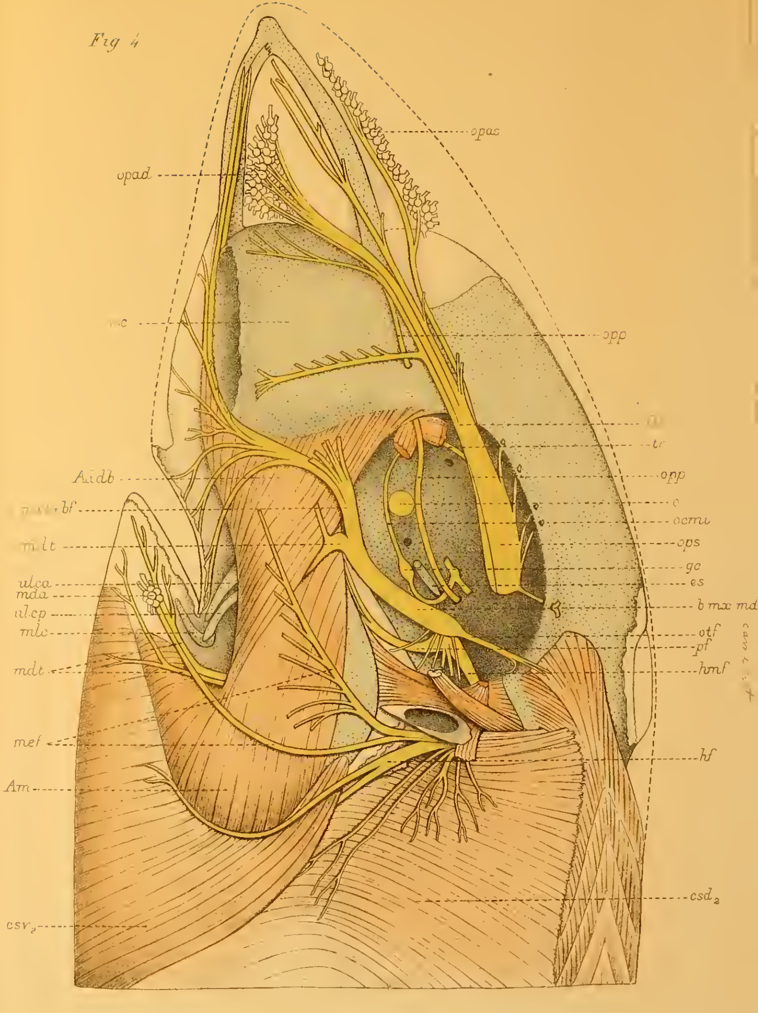


Fig 4



West, Newman chromo

Fig 5

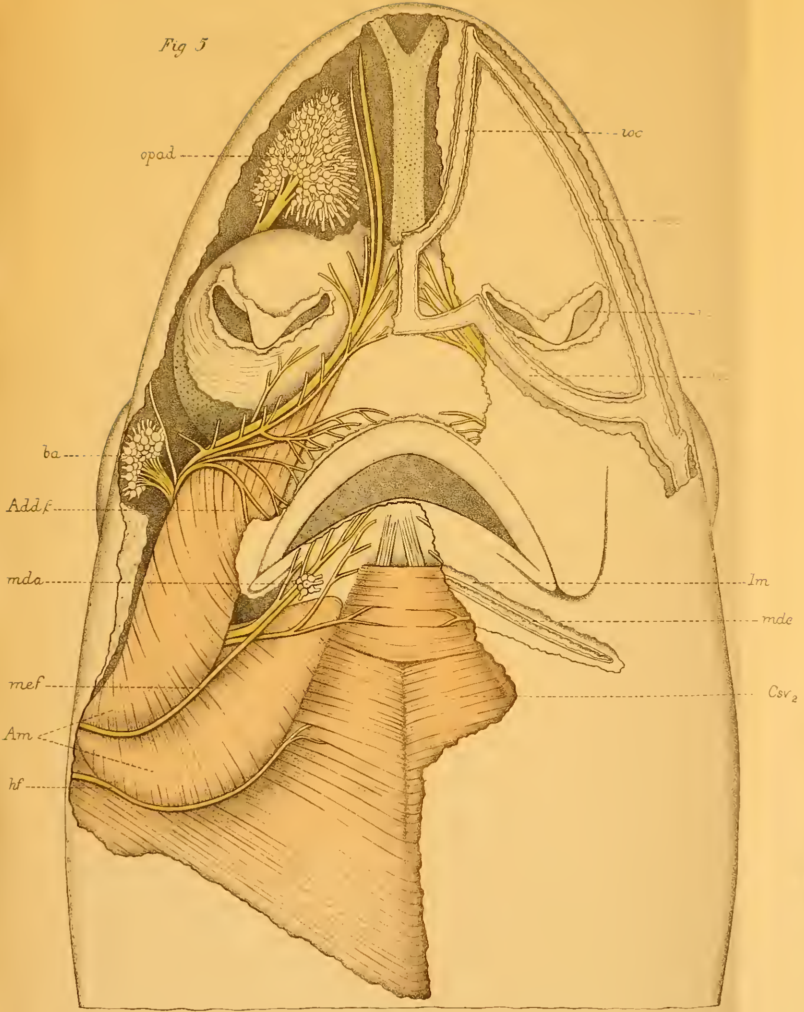


Fig. 6

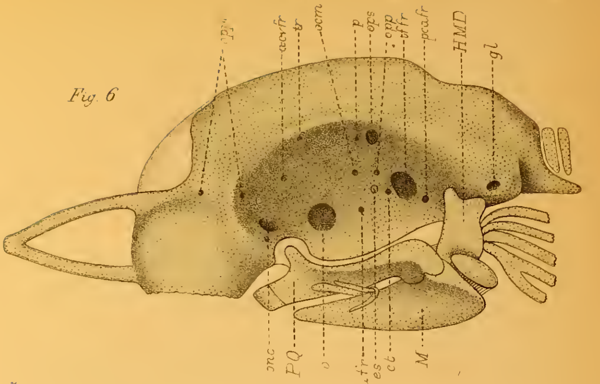


Fig. 7

Fig. 8

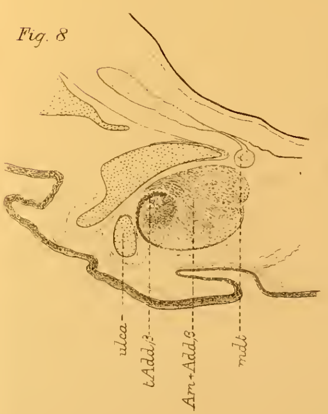
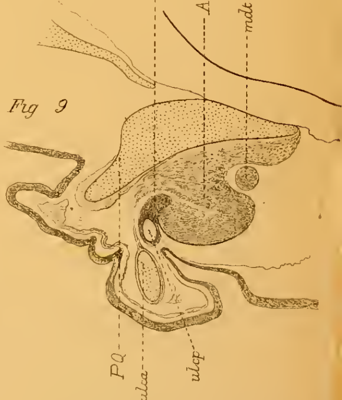


Fig 9



The Anatomy of Scalibregma inflatum, Rathke.

By

J. H. Ashworth, D.Sc.,
Lecturer on Invertebrate Zoology in the University of Edinburgh.

With Plates 13—15.

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1. Introduction.

My attention was drawn to our scanty knowledge of Scalibregma when discussing the affinities of Arenicola with other Polychætes (1900,[1] p. 544). It was found impossible to make any definite statement regarding the affinities of these two genera, owing to the small amount of information available regarding the structure of Scalibregma. This Polychæte has received little attention from zoologists, perhaps on account of its comparative rarity and the somewhat small size of the majority of specimens in museum collections. Most of the references to this animal in zoological literature are mere records of its capture. There are only three or four memoirs which refer, quite briefly, to some details of its structure, and only one, by Danielssen (1859, p. 69), which contains a connected account of its internal anatomy. This memoir contains no mention of the nephridia, although the accompanying figures show structures which are obviously nephridia, but which Danielssen considered to be ovaries. He also stated that Scalibregma is hermaphrodite, and that its nerve-cord is provided with typical ganglionic swellings. Subsequent authors do not throw light on any of these matters. In these points there was such marked difference between Scalibregma and Arenicola, which in other respects seemed to have much in common, that I was anxious to reinvestigate the anatomy of the former as soon as specimens were available, chiefly with the intention of comparing the nephridia, gonads, and nerve-cord of these two genera. The material placed at my disposal has enabled me to study the anatomy and histology of this northern Annelid, and to determine some interesting points connected with most of the systems of organs.

I am grateful to the authorities of the United States National Museum in Washington for the loan of a number of specimens collected on the east coast of America, and to

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[1] The dates in parentheses form references to the literature quoted at the end of this paper.

Dr. Théel, of Stockholm, and Dr. Appellöf, of Bergen, for the gift of several excellent specimens from the coast of Norway.

This work has been done in the Beyer Zoological Laboratories of the Owens College, Manchester, and in the Zoological Laboratory of the University of Edinburgh.

2. Historical Account.

Rathke (1843, p. 182) founded the genus and species Scalibregma inflatum upon specimens obtained at Molde, in Norway. He described the external characters in considerable detail, directing attention to the form of the parapodia in different regions of the body, and to the brown or black structures upon them.

Three years later M. Sars (1846, p. 91) was fortunate in securing a very large specimen (58·5 mm. long), which he described under the name Oligobranchus roseus. He has given a good account of most of the external characters of the animal, but overlooked the black structures on the parapodia. He considered this animal was allied to the newly described genus Eumenia, Oersted, and he also mentioned its general affinity with the Ariciidæ and the Arenicolidæ.

Danielssen (1859, p. 69) has given the only account of the internal anatomy of Scalibregma. The form of the alimentary canal, the circulatory system, the nervous system, the paired segmentally arranged organs—interpreted by him as ovaries,—and the structures he mistook for testes are described in considerable detail and illustrated by clear figures.

In 1873 Verrill (1873, p. 605) described the external features of a new species, S. brevicauda, which had been obtained off Newhaven, Connecticut, U.S.A., and Hansen (1882, p. 34) found among the material of the North Atlantic Expedition specimens which he referred to new species, S. (?) abyssorum and S. (?) parvum. Wirén (1887) made scattered references to some points in the structure of the alimentary canal, and the arrangement of the muscles and the four anterior diaphragms. The other references to Scalibregma in zoological literature are mostly mere records of its capture, chiefly in Norwegian waters.

3. Distribution and Habits.

Scalibregma inflatum is recorded chiefly from the North Atlantic and Arctic Oceans; but it is not restricted to these northern seas. The "Challenger" (see McIntosh, 1885, p. 359) captured this species at two stations in southern seas, viz. at station 141, between the Cape of Good Hope and Marion Island, where numerous specimens were dredged from a depth of 98 fathoms, and at station 169, off the east coast of North Island of New Zealand, where a single specimen was obtained from a depth of 700 fathoms.

It is interesting to find that these southern specimens correspond very closely with those obtained from European seas. McIntosh states that the southern specimens are somewhat smaller than European examples, the largest one taken by the "Challenger" being 18 mm. long. This is not a character of any importance, as the size of Scalibregma varies between wide limits. Most of the northern specimens are little, if any, larger than those taken by the "Challenger." Of eleven specimens sent to me from Bergen, six are between 12 and 15 mm. long, two are incomplete but would probably be about 13 and 20 mm. long; the other three are 26, 35, and 56 mm. long respectively, while eight of the ten complete specimens from the east coast of the United States are between 5 and 9 mm. long. McIntosh remarks that the gills of southern forms are smaller than those of Norwegian examples; but this, again, is a very variable character, depending on the age and size of the specimen. We may conclude, therefore, that the specimens of Scalibregma obtained by the "Challenger" are not distinguishable by any essential and constant character from those taken in the North Atlantic.

S. inflatum occurs in the Arctic Ocean as far eastward as

Cape Grebeni (the southern point of Waigatsch Island) and the Sea of Kara (Théel, 1879, p. 51). It is found off the western shores of Spitzbergen (Malmgren, 1867, p. 77; von Marenzeller[1]), Nova Zembla (von Marenzeller,[2] Théel, 1879, p. 51), and along the western coast of Norway as far southwards as the island of Floroë (Rathke, Sars, Danielssen, Malmgren, Appellöf[3]). Scalibregma is also recorded from the south-western coast of Sweden. Sars[4] found several small examples in Christiania Fjord, and Malm[5] soon afterwards obtained specimens near Göteborg.

Scalibregma occurs on the north, east, and west coasts of Scotland, being recorded from the Shetlands,[6] from St. Andrews,[7] and from Loch Maddy in the Hebrides by McIntosh, and from near Millport in the Firth of Clyde by Kölliker.[8] The last named is the most southerly European station from which Scalibregma has been obtained.

On the western side of the Atlantic this Polychæte has been taken off the western shores of Greenland (McIntosh[9]), and at several stations off the eastern coast of North America, between George's Bank, off Nova Scotia, and Newhaven,

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[1] "Spitzbergische Anneliden," 'Archiv für Naturgeschichte,' 55 Jahrg., p. 129, 1889.

[2] "Die Coelenteraten, Echinodermen, und Würmer der K. K., Österreichisch-Ungarischen Nordpol Expedition," 'Denkschriften der Matem. Naturw. Classe der Kaiserl. Akad. der Wissenschaften,' xxxv, 1877.

[3] "Faunistiske Undersogelser i Herlofjorden," 'Bergens Museums Aaresberetning,' p. 10, No. 11, 1894–5.

[4] 'Bidrag til Kundskaben om Christianiafjordens Fauna,' III, p. 46. Christiania, 1873.

[5] 'Zoologiska Observationer,' p. 88, Kongl. Vet. o Vitt. Samhällets i Göteborg Handlingar. Göteborg, 1874.

[6] "Report on Annelida dredged off Shetland Islands by Mr. Gwynn Jeffreys," 'British Assoc. Report for 1868,' p. 336. London, 1869.

[7] "On the Annelids of St. Andrews," 'British Assoc. Report for 1867,' p. 92. London, 1868.

[8] 'Wurzbürger Naturwiss. Zeitschr.,' p. 243. 1864.

[9] "Annelida obtained during Cruise of H.M.S. 'Valorous' to Davis Straits," 'Trans. Linnean Soc., Zoology,' second series, vol. i, p. 506. London, 1879.

Conn. (Verrill[1]). The specimens sent to me by the Smithsonian Institution were taken at four stations off this coast, the most northerly one being off Nova Scotia, and the most southerly in latitude 40° N.

Although Scalibregma is found in some places in considerable numbers in shallow water (as in some of the fjords of Nordland (see Danielssen, 1859, p. 25), it is more usually obtained by dredging, and sometimes from considerable depths. Those from the Smithsonian Institution were all obtained at depths varying from 43 to 99·5 fathoms, and the "Challenger" specimens were dredged from 98 and 700 fathoms respectively.

Scalibregma burrows in sand, which is often more or less intermixed with mud or clay, to a depth of one or two feet, forming long passages which in some places, as in the fjords of Nordland, are accessible at low water (Danielssen, p. 25). In its mode of life it evidently strongly resembles the common lugworm (Arenicola marina) of our coasts.

4. External Characters (13 Pl.).

The general aspect of Scalibregma inflatum may be described as arenicoliform, but its shape varies considerably in different individuals. The anterior end of the animal is short, and resembles a truncated cone (fig. 1). The following region of the body is inflated to a greater or less degree, the inflation extending sometimes over only four or five segments, but more generally comprising about ten segments. The swollen portion is either globular or more or less cylindrical. In many cases, especially in the smaller specimens, the body swells out abruptly about the fifth or sixth segment, decreasing in diameter almost as suddenly at the end of the inflated portion; but in most of the larger specimens there is a much more gradual transition from the inflated portion to the regions in front of and behind it, as shown in fig. 1.

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[1] "New England Annelida," 'Trans. Acad. of Arts and Sciences,' vol. iv, Part 2. Newhaven, 1882.

Behind the swollen portion the body tapers gradually to the posterior end.

The animal is strongly convex above but flattened below. There is a depressed area along almost the whole length of the mid-ventral line (marking the position of the nerve-cord), which is divided by transverse grooves into a series of squarish or hexagonal areas (fig. 2). In some specimens the position of the œsophageal connectives is also marked externally by two shallow depressions, the metastomial grooves, which pass round the mouth and unite at the anterior end of the mid-ventral groove.

The head or prostomium is distinct and well developed, forming a somewhat quadrangular mass overhanging the mouth, and bearing at each side anteriorly a short rounded tentacular process (fig. 3).

Immediately behind the head there is an achætous peristomial segment, composed of two annuli. The rest of the body of the animal is divided into segments bearing parapodia. Each of the first three chætigerous segments is composed of three annuli, the middle annulus bearing a prominent pad on each side, from which the neuropodium and the notopodium arise. All the following fully-formed segments of the body are divided into four annuli, on the third of which the parapodia are borne (figs. 1, 2). In the large specimen, 56 mm. long (fig. 1), sixty-one segments (in addition to the peristomium and pygidium) may be distinguished. The parapodia are clearly visible on all the segments up to and including the fifty-third; those of the next four segments are very small, the dorsal cirrus being the only easily visible appendage. The last four segments of the animal are divided from one another only by faint grooves, and do not bear parapodia. Following these there is a very short terminal portion or pygidium, which even in large specimens is only about ·3 mm. long. There are four pairs of branched shrubby gills, situated immediately behind the notopodia of the second, third, fourth, and fifth chætigerous segments (for further description of the gills see p. 262).

Apertures.

The mouth is a wide transverse ventral slit between the peristomium and the first chætigerous segment. It is overhung by the prostomium, and is bordered anteriorly and posteriorly by papillæ (fig. 2). The pharynx, when fully protruded, is smooth and globular.

The anus is terminal, and surrounded by four slender anal cirri, two on each side, situated somewhat ventrolaterally (fig. 6). In one specimen there are five cirri, there being three on one side and two on the other, but this is evidently abnormal. In full-grown specimens the cirri are are about ·8 to 1·0 mm. long, and ·05 to ·06 mm. thick. There is a small protuberance on each side of the mid-ventral line of the pygidium, from which the two cirri arise.

The nephridiopores are exceedingly minute and difficult to see. The first nephridium opens on the fourth chætigerous annulus, but as this nephridium is very small its opening can usually be found only in sections. The second nephridium is a little larger, but its opening is almost equally difficult to find. The apertures of the succeeding nephridia, while being small, are however visible in cleared preparations, and occasionally in surface view of favourable spirit preparations. Each nephridiopore is a minute oval aperture, situated ventral and anterior to the neuropodium of the segment on which it opens (fig. 5). The aperture is close to the anterior border of the chætigerous annulus, and it is often obscured by lying in the groove which separates this annulus from the preceding one. In the most favourable specimens in my possession the largest nephridiopores are only about ·06 mm. in diameter. Towards the posterior end of the animal, where the nephridia become smaller, the nephridiopores become correspondingly more difficult to see in surface view, although they may be distinguished in sections in each segment almost to the posterior end of the worm. In a specimen 13·6 mm. long the last visible nephridiopore is only 1 mm. from the posterior end of the animal.

At each side of the prostomium there is a narrow longitudinal slit (fig. 3), which leads downwards, backwards, and inwards into the nuchal organ (for description see p. 269).

There are small structures on the body-wall situated in each segment about midway between the notopodium and neuropodium. At first sight they are liable to be mistaken for apertures, and Levinsen (1883, p. 133) suggested that they were sexual openings. On further examination each of these proves to be a depression, from the floor of which a small elevation arises, the apex of which may be seen a little below the level of the mouth of the pit (figs. 1, 4, 5, *S. O.*). These structures are best seen in the segments just behind the branchial region, but on careful examination they may be seen in all the chætigerous segments of the animal. Sections prove that these are lateral sense organs, similar to the "Seitenorgane" described by Eisig (1887) in the Capitellidæ. A detailed description may be found on p. 270.

Size.

Scalibregma inflatum varies in size between wide limits. Of the twenty-two complete specimens in my possession the smallest is 5 mm. long, and the largest 56 mm. long and 10 mm. broad at its widest part. The latter is one of the largest specimens yet recorded (fig. 1). Sars's specimen was 58·5 mm. long and 5 mm. broad at its widest part; and Rathke's example was one inch and seven lines (about 40 mm.) long and 5 mm. broad. In the specimen 56 mm. long there are sixty-one segments, and a very short pygidium (about ·3 mm. long). Parapodia are clearly visible on the first fifty-three segments, but those of the succeeding segments are very small, or absent altogether. It is interesting to note that in Sars's specimen there are also sixty to sixty-one segments. One of my specimens 35 mm. long contains ova which appear to be almost ripe, so that the animal reaches maturity when little more than half its maximum size.

Colour.

Sars has recorded the colour of his living specimen. The general colour of the body was vermilion red, the parapodia being light yellow, and the gills blood-red. Rathke's specimens were greenish grey or dirty greenish yellow in colour. My spirit specimens are a pale yellowish brown, due to the large number of yellowish granules in the epidermal cells.

5. Parapodia (Pl. 13).

Each of the parapodia throughout the body is clearly divided into a notopodium and a neuropodium, which closely resemble each other in shape and size. In the anterior fourteen or fifteen segments the parapodia consist simply of two blunt conical mammillæ, each bearing a bundle of setæ. Those of the first five chætigerous segments are situated upon large elevations, each of which is borne chiefly by the chætigerous annulus, but also partly by the annulus before and the one behind it. There are also elevations supporting the parapodia of the next nine or ten segments, but they are smaller than those just described (fig. 1). The parapodia of the anterior portion of the body (as far back as the fourteenth or fifteenth segment) are comparatively small, and the setal prominences, which are bluntly conical, project only a little way from the body-wall. In the succeeding segments the parapodia gradually increase in size, and each is supported upon a flattened base, the two rami of the parapodium and the basal outgrowth forming a large lamella, projecting at right angles to the body (fig. 8).

The notopodium of the sixteenth segment of most specimens bears a small cirrus (*Cirr. D*, fig. 1), and in one or two examples a small dorsal cirrus is also present above the notopodium of the fifteenth segment. The parapodia of the fully developed segments behind this bear both dorsal and ventral cirri. The cirri of the middle part of the body are short, blunt conical outgrowths, but further back they become lamelliform or digitiform structures.

Near the posterior end of the animal the parapodia and cirri are small, and on the last three or four segments, which are divided from each other only by shallow grooves, parapodia have not yet been formed (fig. 6). Just in front of these there are a few segments (about four) in which the parapodia have only been recently formed, and in these the dorsal cirri are considerably larger than the ventral ones,—in fact, the latter have not yet appeared in some segments which possess dorsal cirri of moderate size. The dorsal cirri are thus formed before the ventral ones. The notopodium and a few of its setæ are formed before the neuropodium appears.

The cirri are sensory structures, and from their earliest appearance are supplied with stout branches from the lateral nerves given off in each segment from the ventral nerve-cord (Pl. 14, fig. 16).

On each cirrus, a little behind its tip, there is a distinct darker area, which is somewhat oval, reniform, or pyriform in shape (fig. 8). In most specimens this area is very obvious, on account of its brown or black colour, but in some its colour is much lighter. This is not a structure separate from and standing out from the cirrus, as the description by Rathke (pp. 185, 186) would lead one to believe. The darker appearance of this portion of the cirrus is due to the presence within it of a collection of special gland-cells, the dark-coloured glandular mass being visible through the semi-transparent walls of the cirrus. Rathke examined and reported on these dark masses in considerable detail, and rightly inferred that they are similar in structure to the black or brown spots on the notopodia of Nereis dumerilii, which he had described on a previous page as glandular (Hautdrüsen). Sars does not mention them, but Danielssen (p. 75) re-examined them, and came to the conclusion that they are testes, as they are composed of a large number of somewhat coiled tubes, filled with minute elongate bodies, which he took to be "zoosperms." Rathke's interpretation is the correct one; these dark bodies are parapodial glands, the secretion of the cells of which is in the form of minute slender rods (see p. 248). McIntosh (1885, p. 360) remarks that these curved bodies in the parapodia of Scalibregma are probably homologous with those described by Kölliker and Greef in Ephesia (Sphærodorum).

The cirri arise as solid outgrowths of the epidermis. From their earliest appearance they contain gland-cells, which at first are similar to the ordinary flask-shaped or club-shaped glandular cells found in the epidermis of the squarish elevations of the skin seen in the anterior third of the animal (see p. 252 and fig. 12). The gland-cells of the cirri are at first pear-shaped or club-shaped, and only about 10—12 μ long. They stain deeply with hæmatoxylin, and each has a well-marked nucleus. The secretion is at this time of a finely granular nature. As the cirri increase in size the gland-cells elongate, and when the latter become 30—40 μ in length, their secretion is then clearly seen to be in the form of exceedingly thin rod-like bodies. The cells continue to elongate, and in worms only about 15 mm. long the gland-cells are rather more than ·1 mm. long (fig. 10). The greater part of each cell is occupied by a bundle of fine rods, but in favourable specimens the nucleus may be seen towards the rounded inner end of the cell. There is a small amount of connective tissue around the bases of these rod-secreting cells. In the largest specimens at my disposal, 35 mm. and 56 mm. long respectively, the gland-cells are twisted, and so closely packed together that it is almost impossible to determine the limits of the individual cells. They form a compact, deeply staining mass, situated a little behind the tip of the cirrus (fig. 8).

The very fine-pointed ends of the gland-cells open on the free surface of the epidermis. On examination of medium-sized specimens it is seen that most of the glands of the notopodial cirrus open on its dorsal side, while those of the ventral cirrus open chiefly on the ventral wall (fig. 9).

The rods are at first short, and there are comparatively few in each cell, but later they are much more elongate, and present in large numbers in each cell. In the largest specimen (56 mm. long) the fully formed rods are 40—50 μ in length, and about 3 μ in width at their widest point. They are spindle-shaped, and taper gradually from about the middle, where they are thickest, to their very fine-pointed ends. They are sometimes straight, but more usually are somewhat curved, sinuous, or twisted (fig. 11). These peculiar glands are not strictly confined to the cirri. In four of the specimens which have been cut into sections there is, just below each of the neuropodia of two or three of the anterior segments (ranging from the third to the sixth), a collection (or sometimes two) of deeply staining cells in the epidermis. Each of these cells contains a bundle of rods exactly like those above described from the parapodial glands. In two or three cases there is a small bundle of these rod-forming cells, either in or immediately below the epidermis, near the terminal portion of the first or second nephridium. Claparède (1868, p. 15) has noticed the connection of similar rod-containing cells with the excretory pores in certain Hesionids.

Rod-secreting glands similar to those of Scalibregma are known to occur in the skin and subepidermal tissues of a large number of Polychætse. Claparède has described almost indentical structures ("bacilliparous follicles") in the cirri of Phyllodoce, sp. (1863, pl. xi, figs. 19, 20), in papillæ on the neuropodia of Aricia fœtida (1868, pl. xx, figs. 2 *B*, 2 *C*), in Nereis cirratulus, especially in the parapodia and their appendices (1868, pl. xxiv, fig. 1 *L*). A very useful series of figures of these glands, some original and others collected from various authors, is given by Eisig (1887, pl. xxxvii).

6. Setæ (Pl. 13, fig. 9, and Pl. 15, figs. 25, 26).

Both Rathke and Sars described the setæ of Scalibregma as simple, fine, capillary bristles, and they quite overlooked the peculiar furcate setæ which are present in both divisions of the parapodia throughout the body. Hansen (1882, p. 34) first observed these curious setæ in the ventral fascicles of S. (?) abyssorum, S. (?) parvum, and in S. inflatum.

The setæ of S. inflatum are lodged in sacs in the parapodia, and the tips of the bristles project beyond the prominent lips of these setal sacs. On first examining a parapodium only the simple capillary setæ are seen, but after rendering the tissues more transparent by treatment with warm potash solution the furcate setæ become visible. The simple setæ project a long way beyond the mouths of the setal sacs, being exposed for quite half their length, while the furcate setæ are almost entirely enclosed, only their fine tips protruding from the mouths of the sacs (fig. 9).

The setæ of a parapodium may be divided into four groups, there being one group or row of simple setæ and one of forked setæ in each notopodium and neuropodium. The simple setæ of the notopodium and neuropodium form two straight fascicles, projecting from the parapodium in almost parallel or in very slightly diverging lines; but the furcate setæ lie in two bundles, which are usually placed so that while their proximal ends are adjacent their tips are widely divergent, those of the notopodium being directed dorso-laterally, and those of the neuropodium ventro-laterally. The bundles of furcate and simple setæ form two almost vertical and parallel rows in each ramus of the parapodium. The row of forked setæ is usually the more anterior.

The simple setæ are fine capillary structures, attaining a length of about 1·7 mm. in the largest specimen (56 mm. long). They are about 8 μ in diameter at their inner ends, where they are thickest, and taper gradually to a very fine point. They are marked in their proximal portion by very minute longitudinal ridges and furrows. Those setæ which have not been worn by use bear exceedingly minute hair-like processes on their distal third (fig. 26).

The length of the furcate setæ is generally about three fourths that of the simple setæ of the same parapodium. In the specimen, 56 mm. long, they reach a length of 1·2—1·3 mm. They are considerably stouter than the simple setæ, being 15—18 μ in thickness at their inner ends. They taper gradually to the base of the fork, their diameter at this point being only 6—8 μ (fig. 25). The prongs of the fork are sometimes straight, but more usually curved, their very fine tips pointing away from each other. The two rami are not quite equal; in the largest specimens they are 50—65 μ and 65—75 μ in length respectively. The proximal portion of the edge of each prong bears a number of minute curved pointed processes.

In the large worm (56 mm. long) there are fifty to sixty simple setæ, and about twenty to twenty-four furcate setæ in each ramus of the parapodium of the anterior half of the animal.

On clearing the posterior end of another specimen by treatment with warm potash solution the very small setæ present in the newly formed parapodia are seen. Each of the notopodia and neuropodia in this region bears only one or two simple setæ, accompanied by one furcate seta. Both kinds of setæ are therefore present in the parapodia throughout life.

Furcate setæ were first discovered by Malmgren (1867, p. 187) in Eumenia crassa, and were shortly afterwards observed by McIntosh (1868, p. 419, and pl. xvi, fig. 5) in Eumenia (Lipobranchius) jeffreysii. Théel (1879, p. 49, and pl. iii, fig. 47*a*) figures them in Eumenia longisetosa, and Hansen (1882, p. 34, and pl. v, figs. 16—19) in Scalibregma inflatum, S. (?) parvum, and S. (?) abyssorum; but the figures of these authors do not show the minute barbules on the inner side of each prong. McIntosh (1885, pl. xxii *A*, fig. 21) saw the barbules on both prongs of the forked setæ of his southern specimens of S. inflatum, and figured similar setæ from Eumenia reticulata (1885, p. 360, and pl. xxii *A*, fig. 20), and S. Joseph (1894, p. 106, and pl. v, fig. 133) has observed them in Sclerocheilus minutus.

The furcate bristles of Eumenia glabra described by Ehlers (1887, p. 170, and pl. xlv, fig. 4) are remarkable for the great inequality in length of the prongs, one being nearly three times the length of the other. Ehlers (1887, p.

127, and pl. xxxviii, fig. 6) has also figured from Nephthys inermis a forked seta, which is similar to those of Scalibregma, except that the two prongs of the fork are equal in length in the former.

Furcate setæ are also known to occur in the Ariciidæ, having been described by McIntosh (1879, p. 504, and pl. lxv, fig. 7) in Aricia greenlandica, by S. Joseph (1894, pl. v, fig. 116, and 1897, pl. xxi, fig. 172) in A. latreillii and A. lævigata, and by Cunningham and Ramage (1888, pl. xxxviii, fig. 7 E; pl. xl, fig. 8 D) in Scoloplos armiger and Theodisca mammillata. The setæ of these worms are, however, evidently quite different to those of Scalibregma, the fork of the former not being fixed quite so symmetrically upon the shaft, and the tips of the prongs are not fine and pointed, but slightly thickened.

Furcate setæ, agreeing in essential characters with those of Scalibregma—that is, possessing unequal barbuled and finely pointed prongs, are practically confined to the genera Eumenia, Lipobranchius, and Sclerocheilus, which on other grounds have been placed with the genus Scalibregma in the family Scalibregmidæ.

7. Skin.

In the anterior and inflated portions of the animal the annuli bear longitudinal grooves on their dorsal and lateral regions, which subdivide the skin into a series of squarish or oval elevations (fig. 5). These are due chiefly to the fact that the epithelial cells which form them are elongated, columnar cells, while those of the grooves are much shorter, almost flattened cells. Many of the cells of the papillæ are club-shaped, mucus-forming cells, which stain deeply with hæmatoxylin (for other glands of the skin and cirri see pp. 247—249). These cells do not occur in the intervals between the elevations (fig. 12). In some specimens in which there is an excessive amount of inflation of the body, the skin of the inflated region is almost transparent. Behind this region the elevations become less marked, and in the posterior half of the animal the skin is subdivided only by the circular grooves which separate the annuli.

Around the bases of the notopodia and neuropodia of the segments immediately behind the branchial region there are sometimes epidermal elevations of considerable size. These are best developed in old specimens (see figs. 1, 5).

Sections of old specimens show that the yellow-brown colour of the skin is due to the presence of numerous insoluble yellow granules in the epidermal cells. These granules are light yellow when viewed singly, but appear brown in the aggregate.

There is only a small amount of connective tissue between the epidermis and the underlying musculature.

8. Musculature.

Immediately beneath the epidermis there is a layer of circular muscles, beneath which are the longitudinal muscle bands which project into the cœlom (fig. 16). The circular muscles in old specimens usually form a continuous sheet beneath the epidermis, but in younger ones are sometimes subdivided into hollow hoops, of which there are two (occasionally only one) in each annulus (fig. 12).

The longitudinal muscles are interrupted along three lines, viz. on each side at the level of the insertions of the oblique muscles, and mid-ventrally by the nerve-cord (fig. 16). They are thus divisible into three groups, of which the two ventral lie between the nerve-cord and the insertions of the oblique muscles, the other forming an uninterrupted series extending over the dorsal and lateral regions of the body-wall. The ventral bands are rather more strongly developed, especially in young specimens. The longitudinal muscles are covered by a very thin cœlomic epithelium.

The oblique muscles are present throughout the chætigerous segments of the body. They are short, thin, narrow bands arising at the sides of the nerve-cord and inserted into the body-wall immediately dorsal to the level of the notopodial setal sacs (figs. 14, 16). The nephridia are usually almost hidden from sight beneath these oblique muscles.

The parapodial muscles are moderately well developed (fig. 9). Each bundle of setæ is moved by (1) a number (about five to eight) of slender protractor muscle strands attached to the base of the setigerous sac and to the body-wall near the level of the mouth of the sac, and (2) a few short strands which pass from the base of the notopodial setal sac, and are inserted into the base of the neuropodial sac. By contraction of the latter muscles the bases of the setal sacs approximate, and at the same time the distal ends of the two groups of the setæ are caused to diverge.

Into the inner end of each lateral sense organ a special retractor muscle is inserted. The other end of this muscle is attached to the base of the notopodial setal sac (fig. 9).

The position and arrangement of the four anterior diaphragms and the occurrence of small strands of connective tissue, representing septa, accompanying the segmental vessels in the post-branchial region of the body are described below (p. 255).

There is on each side a short muscle band arising from the lateral body-wall and inserted into the inner and lower end of the corresponding nuchal organ. On contraction this muscle serves to retract the nuchal organ, and also, to a small extent, the prostomium. The latter is well supplied with muscles (fig. 15).

There are several strong muscle strands passing from the buccal mass to the neighbouring body-wall. These are the retractors of the proboscis (fig. 14).

Along almost the whole length of the stomach and intestine there is an incomplete ventral mesentery, consisting of numerous separate muscle strands passing from the ventral wall of the stomach to the body-wall close to the nerve-cord.

9. General Anatomy of the Internal Organs.

Fig. 14 shows the appearance of the animal when opened by a dorsal incision. The cœlom is spacious, especially in the inflated portion of the animal. It is subdivided anteriorly by four diaphragms or septa placed transversely at the level of the posterior end of each of the four branchiferous segments. Each diaphragm is inserted at the level of the hinder border of the annulus which immediately follows the chætigerous annulus. The second, third, and fourth diaphragms are perforated by the minute funnels of the first three nephridia.

Behind the branchial region the cœlom is not subdivided by transverse partitions, but is continuous to the posterior end of the animal. In the post-branchial portion of the body each of the segmentally arranged blood-vessels is accompanied by a small strand of connective tissue, which near the nephrostome spreads out slightly and is attached to the body-wall a little above the level of the neuropodium. The gonads are developed near the nephrostome on the surface of the expanded portion of this strand (fig. 21). These narrow bands are the equivalents of the septa of the branchial region and of other Annelids, such as Arenicola grubii and A. ecaudata, in which the transition from the narrow bands to complete septa is well seen (Gamble and Ashworth, 1900, pl. 25, figs. 44, 45).

The stomach and intestine are loosely bound to the mid-ventral body-wall by numerous thin strands of muscular tissue, which form an imperfect ventral mesentery. Just as in Arenicola (Gamble and Ashworth, 1898, p. 14) the stomach is probably swung backwards and forwards by the movement of the body, thus bringing about a thorough mixing of the sand, etc., with the secretion of the œsophageal pouches and of the stomach; the muscle strands forming the incomplete ventral mesentery allow a certain amplitude of swing, as the drawing of the dissection shows. In the specimen, the proboscis of which is strongly retracted, the stomach is probably drawn backwards to its most posterior position, as is shown by the backward trend of the blood-vessels.

The intestine is probably moveable in a similar manner, but to a less extent, as the blood-vessels which pass between the subintestinal vessels and the nephridia and body-wall are capable of considerable extension without injury (see fig. 14).

From the level of the fourth diaphragm to that of the fourteenth seta there are six rather long median blood-vessels running from the ventral vessel to the mid-ventral wall of the stomach, and paired segmental vessels pass right and left from the ventral vessel to each parapodium (and corresponding nephridium) up to the fourteenth. From the fifteenth seta to the end of the animal there are two segmental vessels, an afferent and an efferent, on each side.

The nephridia are to a large extent hidden beneath the numerous oblique muscle bands, and even when exposed by dissection are difficult to see, on account of their small size; they are usually only about ·25 mm. in diameter.

10. Cœlom.

The cœlom is spacious, especially in the inflated region of the animal. It is subdivided by septa only in the branchial region. In the rest of the body the septa are very small, being represented by a thin strand of tissue running alongside the afferent nephridial vessel.

The cœlomic fluid is, as far as can be judged from spirit specimens, very similar to that of Arenicola (Gamble and Ashworth, 1898, p. 29, and pl. 5, fig. 24). It contains the reproductive cells in various stages of growth, and cœlomic cells, some fusiform about 30 μ long, and others spherical or amœboid.

The reproductive cells collect principally in the space between the oblique muscles and the ventral body-wall, especially in ripe females, in which this space is crowded with ova.

11. Alimentary Canal.

Danielssen (1859, p. 69) described the general form of the alimentary canal, pointing out its various divisions, and drawing attention to the nature and probable functions of the œsophageal pouches, and to some details of the structure of other parts of the digestive tract, e. g. he observed the ciliated epithelium lining the œsophagus. Wirén (1887, pp. 30, 37) referred to some points in the histology of the œsophagus and stomach.

The mouth (fig. 2) is a transverse slit, situated ventrally between the peristomial and the first chætigerous segments, through which the smooth, spherical, eversible pharynx or "proboscis" may be extruded. The mouth is bordered in front and behind by papilliform elevations of the skin. The pharynx, when fully protruded, is a smooth, globular structure, not provided with spines or any other armature. When it is withdrawn the anterior part of the alimentary canal—the part lying in front of the first diaphragm—forms a spherical mass, from which muscle strands pass to the neighbouring body-wall (fig. 14).

The œsophagus is a narrow cylindrical tube about 8—9 mm. long (in the specimen 56 mm. long), bearing just in front of the fourth diaphragm a pair of hollow glandular pouches, which in this specimen are about 2 mm. long and 1·8 mm. wide. Each is a somewhat heart-shaped sac, attached to the wall of the œsophagus by its apex, its free wider end being bi- or tri-lobed. The two pouches are united in the middle line, either directly or by a small median sac, into which both lateral pouches open. They discharge their secretion into the œsophagus through a small duct leading from the median sac.

About the level of the sixth to eighth setæ the œsophagus passes somewhat suddenly into the much wider stomach, which even in spirit specimens still bears traces of the bright orange-yellow colour which Danielssen noticed in fresh specimens. In all the specimens examined the walls of the stomach are folded, but whether these folds are natural it is impossible to state with certainty. The walls of the stomach and intestine are marked by a number of parallel lines which pass round the tube from the ventral side to the dorsal vessel; these are the blood-vessels or sinuses (see below) similar to those described in Arenicola.

About the level of the fourteenth to sixteenth setæ the stomach passes gradually into the intestine, which is a cylindrical tube narrowing slightly towards the anus.

The ventral wall of the anus is slightly notched in the middle line, and on each side of the notch is a protuberance from which the two anal cirri arise (fig. 6).

As pointed out above (p. 255), it is moderately certain that the stomach, and to a less extent the anterior part of the intestine, are swung backwards and forwards during digestion. In addition to this the passage of the contained sand, etc., is aided by the strong peristaltic movements of the anterior part of the intestine which have been observed by Danielssen (1859, p. 70).

The alimentary canal of most of the specimens was distended with fine sand and débris in which quartz grains, spicules, frustules of diatoms, and Foraminifera were clearly recognisable.

Histology.—The œsophagus is lined throughout by ciliated columnar cells. There are no gland-cells in this part of the alimentary canal. The ciliated cells are supported by a thin layer of muscle-fibres. The walls of the œsophageal pouches are raised internally into a number of folds, which are at first mere ridges, but increase in size with the growth of the animal. Each fold consists of two layers of epithelial cells, between which is a blood-sinus, slightly enlarged, near the inner edge of each fold (fig. 23).

On the external surface of the pouches there is a network, apparently a blood-sinus, with which the sinuses of the folds are continuous. The cells lining the cavity of the œsophageal pouches are cubical or flattened, and are not ciliated. The protoplasm of these cells usually contains an enormous number of minute spherical granules (or cavities from which the granules have been dissolved), which give rise to the glandular secretion (fig. 24). The latter may often be seen in masses of considerable size in sections of the hinder portion of the œsophagus and the anterior portion of the stomach.

The stomach is lined by columnar cells which are strongly ciliated. Among these there are numerous glandular cells which are swollen with granules of secretion and stain deeply with hæmatoxylin. There is an exceedingly small amount of muscular tissue in the walls of the stomach.

The columnar or cubical cells which line the intestine are supported by a thin muscular layer. In the cells of the dorsal and lateral walls of the intestine of large specimens there are very numerous yellow granules, probably chlorogogenous. There is a well-marked ventral groove, the cells of which are columnar and bear long cilia, running along the whole length of the intestine to the anus (fig. 16). I have traced this groove forwards as far as the level of the fifteenth or sixteenth setæ. The function of this groove is probably the same as in Arenicola, viz. to carry backwards along the intestine the digested substances which have been extracted from the sand. In some specimens food particles may be seen in the groove surrounded by a thin covering of mucus. Towards the posterior end of the intestine the whole of its inner wall appears to be ciliated, and the cilia seem to be especially strongly developed in the last few segments. There are two cords situated in the ventral wall of the intestine below the ciliated groove. These, which are best developed in old specimens, are apparently nervous (see p. 268).

12. Vascular System (fig. 14).

Danielssen (1859, p. 70) has described and figured some of the principal parts of the vascular system, but as his account is not complete, and is incorrect in some respects, I propose to describe the vascular system as seen in the dissection of my largest specimen (56 mm. long).

The dorsal vessel arises near the anus, and runs along the whole length of the alimentary canal, breaking up into capillaries on the pharynx. It is closely adherent to the gut, and receives a large number of fine vessels (or lacunæ; see below, p. 261) from the walls of the stomach and intestine. Near the anterior end of the stomach the dorsal vessel presents a well-marked enlargement, which is apparently constant, as it is present in the other specimens examined. In my largest example this swelling, which, following Danielssen, we may call the blood-reservoir, is 7 mm. long and 1·2 mm. thick in its widest part. Anterior to this the dorsal vessel resumes its normal diameter for a length of about 4—5 mm. and then abruptly dilates into a conical bulb, which Danielssen named the heart, about 1·5 mm. in diameter. The vessel then narrows to its previous size, and gives off four pairs of stout afferent vessels which run along the corresponding diaphragms to the gills. On reaching the pharynx the dorsal vessel divides into two branches, which soon break up into smaller vessels supplying the pharynx, buccal mass, brain, etc.

The ventral vessel arises near the mouth, by the union of small vessels from the prostomium and peristomium. It runs along the whole length of the animal just above the nerve-cord. Soon after its origin it receives four pairs of efferent branchial vessels, and thus becomes almost at once a thick trunk. In each of the post-branchial segments the ventral vessel gives off a pair of slender vessels supplying the nephridia, setal sacs, and neighbouring tissues. Besides these paired branches the ventral vessel gives off to the stomach six median vessels, the first of which is situated just behind the fourth diaphragm, and the last at the level of the thirteenth setæ. In the posterior portion of the animal, behind the twentieth segment, the ventral vessel bears a large number of short, blind, usually curved outgrowths, which are covered with a layer of cells, probably chlorogogenous, and corresponding to the similar tissue clothing the blind outgrowths of the ventral vessel of Arenicola marina (Gamble and Ashworth, 1898, pl. 2, fig. 5).

Along the whole length of the intestine there is a pair of subintestinal sinuses situated one on each side of the ventral groove of the intestine (figs. 14—16). These may be traced from behind forwards as far as the level of the fifteenth setæ, then they taper rapidly and disappear. Anterior to this point the stomach receives blood only from the six median vessels above referred to. In each segment, from the fifteenth to the end of the body, a pair of vessels collecting blood from the nephridia and setal sacs opens into the subintestinal sinuses.

On the walls of the stomach and first part of the intestine there are numerous fine blood-streams, which carry blood from the ventral portion of the gut into the dorsal vessel. These are not distinguishable on the posterior part of the intestine, as this portion of the gut is surrounded by a sinus, by means of which blood is conveyed from the subintestinal sinuses to the dorsal vessel. The whole of the blood in the walls of the stomach and intestine is contained in sinuses; the intestine, as seen in section, appears to be quite enclosed in a blood-sinus. The subintestinal sinuses are somewhat specialised parts of the general sinus. The dorsal vessel is not distinct from the sinus in the posterior part of the animal, but from the level of the twelfth setæ (i. e. a point a little behind the blood-reservoir) it is distinct, and has a wall of its own.

In Arenicola the blood in the walls of the stomach and intestine is apparently contained in vessels in young specimens, but in sinuses in old specimens (Gamble and Ashworth, 1900, p. 460); but even in the latter it is sometimes difficult to determine whether the gastric plexus is formed of vessels or sinuses. In Scalibregma the blood in the walls of the stomach and intestine is certainly contained in sinuses, which in the posterior part of the intestine are large.

The body-wall and nerve-cord are very sparingly supplied with blood. No vessels are distinguishable in the body-wall, except in immediate proximity to the setal sacs, and these vessels are few and small.

The walls of the heart and blood-reservoir are very thin, and their structure is difficult to determine. The walls are composed of a layer of peritoneal epithelium within which a very thin sheet of muscle-fibres may be distinguished. In some sections an exceedingly delicate endothelium appears to be present, but this is difficult to distinguish with certainty. There is no trace of heart body such as is present in the dorsal vessel of some other Polychætes.

Danielssen states that the blood-reservoir and the heart are contractile, alternately expanding and contracting with considerable force, driving the blood forward to the gills. The blood-plasma is red and the corpuscles are few in numbers. They are spherical or ellipsoidal cells, 6—9 μ in diameter, and have prominent nuclei. It is very difficult to ascertain where they are formed, but apparently some arise from the cells lining the wall of the dorsal vessel, especially in the region of the heart and blood-reservoir. In one specimen there is a mass of corpuscles in the ventral vessel immediately behind the fourth diaphragm. These corpuscles resemble in appearance and in reaction to stains the cells lining the wall of the vessel in their immediate neighbourhood. Possibly corpuscles are formed at various points in the vessels.

13. Gills.

The four pairs of gills are shrubby, much-branched outgrowths of the body-wall situated immediately above and behind the notopodia of the second, third, fourth, and fifth chætigerous segments (fig. 1).

Rathke describes the gills as being present on the fourth to seventh segments, and figures three chætigerous segments anterior to the first pair of gills; but other authors describe the gills as being situated on the second to fifth segments. It seems unlikely that Rathke's specimen, while agreeing very closely with other specimens obtained from the same locality, should differ from these only in the position of the gills. It seems probable that in this respect Rathke's account is incorrect.

The first gill is considerably smaller than the other three, which are nearly equal in size. The branches of each gill spring from a single stem, which is short and stout, and soon divides into two main branches, one of which is directed dorsally and the other ventrally (fig. 4). Each of these usually divides again into two, and these branch freely, sometimes dichotomously, or often dividing into three.

In the living animal the gills are red and the fine branches reddish yellow, due to the contained blood (Sars). The gills are hollow, each containing a prolongation of the cœlom. Their walls are composed of single layers of epithelial cells, within which is a delicate cœlomic epithelium surrounding the axial cavity. Between these two layers is a thin sheet of muscle-fibres, upon the presence of which the contractility of the gill depends.

The gills are supplied with blood by four pairs of afferent vessels given off from the dorsal vessel, and they return blood by a corresponding number of efferent trunks to the ventral vessel (fig. 14). The position of the vessels and the circulation of the blood in the gills is difficult to make out from my material, as the gills are almost bloodless in all the specimens.

14. Central Nervous System.

Danielssen (p. 72) has given a brief account of the nervous system. He figures (pl. i, fig. 3) the nerve-cord as a double chain, upon which there are ganglia in the middle of each segment, each giving off a pair of nerves to the body-wall. From the œsophageal connectives three fine nerves are given off on each side. The brain, which consists of two masses connected by a transverse commissure, also gives off three nerves on each side, which run forwards.

I cannot agree with Danielssen on several of these points, and especially on the ganglionation of the nerve-cord. I find that the cord is of almost uniform thickness, there being no ganglia visible either in dissections or in horizontal sections.

The central nervous system closely resembles that of

Arenicola, especially that of A. claparedii (Gamble and Ashworth, 1900, p. 469), with which it agrees even in many of its details.

The Brain.

The brain is lodged in the middle portion of the prostomium (fig. 15). It is somewhat A-shaped, the single anterior lobe being in contact with the anterior face and dorsal wall of the prostomium, and the two posterior lobes lying in contact with the inner sides of the two nuchal grooves. In some specimens the anterior brain-lobe is not in close contact with the dorsal prostomial epithelium along its whole length, but in the posterior half is separated from the epithelium by a thin sheet of muscle-fibres. The brain is placed in a slightly slanting position, its anterior lobe being situated more dorsally than the posterior lobes.

The anterior lobe is almost entire, the only trace of division being a very slight groove along its ventral surface; but the two posterior lobes of the brain are separated from each other by a considerable space lined by cœlomic epithelium, and containing muscle-fibres and blood-vessels.

The dorsal and lateral portions of the anterior brain-lobe consist chiefly of small oval or pyriform cells, some with small deeply-staining nuclei, others with vesicular nuclei, with one or two small dark nucleoli. A few larger cells are found here and there. The ventral part of this lobe of the brain consists chiefly of a delicate neuropile.

The anterior brain-lobe gives off a pair of moderately stout nerves to the hollow tentacles (*N. Tent.*, fig. 15). The nerve spreads out just beneath the epidermis of the base of the tentacle, gradually thinning out towards the tip. The stout œsophageal connectives arise from the brain a little further back, i. e. about the middle of its length. The tentacular nerves receive fibres from the dorsal and ventral part of the anterior brain-lobe, and there is a considerable mass of cells immediately below and to the outer side of the origin of each of these nerves. The connectives also receive fibres from the dorsal and ventral portions of the brain, and there is a group of larger nerve-cells just below their point of origin. The posterior brain-lobes consist of nearly equal parts of cellular and fibrous elements. The fibrous matter is covered internally by a thin layer of cells, but externally has a thick coating of ganglion cells, which are closely applied to the nuchal epithelium. This mass of cells forms a large ganglionic centre. The posterior brain-lobes are broad in front where they are fused with the anterior part of the brain, and in this region there are numerous comparatively large nerve-cells, especially on the inner faces of these posterior lobes abutting on the cœlomic cavity. On tracing these lobes backwards along the inner side of the nuchal organ, it is seen that the cells decrease rapidly in quantity, and each lobe is continued as a fibrous tract or nerve, which is accompanied by only a very thin covering of cellular elements (*N. Nuc.*, fig. 15). This divides into two or three nerves near the posterior end of the nuchal organ. The nerves lie between the epithelium and the sheath of the organ.

There is a little neurilemma on the dorsal and ventral faces of the brain, from which strands pass inwards, supporting the nervous elements.

The above is a description of the brain of moderately young specimens 13 to 14·3 mm. long. The average measurements of the brain of five such specimens are ·23 mm. long, ·22 mm. broad, and ·16 mm. deep. As the animal increases in size the brain not only grows in bulk but undergoes considerable changes in appearance. In a specimen of 56 mm. long the brain is ·35 mm. long, ·5 mm. wide, and ·35 mm. deep. The fibrous portion of the brain in this specimen is proportionately larger and much more complex, and the neuroglia is better developed than in smaller specimens. The nerve-cells, some of which are 30 μ in diameter, are aggregated into definite groups, separated by masses of fibrous tissue. As in younger specimens the fibrous elements are chiefly internal, and are covered by the cells. At the point of origin of the connectives the fibrous matter is exceedingly abundant, and here, too, on each side are a few large unipolar cells with prominent nuclei. There seems to be a definite nerve-tract arising from this mass of cells and passing into the connective. The fibres of the connective appear to be derived almost entirely from the anterior and middle portions of the brain, only a very small proportion being derived from the posterior lobe. In the posterior lobe there is also a number of larger cells, but the fibrous and cellular elements are in almost the same proportion as in younger specimens.

The Œsophageal Connectives.

The connectives arise from the brain, slightly anterior to the middle of its length. They run just beneath the epidermis, and at first fall nearly vertically downwards near the middle line, then diverge sharply, pass round the mouth, and unite just anterior to the level of the second chætigerous annulus to form the nerve-cord. The course of the connectives is marked externally by the metastomial grooves, which are well seen only in comparatively few specimens.

The connective of each side gives off nerves to at least two, and sometimes three, annuli, through which it passes, and also a nerve through which it runs along the sides of the mouth to the eversible part of the pharynx. The former nerves are situated just beneath the epidermis; the latter nerve, which also supplies the upper lip, may be traced by the aid of its distinct sheath for some distance along the dorso-lateral region of the pharynx between the epithelial and muscular layers, and is probably in connection with the stomatogastric system.

The connectives are composed chiefly of fibrous matter, but there is a thin coating of cells on the external face, and at the point of union of the two connectives there are several larger nerve-cells. The connective is enclosed in a sheath of neurilemma, which is better developed in old specimens, and in the latter sends ingrowths which partially subdivide the connective into two or three.

The Nerve-cord.

The most striking point in Danielssen's description of the nerve-cord of Scalibregma is the ganglionation. I am unable to find any trace of the segmentation or ganglionation of the nerve-cord either in dissections or in sections taken in various planes. Ganglion cells occur, apparently evenly distributed along the whole length of the cord on its lateral and ventral faces, as in Arenicola (Gamble and Ashworth, 1900, p. 480). In most species of Arenicola, however, an indication of the segmentation of the cord is afforded by the presence of giant-cells placed at regular intervals along the cord near the posterior boundary of each segment. In Scalibregma there are no such landmarks, giant-cells and giant-fibres are entirely absent.

The nerve-cord of Scalibregma is not cœlomic in position in any part of its course. It is situated in the body-wall outside the layer of circular muscles, and in close contact with the epidermis (fig. 16).

The cord gives off a pair of nerves situated in each interannular groove in the basal portion of the epidermis (fig. 12). The nerves which lie in the groove immediately behind each chætigerous annulus are larger than the rest. Besides these there is a pair of moderately large nerves given off opposite the middle of each chætigerous annulus, which also run between the epidermis and the circular muscles. Each of these nerves (fig. 16) gives off (1) a branch passing into the base of the ventral cirrus, and spreading out beneath the epidermis; (2) a branch to the lateral sense organ; (3) a branch to the dorsal cirrus. The nerve then continues dorsally along the annulus, gradually tapering, and becoming very difficult to trace. The nerve to each cirrus comes into close contact at one point with, and sends fibres to, the corresponding setal sac near its mouth.

In the posterior portion of the animal the nerve-cord lies in very close relation to the epidermis, which is here very thin.

Near its termination in the tail segment the cord gives off a pair of comparatively large nerves supplying the anal cirri.

In transverse section the nerve-cord is oval in shape, being flattened from above downwards (fig. 17). In some specimens it is very much flattened in the posterior region of the animal, whereas in others it is not so compressed.

Ganglion cells occur along the whole length of the cord, being placed on the ventral face and at the ventro-lateral angles. These cells are small and subequal, although here and there a few larger cells may be seen generally situated near the median line in the fissure between the two fibrous tracts. The fibrous matter of the cord is partially subdivided into two by a median vertical sheet of neuroglial tissue, the fibrillæ of which form, in transverse section, a network, more obvious in the ventral portion of the cord. In horizontal sections the neuroglial fibrillæ form wavy strands resembling the neuro-fibrillæ, but the former are generally more deeply staining than the latter.

In older specimens there is a proportionately greater amount of fibrous matter in the cord, and the cells are restricted almost entirely to the ventral face, and most of them are situated in the small fissure between the fibrous tracts, there being very few at the ventro-lateral angles of the cord. In such specimens (30—56 mm. long) the neurilemma sheath and neuroglial network are more highly developed than in younger specimens.

The brain and nerve-cord, and especially the latter, are poorly supplied with blood.

There are two cords (fig. 16, *Int. N.*), best developed in old specimens, running along almost the whole length of the intestine. They are situated in the ventral wall just below the ciliated groove. They are composed chiefly of fibrous elements, but cells are present at frequent intervals. From their appearance and structure they seem to be nervous, but I have been unable to find any connection between them and any other part of the nervous system. The cords become gradually smaller as they approach the posterior end, and finally coalesce. They may be traced as far as the anus.

15. Sense Organs.

The sense organs are (1) the epithelium of the prostomium and tentacles, (2) the nuchal organ, (3) the lateral sense organs, (4) the dorsal, ventral, and anal cirri. Probably also the long capillary setæ should be added to this list. There are no eyes or otocysts.

Prostomial Epithelium.

The epithelium of the anterior and dorsal faces of the prostomium and its tentacles consists of columnar cells, among which slender fusiform sense organs may be distinguished. The latter are generally seen in small groups, and their slender tips are level with or project slightly beyond the outer surface of the cuticle. The bases of these cells are in intimate relation to either the cells of the brain itself or the fibres of the nerves which supply the two tentacles.

The Nuchal Organ (figs. 3, 15).

On each side of the prostomium there is a narrow longitudinal slit which leads inwards and downwards into the blindly-ending nuchal organ. In sections the inner ends of the two nuchal organs are seen lying close together near the middle line, below and behind the brain. The character of the epithelium lining the organ varies considerably. Near the mouth of the depression the epithelial cells are short, columnar, or cubical, and stain lightly, but towards the inner end they rapidly increase in length, and here they are long, narrow, columnar, and deeply-staining, and many of them in the terminal portion are ciliated. In some specimens there is quite a sharp line of demarcation between the cubical and elongate cells. In favourable sections sense-cells may be seen among the columnar cells in the middle and inner portions of the organ. From the inner ends of these fusiform sense-cells slender fibrils may be traced to the adjacent nerve, which is in continuity with the posterior lobe of the brain. The epithelium lining the inner or terminal portion of the organ is strongly folded, and suggests that this section of the organ is to a certain extent eversible. Possibly the small papilla noticed by Sars in S. inflatum (1846, fig. 21), and by Hansen in S. (?) parvum (1882, p. 34, and pl. v, fig. 8), may be the nuchal organ only partially withdrawn. The retraction of the nuchal organ is effected by a small muscle arising from the body-wall at a point about midway between the notopodial and neuropodial sacs of the first chætigerous segment, and inserted into the inner end of the organ (*Nuc. Retr.*, fig. 15).

Dorsal, Ventral, and Anal Cirri; Setæ.

As pointed out in the section dealing with the ventral nerve-cord, there is a pair of nerves given off in each segment, supplying among other structures the parapodial cirri and the setal sacs. The nerves to the cirri spread out beneath the external epithelium. The nerves which supply the cirri send fibres to the setal sacs near their mouths; these may be traced for a short distance along the sacs towards their inner ends, but owing to their small size they are soon lost from view. They probably end among the bases of the setæ, as Retzius[1] has shown for Arenicola.

The anal cirri are abundantly supplied with nerves by a pair of trunks given off near the termination of the cord. Each cirrus is an epidermal outgrowth, along the whole length of which there is an axial nervous strand. The nerve is surrounded only by a single layer of epidermal cells.

16. THE LATERAL SENSE ORGANS.

These are the most interesting sense organs of Scalibregma. Levinsen (1883, p. 133) noticed the prominent lips guarding the depression into which the sense organ is withdrawn, but he mistook the structure for an aperture "probably sexual." Théel (1879, p. 49) observed a papilla

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[1] 'Biolog. Foren. Forhandl.,' Band iii, Hefte 4—6, p. 85, 1891.

between the two rami of each of the parapodia of Eumenia longisetosa, but he did not recognise the nature of these papillæ.

Our knowledge of lateral sense organs of this kind is due almost entirely to Eisig, who has described their relations and structure in his monograph of the Capitellidæ (1887).

The lateral sense organs of Scalibregma occur in each chætigerous segment throughout the whole length of the body, midway between the notopodium and neuropodium (fig. 1, *S. O.*). The sense organs on the first and second chætigerous segments are small rounded eminences, very difficult to distinguish in surface view, even with a moderate magnification. Those of the succeeding segments are, in preserved specimens, generally sunk and hidden in a depression bordered by prominent lips of epidermis (figs. 4, 5). The essential portion of the organ is liable to be overlooked, and the depression, by reason of its prominent lips, may then be readily mistaken for an aperture. The sense organ itself is a papilla arising from the bottom of the above-named depression, its free, oval, curved surface bearing a very narrow, dark, almost flat area, running dorso-ventrally. The sense hairs arise from this darker area or "hair field" (Eisig), which, in the largest organs of a specimen 56 mm. long, is only about 50 μ long and 10—15 μ broad. In this specimen the surface of the free pole of the largest papillæ is about 250 μ long and 90 μ broad.

The sense organs are best developed in the region of the body just behind the gills. In the posterior third of the animal they gradually decrease in size, and in the last five or six segments they are difficult to find even in sections. About the sixth or eighth segment from the posterior end the organ is recognisable as a minute oval elevation, measuring about 15 μ along its longer diameter (fig. 7).

The structure of these organs can be best studied in thin transverse sections of specimens about 15 mm. long (figs. 28, 29). The organs have attained almost the same stage of growth even in specimens only 5—7 mm. long.

The sense hairs form a dense tuft, covering the flattened area in the middle of the free surface of the papilla. They are moderately stiff hairs, attaining a length of about 40—50 μ, but they are exceedingly delicate, being less than 1 μ thick at their bases. There are a hundred or more hairs in each of the sense organs in the anterior and middle regions of the body. The whole papilla is covered by the thin cuticle continuous with that covering the general epidermis, but over the hair field the cuticle is exceedingly thin, and is pierced by the sense hairs. Beneath the cuticle, over the greater part of the surface of the sensory papilla, there is a layer of columnar or cubical epidermal cells, but in the hair field there is a striking departure from this arrangement. Here, below the cuticle, are long, exceedingly thin columnar cells, closely and regularly arranged. These rods are in most specimens 12—15 μ long (but in the largest specimen, 56 mm. long, they attain a length of 20—25 μ) and about 1 μ wide. They stain darkly, but not quite homogeneously, there being a more deeply-staining, elongated, flattened nucleus near the distal end of each rod. Each rod bears only one or two hairs. The rods are continued inwards as delicate fibrils, many of which may be traced into continuity with the delicate drawn-out ends of pyriform or fusiform ganglion cells, which occupy the axis of the sensory papilla. Many of these ganglion cells are clearly bipolar, the outwardly directed process being, as described above, in connection with the base of a rod, the inward process passing into the nervous mass formed by the spreading out of the spinal nerve in the basal portion of the sensory outgrowth. In older specimens especially, the ganglion cells are nearly all obviously bipolar. These ganglion cells are few in number, there being only about eight or ten in each sense organ. They are usually about 15—20 μ long, and about 8—10 μ wide, and their large nuclei are 6—8 μ in diameter. Occasionally, especially in large specimens, cells 30 μ long with nuclei 8—12 μ in diameter may be seen.

There are other ganglion cells generally aggregated into a small mass near the base of the papilla, but these cells are rather smaller and more spherical than those described above.

At the base of the papilla, around the nervous axis, there are numerous very deeply staining nuclei-like bodies, about 4—5 μ in diameter. According to Eisig (1887, p. 505) these are to be regarded as nuclei of multipolar ganglion cells which have been deprived of their cellular substance. These nuclei are situated upon a network of fine fibres, probably nervous, since they are in close relation to the fibrils of the branch of the spinal nerve supplying the sense organ. These fibres probably represent the protoplasmic part of the cells of which the deeply staining bodies are the nuclei. These and the basal ganglion cells are more numerous on the ventral side of the axis of the organ than on the dorsal side. This is probably accounted for by the fact that the branch of the spinal nerve enters the papilla on the ventral side. The nerve, soon after entering the sensory elevation, turns nearly through a right angle, and then runs along the axis of the papilla, its ultimate branches terminating among the ganglion cells and bases of the rods (fig. 30).

Inserted into the base of the sensory papilla there is a retractor muscle, the fibres of which spread out fanwise on the basal part of the nervous substance of the sense organ (figs. 16, 29). In some cases the muscle-fibrils extend inwards into the papilla as far as the ganglion cells. In favourable specimens the intimate relation of these muscle-fibrils and the nerve-fibrils may be clearly seen, and it appears probable that there is an arrangement similar to that shown by Eisig for the Capitellidæ (1887, p. 505), viz. that fine processes of the ganglion cells end in the fibrils of the retractor muscle. The muscle is attached to the inner end of the notopodial setal sac.

The position of the sense organ between the two projecting setal sacs affords it considerable protection, and additional protection is given to the sensory area by its withdrawal into a depression of the epidermis by means of the special retractor muscle. Some such arrangement is necessary to prevent injury to the delicate sense hairs when the animal is burrowing in the sand.

The sense organs differ widely in structure according to their age and the size of the specimen from which they were taken. Very young organs may be seen in sections of the last few segments of an animal.

Sense organs are clearly distinguishable in about the third segment in front of the tail segment (fig. 27). The rods are exceedingly small and difficult to see; they occupy an area equivalent to that of one or two epidermal cells. The sensory area is only 10 μ long. Below the rods are two or three small ganglion cells about 8—10 μ long, and below these are about twenty deeply staining nuclei. In the next anterior segment the rods are rather more obvious, being 5—6 μ long, and in the segment further forward the sense hairs are clearly visible, and have attained a length of about 5—6 μ. In these posterior segments the rods, ganglion cells, and nuclei are closely compressed, and their relations are difficult to determine; but further forwards, as the sense organs increase in size and the various structures become better differentiated, their connections with each other may be more readily seen. The foregoing description on pp. 272, 273, is taken from fully developed sense organs of specimens 13—15 mm. long. In older specimens there are still further changes (fig. 30). The axial portion of the organ becomes more fibrous, the ganglion cells undergo little change, but there are very many more of the deeply staining nuclei at the base of the organ than in younger specimens. The rods also stain more homogeneously, their nuclei being almost invisible, their position being indicated by a slightly darker area in each rod.

Occurrence of Lateral Sense Organs in other Polychæta.

Lateral sense organs are proved to occur in only a very few Polychæta. They are found in the Capitellidæ (with the exception of Capitella), and their relations and structure have been exhaustively investigated by Eisig (1887, p. 494). E. Meyer[1] has described the small and simple "Seitenorgane" of Polyophthalmus pictus. These are, I believe, the only hitherto published accounts of the lateral sense organs of Polychætes.

These sense organs of Scalibregma closely resemble those of Capitellidæ, except that in the latter there are no large ganglion cells beneath the rods. I have also found similar sense organs in specimens of Eumenia crassa and Lipobranchius jeffreysii, which reached me when this paper was almost completed. In the two latter genera, the depression in which the sense organ is lodged is easily visible on each side midway between the notopodium and neuropodium of each chætigerous segment. In several cases the sensory papilla and the "hair field" can be clearly seen within the depression.

From an examination of published figures of Polychæta it appears probable that "Seitenorgane" are rather more widely distributed than is generally supposed, for there are certain structures shown in these figures which strongly remind one of lateral sense organs, both by their position and appearance. It was stated above (p. 270) that the apertures of the depressions containing the sense organs of Scalibregma have been mistaken by earlier observers for sexual openings. It is probable that certain apertures described as occurring in a corresponding position in other genera may eventually be shown to be depressions lodging sense organs. S. Joseph (1898, p. 371, and pl. xxi, figs. 187, 188) noticed in Ophelia neglecta an oval pore opening into a goblet-shaped depression situated between the two rami of nearly all the parapodia. Kükenthal[2] has also figured a structure in a corresponding position in the

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[1] "Zur Anatomie und Histologie von Polyophthalmus pictus," 'Archiv für mikros. Anat.,' Band xxi, p. 791. Bonn, 1882.

[2] "Über das Nervensystem der Opheliaceen," 'Jenaische Zeitschr. f. Naturw.,' Band xx, p. 510, and Taf. xxiii, fig. 24. Jena, 1887.

parapodia of Ophelia limacina, and Rathke (1843, p. 202, and Tab. x, fig. 15; p. 203, and Tab. xi, fig. 14) has described small apertures similarly situated in Ammotrypane œstroides and in A. (= Ophelia) limacina. He believes these to be ovipores.

The papilla figured by Théel (1879, pl. iii, fig. 46^{20}) between the notopodium and neuropodium of Eumenia longisetosa is almost certainly a sense organ. There are, in some specimens of Arenicola cristata (Gamble and Ashworth, 1900, p. 443, and pl. 24, fig. 33), small papillæ, or sometimes depressions, corresponding in position to that of the above-described sense organs, but whether these structures in Arenicola are sensory could not be determined, owing to the defective preservation of the specimens examined.

The Morphology of the Lateral Sense Organs of Polychæta.

The morphology of the lateral sense organs of Capitellidæ has been exhaustively treated by Professor Eisig (1887) in his classical monograph of this family of Polychætes. In the spring of last year, while working in the Zoological Station in Naples, I had the privilege of discussing this question with Professor Eisig, and I am grateful to him for so carefully explaining to me his views upon this subject. He believes that these sense organs are modified cirri, and bases his conclusions on the following arguments. (1) The known sensory nature of cirri, as indicated by the presence on the cirri of some Polychætes of fine stiff hairs. (2) If a gradual shortening of a cirrus took place, the free nerve endings would become more and more aggregated at the free pole of the papilla, thus producing an organ of the same shape and general structure as a "Seitenorgan." (3) Each of the lateral sense organs of Capitellidæ, being situated immediately dorsal to the neuropodium, is considered by Eisig as equivalent to the dorsal cirrus of the neuropodium. He turns for confirmation and support to the parapodia of the

Glyceridæ. In this family the parapodium is not so obviously biramous as in many others, and he considers the whole parapodium of the Glycerids is really a neuropodium (the notopodium being absent) equivalent to that of Capitellids. In this case the dorsal cirrus present on the parapodium of Glycerids would occupy a position corresponding to that of the sense organ on the neuropodium of Capitellids. But, in my opinion, the evidence afforded by the study of the comparative morphology of the parapodia of Glycera and other Polychætes is against this argument and the conclusions drawn from it by Eisig.

The parapodia of several of the Glyceridæ are, at first sight, single outgrowths, in some species the division into two being only feebly marked. Each parapodium is, however, essentially biramous, as is shown by (1) the bifid tip of the parapodium; (2) the setæ are implanted in it in two more or less distinct divergent bundles. These points may be at once verified by reference to the figures of parapodia of several species of Glycera which Eisig has collected and placed on the last plate of his monograph (see Taf. xxxvii, and note especially G. capitata, fig. 31). The chief differences between the parapodia of the various species of Glycera are traceable to the varying amount of compression and approximation of the parts of the parapodium. In some cases the two rami are so closely approximated that the mouths of the two setal sacs are almost confluent, but even in these cases, on tracing the setæ to their inner ends, it is usually seen that they fall into two distinct and separate groups—a notopodial and a neuropodial. There are usually two acicula in each parapodium, one in the dorsal and the other in the ventral ramus. These acicula are points of insertion of the muscles which move the parapodium and setæ, and the presence of two indicates the essentially bifid character of the parapodium by pointing to the fact that there are two sets of muscles for moving the setæ, one for each bundle (see McIntosh, 1885, pl. xlii, figs. 5, 6, 8, 10).

It is, therefore, most probable that the parapodium of the

Glyceridæ is truly biramous, each ramus bearing a group of setæ. Moreover, the notopodium and neuropodium of Glycerids are equivalent to the correspondingly named structures in other Polychætes, the sole difference being that in the former the typical parts of the parapodium have become more closely approximated and merged into one another than is usual.

This may be further emphasised by a comparison of the parapodia of Glycera and Scalibregma. There is no difficulty in homologising the parts common to both. The parapodium of each of these genera bears two bristle bundles —a notopodial and a neuropodial—and also a dorsal and ventral cirrus. In addition there is in each parapodium of Scalibregma a structure not represented in Glycerids,—the lateral sense organ, which is situated between the two rami in a position corresponding to that of the "Seitenorgane" of the Capitellid parapodium.

Eisig's assumption that the whole parapodium of Glycerids is equivalent to the neuropodium of Capitellids does not appear therefore to hold good. The facts cited above go far towards proving that the Glycerid parapodium contains a notopodium and a neuropodium morphologically equivalent to, but less distinct than, those of Capitellids. If this be admitted, then the assumed homology of the "Seitenorgane" of Capitellids with the dorsal cirrus of Glycerids falls, as the two structures are not in the same morphological position, and have not the same relationship to the respective rami of the parapodia, for the dorsal cirrus is an appendage on the dorsal side of the notopodium, whereas Eisig contends that the "Seitenorgan" represents the cirrus on the dorsal side of the neuropodium.

After a careful examination of the lateral sense organs of Scalibregma, I have come to the conclusion that they are not very intimately related to either ramus of the parapodium, they occupy a position between the two rami. Moreover, a study of the excellent figures which Eisig has given of these organs in the Capitellidæ shows that they are not related to the neuropodium, and, indeed, if they are connected with one or other division of the parapodium, their relation is rather with the dorsal ramus than with the ventral. The sense organs in several of the Capitellidæ are considerably nearer the notopodium than the neuropodium, especially in the thoracic region (see, for example, Eisig, 1887, Taf. ii, fig. 8; Taf. xxiv, fig. 3; and Taf. xxvii, fig. 16). The sense organ may be separated from the neuropodium by a considerable interval, containing some other structure, e. g. see Eisig's Taf. xvi, fig. 3, which gives a lateral view of the abdomen of Dasybranchus, each of the sense organs of which is situated some distance from the corresponding neuropodium, and a gill is interposed between the neuropodium and the sense organ. The retractor muscle of the sense organ is, in some genera, derived from the same group of muscles as the protractors of the notopodial setæ, as in Scalibregma (see p. 273, and Pl. 13, fig. 9). In these cases the retractor of the "Seitenorgane" is attached to the inner end of the notopodial setal sac (see Eisig's figure of Notomastus lineatus, Taf. x, fig. 10). The muscles of the neuropodial setæ are never in any way connected with the lateral sense organs.

There is evidently, therefore, little reason for regarding the lateral sense organs of Capitellids even as closely related to the neuropodium, as in those cases in which the sense organs are to some extent associated with one of the rami of the parapodium, the association is invariably with the notopodium and not with the neuropodium. I conclude, however, that the sense organ is not to be regarded as an appendage of, or as intimately associated with, either ramus of the parapodium; it is on neutral ground between the two rami.

I am unable to suggest any alternative to Eisig's hypothesis to explain the origin of lateral sense organs in Polychætes. It may be pointed out that these organs have arisen in a well-protected position near the path of a large nerve—the annular nerve. In course of time the epidermis of this protected area has become much more sensitive than the less favourably situated cells around, and the former has gradually received a larger nerve supply. The definite sense organ has resulted from a gradual conversion of a number of these protected epidermal cells, perhaps at first into fusiform sense cells, similar to those met with on the cirri or on the general body surface of some Polychætes. These became further differentiated forming rod-like sense elements, and the nervous apparatus connected with their bases became increasingly complex. As shown above (p. 274), when the sense organ appears in the newly-formed segments near the posterior end of Scalibregma, it is distinguishable only by reason of the differentiation of very few epidermal cells into rod-like sense cells, and the presence beneath them of certain nerve-cells; it is never cirriform at any period of its growth.

17. Nephridia.

The character of the nephridia of Scalibregma is practically unknown. All our information regarding these organs is contained in Danielssen's account (1859), in which they are described as the female reproductive organs. In his specimen, which was a large one, he found forty to forty-two pairs of tubular yellowish bodies, one pair in each segment of the animal "from the sixth to the anal segment." Those lying in the sixth to the thirteenth were larger than the others, being about four lines (8 mm.) long. These sac-like bodies were ciliated internally and filled with an enormous number of roundish cells, many of which contained yellowish-green granules. Danielssen believed these organs to be ovaries from which all the ova had been discharged into the cœlom, as at that time of the year (June) the cœlomic fluid contained an enormous number of ova.

The nephridia are almost hidden from view by the oblique muscles which are present in each chætigerous segment throughout the body (fig. 14). The nephridia of Scalibregma are not large sac-like organs as in Arenicola, but slender loops, each formed by a tube bent once upon itself, The nephridium may, for purposes of description, be divided into four regions: (1) the funnel, (2) the fine straight tube which leads directly backwards from the funnel into (3) the loop formed by a U-shaped tube, the two limbs of which are parallel and close together, the second limb leading into (4) the short terminal tube of the nephridium (fig. 18). The only part of the nephridium visible without dissection is the loop, which is generally seen through the intervals between the oblique muscle bands.

The funnel is very small; even in large worms it is seldom more than ·4 mm. in diameter. The opening is generally directed ventrally. Both lips are simple, and bear no processes. The dorsal lip is larger than the ventral one, and overhangs the aperture like a hood. Occasionally in large nephridia the dorsal lip is slightly folded. The funnel is difficult to see because it is partially hidden by several blindly ending processes of the afferent nephridial vessel, which are bound to the funnel by a strand of connective tissue which represents the septum in the post-diaphragmatic segments (see p. 255). The funnels of the first three nephridia are situated on the anterior faces of the second, third, and fourth diaphragms respectively.

The funnel leads into a short ciliated tube, which generally runs directly backwards. This portion, even in the largest nephridia, is only about 1 mm. long, and its lumen is small (about ·04 mm. in diameter).

The two limbs of the loop of the nephridium, which form the excretory part of the organ, are closely applied together. Each is ciliated. The lumen of the straight tube of the nephridium undergoes a gradual enlargement as this tube merges into the first limb of the loop, the lumen of the latter portion being about ·08 mm. wide in large specimens. A little more than halfway along the first limb of the loop there is a distinct narrowing of the lumen, which throughout the second limb is only about ·04 mm. in diameter, so that the two limbs of the loop may be easily distinguished in section by the relative sizes of their cavities (see fig. 16).

The loop is nearly 4 mm. long in the largest nephridia. In young nephridia the lumina of the two limbs of the loop are about equal in size.

The terminal portion of the nephridium is generally bent almost at right angles to the loop. It is seldom longer than ·5 mm. It is not distinguished from the adjacent portion of the loop by any external structural character, except in a few cases in which there is a slight dilation of the terminal tube just before reaching the nephridiopore (fig. 18).

The first nephridium is very small, being only 1·5 mm. long in a large worm. The sixth is usually the largest, being 4 to 5 mm. long. In most of the nephridia of large specimens and in the first ten or fifteen nephridia of specimens about 15 mm. long the loop is the most obvious part of the nephridium, the straight tube being only one half to one fourth its length; but the young nephridia found in the posterior segments have very short loops, considerably shorter than the straight tube of the same nephridium (fig. 21).

The nephridiopores are small oval apertures. The first is situated just below and slightly anterior to the fourth neuropodium, but this is so minute that it can usually be seen only in sections. The others may usually be found either in surface view of favourable spirit specimens, or in specimens cleared in oil (fig. 5). The pores are about ·04—·06 mm. along their longer diameter (see also p. 244).

Histology.—The lips of the nephrostome are lined by a single layer of elongate columnar cells with well-marked nuclei. The cilia are better developed on the dorsal lip (fig. 19). The straight tube behind the nephrostome is lined by almost cubical ciliated cells, the nuclei of which are small and spherical, and lie close to the lumen of the tube. The cells of the loop are larger than those of the preceding portions of the nephridium. In surface view they appear pentagonal or hexagonal, and are closely fitted together at their borders. Their protoplasm contains (in preserved specimens) numerous cavities which in life were probably filled with excretory substances (fig. 20). In some specimens there are numerous small masses of excretory granules distributed throughout the cells of the loop. These granules appear dark brown or black when seen in masses, but yellow or light brown when examined singly. In some specimens the deposits are in the form of yellowish needle-shaped crystals. The nuclei of these cells are very small, and situated very close to the lumen. The terminal tube closely resembles the adjacent part of the loop, except that there are fewer concretions in the former. On approaching the nephridiopore the wall of the tube becomes thinner (fig. 20), and in some specimens the cells of this part are not ciliated. There is no muscular tissue in the walls of any part of the nephridium.

In some specimens Coccidian parasites, which in section strongly resemble ova, are embedded in the cells of the loop.

The nephridium is covered by a very thin layer of peritoneal epithelium, and the blood-vessels seen on the funnel only lie between the peritoneum and the bases of the excretory cells.

Blood Supply.—The nephridia are supplied with blood by branches of the afferent branchial vessels which are given off from the dorsal vessel (as in the case of the first three nephridia) or by the segmentally arranged branches of the ventral vessel (fig. 14). The latter vessels usually bifurcate near the setal sacs, one branch passing to the nephrostome and the other to the body-wall; the latter vessel usually bears blind outgrowths which partially obscure the nephrostome.

The nephridia receive only a small amount of blood, the whole of which apparently goes to the funnel (and to the rudimentary septum on which the gonads are formed). I have not found vessels on any other part of the nephridium.

The first three nephridia return blood to the second, third, and fourth efferent branchial vessels. The nephridia of the fifteenth and following segments return blood to the subintestinal vessels.

It is interesting to compare Danielssen's observations with the foregoing. He evidently saw only the loops of the nephridia, the two limbs of which are indicated in some of the anterior nephridia of his figure (pl. i, fig. 1); in these nephridia the anterior limit is drawn broader than the posterior, as is usually the case in large specimens. He apparently overlooked the first two nephridia, which are small and difficult to see, as they are partially hidden by the diaphragms. He describes the first nephridium as situated in the sixth segment and immediately behind the last diaphragm. This is really the third nephridium, as may be seen from a glance at fig. 14. The yellow granules observed by Danielssen in the cells of the nephridia were probably excretory.

18. Reproductive Organs.

Danielssen (1859, pp. 73—76) described Scalibregma as hermaphrodite. He examined the tubular nephridia, and concluded they were ovaries from which all the ova had been discharged into the cœlom. The parapodial glands present on the dorsal and ventral cirri from the sixteenth to within a few segments of the posterior end of the animal were mistaken by him for testes, and the minute rods which they contain were supposed to be spermatozoa. Scalibregma is not hermaphrodite, it is diœcious. As pointed out above (p. 280), the paired segmental tubular organs are nephridia, and the structures in the cirri are (p. 247) modified epidermal glands which, instead of producing a liquid mucous secretion, give rise to rod-like bodies which may be discharged on the surface of the cirri.

For a considerable time I was unable to locate the gonads, as they are extremely small. The nephrostome is connected to the body-wall by a thin sheet of tissue, which probably represents the septum of the segment. On the surface of this strand, and especially in the region of the smaller lip of the funnel, there is a collection of loosely arranged cells produced by proliferation of the peritoneal cells covering the base of the funnel and the neighbouring portion of the septum. These cells are the very young reproductive cells. They are found only in the region of the smaller lip of the nephrostome, and for a little distance along the outer side of the straight tube of the nephridium where this organ is in contact with the rudimentary septum. Gonads are present on all the fully grown nephridia, but those on the first and second nephridia are very small. The gonads connected with the first three nephridia are situated on the smaller lips of the funnels and on the neighbouring portions of the anterior faces of the last three diaphragms.

The nuclei of the reproductive cells are large and deeply staining.

It is not possible, I think, to distinguish the sex of a specimen by examination of the cells of the gonad, because they are shed into the cœlom when so small that they have not become sufficiently differentiated to be recognisable as either young ova or young spermagonia. It is only after an examination of the more mature sexual products usually found in the cœlom that the sex of the specimen can be determined.

The reproductive cells leave the gonad when about 10—12 μ in diameter. They increase in size in the cœlom, and by the time they have reached 15 μ in diameter their nature may be determined, as in males division of the cells now takes place, and in females the cells are recognisable as young ova. The ovum continues to grow in size, and its protoplasm—which up to this point has been clear and homogeneous — gradually becomes loaded with spherical yolk granules about 1 μ in diameter, which stain deeply with hæmatoxylin. The largest ova in my specimens are ·12 mm. in diameter; these are probably almost ripe. The nucleus is excentric and vesicular, about 30 μ in diameter, and has a prominent deeply staining nucleolus. The peripheral layer of protoplasm is almost free from yolk granules, but these granules are moderately uniformly distributed throughout the other parts of the protoplasm. The vitelline membrane of these ova is thin.

The spermatozoa develop exactly as in Arenicola (Gamble and Ashworth, 1898, p. 32, and pl. 5, figs. 29—34). The spermagonia fall into the cœlom, and after several divisions give rise to spherical or disc-shaped hollow masses of spermatids. The central cavity of each mass contains a small coagulum, the remains of the blastophore.

By what means the genital products escape is difficult to say. The nephridia are much too small to serve as oviducts, as the width of the lumen of the narrow tube immediately following the nephrostome is only about one third the diameter of a ripe ovum. It is possible that the spermatozoa escape by means of the nephridia. The escape of genital products has been seen by Danielssen, who observed that one of his specimens extruded eggs through a small rupture in the body-wall which appeared when the animal was strongly contracted.

19. The Family Scalibregmidæ.

The family of the Scalibregmidæ was established by Malmgren (1867, p. 186) to contain Scalibregma inflatum, Rathke, and Eumenia crassa, Oersted, there being only one species of each genus known at that time. Since then other species and genera have been described as allied to the foregoing, and have been included in the family, although in some cases their characters do not agree with those of the original genera in one or more important respects. The classification of this family is therefore at present in considerable confusion, and this is further increased by the almost inextricable entanglement of the three principal genera—Scalibregma, Eumenia, and Lipobranchius. The position is rendered more difficult by the fact that some of the species of these genera have been only briefly described, and are known only from the external characters of a single specimen, and this sometimes a mutilated one.

The original description of Scalibregma by Rathke (1843, p. 182), and of Eumenia by Oersted (1844, p. 99), mentions the presence of gills as one of the diagnostic characters; and Levinsen (1883, p. 133) includes this among the characters of the family Scalibregmidæ, but qualifies the statement by adding that gills are present only in older worms, or may also be present in younger individuals.

Hansen (1882, pp. 34, 35) described a gill-less worm obtained by the Norwegian North Atlantic Expedition as Scalibregma (?) parvum, and McIntosh (Eumenia jeffreysii, 1868, p. 419; and E. reticulata, 1885, p. 360), Théel (E. longisetosa, 1879, p. 49), and Ehlers (E. glabra, 1887, p. 169) have referred other gill-less specimens to the genus Eumenia. Levinsen (1883) renamed Théel's specimen Scalibregma longisetosum; but this is not satisfactory, as an abranchiate species is thus placed in a genus one of the distinctive characters of which is the presence of gills. Cunningham and Ramage (1888, p. 655) recognised that specimens similar to those named by McIntosh Eumenia jeffreysii did not belong to the genus Eumenia; they considered them to constitute a new genus—Lipobranchius. The absence of gills in his specimens (which were 35—37 mm. long) was carefully considered by Théel (1879) before naming them Eumenia longisetosa. Possibly with a view of accounting for the absence of gills in these specimens, or at any rate of minimising the value of these organs as diagnostic, he states that the gills of Eumenia crassa do not begin to grow until the animal has attained a length of 40—50 mm. The absence of gills in E. longisetosa might, therefore, be due to the fact that the specimens were young ones in which gills would have appeared later. But this seems scarcely probable, and Théel's statement regarding the formation of the gills of E. crassa at a comparatively late stage of the animal's growth also seems extraordinary, as in many branchiate Polychætes the gills are formed in early life when the animal is quite small, e. g. a specimen of Arenicola marina 4 mm. long already bears the full number (thirteen pairs) of gills. Théel's statement, moreover, does not agree with that of at least one author, viz. Johnston (1865, p. 221), who describes a specimen of E. crassa which bears gills and is only one inch and a quarter (about 31 mm.) long. I am indebted to Dr. Théel for two specimens of E. crassa, 29 and 35 mm. long respectively, each of which bears four pairs of gills. Another specimen in my possession, obtained off the south coast of Nova Scotia, is 31 mm. long, and also bears the same number of gills. It would, I think, be better to consider the gills as one of the diagnostic characters of the genus Eumenia, and to consider that Théel's specimens, named by him E. longisetosa, do not really belong to this genus, from which it differs in other respects (see p. 292).

S. Joseph (1894, p. 103) has evidently resolved to maintain the branchiate character of the genera Scalibregma and Eumenia, for he divides the family of the Scalibregmidæ into two sections :

(1) Those with gills—Scalibregma, Eumenia.

(2) Those without gills — Sclerocheilus, Lipobranchius.

In the last-named genus he would place L. jeffreysii, Cunn. and Ram. (= Eumenia jeffreysii, McIntosh), and two other abranchiate species of Eumenia, viz. E. reticulata, McIntosh, and E. glabra, Ehlers. The genus Lipobranchius in his hands thus becomes a somewhat heterogeneous assembly, the members of which agree in general shape and absence of gills, but differ in other characters quite as important, e. g. the prostomium and parapodia. S. Joseph's classification is therefore not entirely satisfactory, and requires some modification.

Before proceeding further it will be advisable to review the chief characters of each of the genera already known, beginning with the best known genera and species.

The genera Scalibregma and Eumenia are very similar, and it is not easy to find many characters by which they may be distinguished.

Taking the species S. inflatum and E. crassa as typical of the respective genera, we may say that the former is more or less arenicoliform, while the latter is maggot-like and tapers only slightly at each end. The most obvious external difference is found on examining the parapodia. In S. inflatum the parapodia from the fifteenth segment to the posterior end project outwards some distance from the body, forming vertical laminæ bearing dorsal and ventral cirri. Each of the parapodia of E. crassa is formed by two mammillæ which arise separately from the body-wall and bear the setæ; cirri are absent. There are also anal cirri in S. inflatum, but none in E. crassa.

The gills of these two Annelids are closely similar. In Oersted's description of E. crassa it is stated that gills are found in the six anterior segments, and Johnston states that they are "confined to the first six segments."

Théel (1879) finds only four pairs of gills. In each of the three specimens in my possession (two from the coast of Sweden and one obtained off Nova Scotia) I find only four pairs of gills situated in the second to fifth chætigerous segments, thus exactly agreeing in number and position with those of Scalibregma. The first gill of my specimens of E. crassa is small, and the fourth is the largest. It is scarcely probable that any other gills would have been formed in these specimens, which are about 30 mm. long and practically mature, as determined by an examination of the sexual products in the cœlomic fluid. There is, therefore, some difference of opinion with regard to the number of gills present in Eumenia crassa. It will be noted that Johnston does not definitely state that there are six pairs. I have been unable to procure a specimen bearing more than four pairs of gills, and though inclining to the opinion that this is the normal number of branchiæ, I cannot settle this question definitely until a much larger number of specimens is available for examination.[1]

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[1] Cunningham and Ramage (1888, p. 655, and pl. 42, fig. 18) describe and figure a specimen named E. crassa, dredged in the Firth of Forth, which differs in several respects from specimens described by other authors. The parapodia of their specimen are lamelliform, project prominently from the

The prostomium of Scalibregma inflatum may be described as almost T-shaped, the two horizontal limbs of the letter representing the tentacular processes. The head of Eumenia crassa is more deeply divided in the middle line, and its lateral angles are rounded, and not prolonged into tentacular processes (fig. 13).

These two Polychætes agree in the position and relations of the nuchal grooves and peristomium; in the appearance and structure of the skin; in possessing two kinds of setæ, capillary and furcate, in each of the rami of the parapodia; in the presence of a sense organ between the rami of each parapodium.

Internally there is also a strong resemblance between these two worms. (My specimens of Eumenia crassa were unfortunately not in good condition internally, and I was unable to determine some of the finer structural details.) They agree in the following respects:—the general form and relations of the alimentary canal, the situation of the four anterior diaphragms, the musculature, the non-ganglionated nerve-cord, the nephridia, each with simple funnel leading into a slender tube bent once upon itself, a considerable part of the proximal limb of the loop being wider than the distal limb.

Scalibregma inflatum and Eumenia crassa differ only (so far as their anatomy is at present known) in the

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body-wall (see fig. 18 B), and bear large flattened leaf-like dorsal and ventral cirri. All other authors agree that the parapodia of E. crassa are without cirri. In the Firth of Forth specimen there are six pairs of gills stated to occur in front of the notopodium of the first six chætigerous somites. In other recorded specimens of this Polychæte the gills are situated behind the corresponding notopodia. The prostomium of the Forth specimen terminates in two diverging tentacles, thus differing from others (see above, p. 290). These points taken in conjunction with the fact that the specimen described by Cunningham and Ramage is an elongate worm gradually tapering from about the eighth or tenth segment to the posterior end, whereas all other recorded specimens are maggot-like, shows that this specimen, if it be E. crassa, is quite different from any other example of this animal recorded from the time of Oersted (1844) up to the present.

shape of the prostomium, the character of the parapodia, and the presence in the former genus of parapodial and anal cirri.

Lipobranchius jeffreysii agrees closely with Eumenia crassa, except that in the former there are no gills. The absence of gills cannot be ascribed to the youth of the specimens, for three of those in my possession are 32, 38, and 40 mm. long respectively, and are almost mature, having ova ·09 mm. in diameter in the cœlomic fluid. These cannot, therefore, be regarded as immature specimens of E. crassa upon which gills would afterwards have been formed, and moreover gills are present in specimens of E. crassa before they reach this size; there are four pairs of gills in a specimen 29 mm. long. Lipobranchius jeffreysii agrees with E. crassa in the shape of its prostomium, and the character of its parapodia, which are without cirri; in fact, given a specimen from which the first six segments have been removed, it would be a matter of some difficulty to determine to which genus the specimen in question belonged.

Among the specimens of Scalibregma sent to me from the United States National Museum there are five small worms 4·6 to 8 mm. long, which have no gills, but otherwise are indistinguishable from Scalibregma. I find that these are not, as I at first supposed, young specimens; some at least are almost sexually mature, e. g. the specimen 8 mm. long contains large ova (·1—·11 mm. in diameter). These, therefore, cannot well be regarded as young specimens of Scalibregma; had they been such their gills would already have been quite obvious structures, for Scalibregma acquires its gills at an early age; a specimen 5 mm. long already bears the full number (four pairs) of well-developed gills. If, therefore, the branchiæ are to be regarded as one of the diagnostic characters of the genus Scalibregma, these abranchiate specimens do not belong to the genus. I propose to call them Pseudoscalibregma.

Several Polychætes have been described which agree with Scalibregma in general characters, but are without gills;

these might also be placed in the genus Pseudoscalibregma. S. parvum, Hansen, S. (Eumenia) longisetosum, Théel, and Eumenia reticulata, McIntosh, probably belong here.

S. parvum agrees very closely with the abranchiate specimens of Scalibregma in my possession in the shape of the prostomium and in the parapodia, which from the twelfth segment to the posterior end of the animal form projecting laminæ, each bearing a dorsal and a ventral cirrus.

Théel's Eumenia longisetosa differs markedly from E. crassa in several respects, e. g. in the former the prostomium is prolonged at each side into a well-marked tentacular process; and though the first eleven pairs of parapodia are small, those of the twelfth and following segments bear leaf-like cirri. Levinsen (1883, p. 133) and von Marenzeller (1892, pp. 401, 426) have realised that Théel's specimens are more closely allied to Scalibregma than to Eumenia, and have accordingly renamed them Scalibregma longisetosum. The latter author suggests that the specimens (which are about 12 mm. long) described by Hansen as S. parvum are merely young forms of Théel's species, and from a comparison of the descriptions and figures of the prostomia and parapodia I consider the evidence supports this view very strongly. S. parvum and S. longisetosum are, however, abranchiate, and should be separated on that account from the genus Scalibregma.

Eumenia reticulata, McIntosh, is evidently nearly related to the foregoing, for its prostomium is prolonged into tentacles, and its parapodia from the fifteenth segment onwards to the posterior end of the body form projecting lamellæ, which McIntosh compared to those of Théel's specimens. McIntosh (1885, p. 361) remarks that "one of the specimens presented the aspect, dorsally, of Scalibregma without the branchiæ."

Eumenia glabra, Ehlers, differs so considerably from any of the species mentioned above, that it is doubtful whether it should be included in any of the hitherto described genera.[1] Its prostomium is drawn out into two well-marked tentacular processes, but its skin appears to be smooth, and (in the figures) bears no signs of secondary annulation, and the parapodia do not project prominently from the body. The posterior end of the animal forms a thin tail, upon the end of which the anus opens. It is distinguished from Eumenia and Lipobranchius by its prostomium and skin, and from Scalibregma by its parapodia and skin.

There still remain for consideration two members of the family, viz. Sclerocheilus minutus, Grube, and Lipobranchius intermedius, S. Joseph. The former was discovered and briefly and somewhat incorrectly described by Grube[2] in 1863, but this description has been revised and extended by S. Joseph (1894, p. 103). The animal is small, only about 5—20 mm. long, and is found living in oyster-shells. The head is of moderate size, and bears two blunt tentacular processes. There are eversible nuchal organs at the sides of the prostomium. The parapodia contain capillary and furcate setæ, and those of the second segment (the peristomium being achætous) also contain stout acicular setæ which are curved near the tip. Behind the twenty-second segment each parapodium bears a small digitiform cirrus below the neuropodium. This is not a gill, as it contains no vessels; it is evidently sensory, as indicated by the presence of fine stiff hairs upon it. The skin is sculptured as in Scalibregma. There are no gills. There are five[3] (or rarely six) cirri around the anal aperture. The alimentary canal resembles that of the other members of the family except that there are no œsophageal pouches. The brain and nerve-cord agree with those of the other members of the family,

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[1] Ehlers (1887, p. 170) evidently doubted whether this animal should be included in the genus Eumenia, for he says, "Ich stelle diese Art vorläufig in die Gattung Eumenia."

[2] "Beschreibung neuer oder weng bekannter Anneliden, Sechster Beitrag," 'Archiv für Naturgeschichte,' Jahrg. xxix, Band i, p. 50. Berlin, 1863.

[3] Grube describes and figures four anal cirri.

and the nephridia are formed on exactly the same plan as those of Scalibregma, each nephridium being a delicate tube, the excretory portion of which is once bent upon itself. S. Joseph believes that the nephridia act as genital ducts, but this seems improbable, if not impossible, as the lumen of the nephridium is too small to permit the passage of a ripe ovum (judging from S. Joseph's figures, pl. v, figs. 137, 142). The animal derives its name from two plate-like pigmented structures on the head, which Grube believed to be "horny" and protective, but S. Joseph describes them as eyes.[1]

This animal is most closely allied to the gill-less forms of Scalibregma (Pseudoscalibregma), with which it agrees in general shape, in the characters of the prostomium, furcate setæ, nephridia, and nervous system, but differs from them in possessing strong setæ in the second segment, the presence of eyes (?), and the absence of dorsal cirri.

According to S. Joseph (1894, p. 113), his new species Lipobranchius intermedius is very similar in almost all respects to Sclerocheilus minutus, with the exception that the former bears no eyes upon the head and no cirri upon the parapodia. It seems to me that this animal is not a Lipobranchius; it differs from that genus in at least two important respects, viz. the shape of the prostomium and the possession of strong acicular setæ in the first parapodium. This animal is more nearly allied to Sclerocheilus than to any other member of the family of Scalibregmidæ. It may for the present be named Asclerocheilus intermedius, a name which indicates its relationship to Sclerocheilus, and at the same time reminds us that the pigmented plates, the distinctive character of the latter genus, are absent from the former.

It would have been better had the preparation of the following table of characters and classification been post-

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[1] S. Joseph (p. 105) states that these pigmented areas occur on the dorsal surface of the head; while Grube describes and figures them (p. 50, and Taf. v, fig. 3 *b*) on the ventral face of the prostomium near the mouth.

poned until I had been able to examine many more specimens of some of the species therein mentioned. There seems little prospect of obtaining further material for some considerable time, and I have therefore appended the table, although it cannot be regarded as a final one, as it is deficient in several respects. It is based largely on the results recorded in the former part of this paper, supplemented by the diagnosis of the authors responsible for the various species.

The Scalibregmidæ form a moderately compact family, the characters of which may be thus stated.

SCALIBREGMIDÆ.

Limnivorous Polychæta, arenicoliform or maggot-like in shape. Gills, if present, confined to the first five (or six, according to Johnston) segments. Prostomium small, in some drawn out at its antero-lateral angles into short processes; in others its two lobes are blunt and rounded; bordered laterally by the two nuchal grooves through which the eversible nuchal organs may be protruded.

Parapodia consist of almost identical notopodia and neuropodia, each bearing setæ of two kinds, viz. simple capillary setæ, and furcate setæ with unequal, barbuled, pointed limbs. Between the two rami of each parapodium there is in most species a small sense organ, which may be withdrawn into a shallow depression of the epidermis. The segments are subdivided into annuli, and the skin, especially in the anterior part of the body, is usually raised into squarish or oval elevations. Internally there are four transverse diaphragms situated at the posterior end of the first, second, third, and fourth chætigerous segments. The eversible pharynx is smooth, there being no armature whatever. The heart is median and is an enlargement of the dorsal vessel. There is a pair of nephridia in each segment except in a few of the anterior ones. Each nephridium is a narrow ciliated tube, the excretory part of which is bent once upon itself; the funnel is small. Diœcious, gonads microscopic.

Found in the temperate seas of the Northern and Southern Hemispheres, and in the colder seas of Northern Europe.

I. Body arenicoliform, prostomium more or less T-shaped, the antero-lateral angles being drawn out to form short tentacular processes.

A. The parapodia of the segments behind the twelfth or fifteenth project prominently at right angles to the body, each forming a laminate appendage bearing a dorsal and a ventral cirrus. Body often swollen anteriorly.

1. Scalibregma.—Gills present on the anterior segments.

S. inflatum, Rathke (Oligobranchus roseus, Sars). Four pairs of gills in chætigerous segments 2—5. Four anal cirri.

S. brevicauda, Verrill. Four pairs of gills on segments 2—5. No anal cirri described.

S. (?) abyssorum, Hansen. Anterior part only known, from one specimen. Three pairs of gills on segments 2—4. The prostomium bears very short tentacles.

2. Pseudoscalibregma.—No gills. No anal cirri described.

P. longisetosum. (Eumenia longisetosa, Théel.) The eleventh or twelfth and following parapodia bear cirri.

P. parvum. (Scalibregma [?] parvum, Hansen.) Cirri present on the parapodia of the twelfth and following segments. This may be a young form of the preceding species.

P. reticulatum. (Eumenia reticulata, McIntosh.) Cirri on the fifteenth and following segments.

B. The parapodia do not form laminate appendages, and are without dorsal cirri. Ventral cirri, if present at all, are digitiform and confined to the posterior region. Each parapodium is composed of two simple rounded elevations, in which the setæ are lodged.

3. Sclerocheilus.—Two triangular masses of pigment on the prostomium. Strong, curved, acicular setæ are found in the first chætigerous segment. The parapodia in the posterior segments of the animal bear ventral cirri. Four anal cirri present.

S. minutus, Grube.

4. Asclerocheilus.—Pigment masses absent. Curved acicular setæ finer than those of Sclerocheilus are present in the first three chætigerous segments. No ventral cirri.

A. intermedius. (Lipobranchius intermedius, S. Joseph.)

II. Body of animal maggot-shaped. Prostomium distinctly divided anteriorly into two by a median groove; each half of the head is blunt and rounded; there are no tentacular processes. The parapodia do not form projecting lamellæ, and do not bear cirri. Each parapodium is composed of two simple rounded elevations which arise separately from the body-wall. Anal cirri absent.

5. Eumenia.—Four (or six) pairs of gills present on chætigerous segments 2—5 (or on the first six according to Johnston).

E. crassa, Oersted.

6. Lipobranchius.—Gills absent.

L. jeffreysii, Cunningham and Ramage. (Eumenia jeffreysii, McIntosh.)

20. Affinities of the Scalibregmidæ.

The Scalibregmidæ, as references in the previous portion of this paper have shown, resemble the Arenicolidæ in many of their structural features, and they also agree in some points with the Opheliidæ. These three families have several points in common, as they are limnivorous, and present certain of the peculiarities characteristic of such Polychætes.

They have a spacious cœlom, subdivided anteriorly by diaphragms, and non-septate in the middle part of the animal; the alimentary canal consists of an eversible pharynx, followed by an œsophagus bearing a pair of lateral glandular outgrowths, a dilated stomach with glandular walls, and a straight intestine, usually with a ventral groove; the blood-vessels of the middle region of these animals are so arranged as to leave the stomach considerable freedom of movement, all the blood-vessels to the stomach passing to its ventral wall, and being arranged so that they can accommodate themselves to the backward and forward motion of this part of the gut.

The Scalibregmidæ agree with the Arenicolidæ in the above-named characters, and in the general shape of the body, the subdivision of the segments into annuli, the sculpturing of the skin, the small-lobed prostomium (which, in some specimens of Scalibregma, is quite comparable to that of Arenicola claparedii), and the presence (in Scalibregma and Eumenia) of gills of a similar type. The brain and non-ganglionated nerve-chain of Scalibregma resemble those of the marina section of the genus Arenicola. There are also points of difference between these two families which are of considerable importance. In the Scalibregmidæ the two rami of the parapodia are practically identical, but in the Arenicolidæ the notopodium is a conical elevation, and the neuropodium a cushion-like outgrowth. In members of the latter family the neuropodium bears crotchets only, and the notopodium bears capillary setæ; in the Scalibregmidæ both rami of the parapodia bear two kinds of setæ, capillary and furcate, the latter being characteristic of the family. In some of the Scalibregmidæ the parapodia form laminate appendages bearing dorsal and ventral cirri, which are absent in Arenicola (cirri are very rarely seen in the posterior region of American specimens of A. cristata). The gills of Scalibregma and Eumenia are confined to the first five (or six) segments; they are never present in the first seven segments of Arenicola.

The dorsal vessel of Scalibregma is dilated just behind the fourth diaphragm to form the heart, which is therefore a median structure, thus differing entirely from the hearts of Arenicola, which are paired, and not directly connected with the dorsal vessel. The nephridia of Scalibregmidæ are minute but numerous, and the simple microscopic funnel leads into a slender U-shaped excretory tube. The nephridia of Arenicola are fewer in number, and are wide sacs, each with a large funnel fringed with ciliated vascular processes. Several of the Scalibregmidæ bear complex, segmental, lateral sense organs, which are not found in Arenicola.

The Scalibregmidæ have only a few features in common with the Opheliidæ. Besides the points mentioned above as common to the three limnivorous families, they agree in the great development of the muscles of the ventral body-wall (especially in Eumenia and Lipobranchius), the nerve-cord without ganglia, the dorsal heart, and the principal features of the circulatory system. The resemblances may be best seen on comparing the Opheliid Ammotrypane œstroides with Eumenia and Scalibregma. The Opheliidæ and Scalibregmidæ differ in their nephridia, those of Opheliids being comparatively few and sac-like; in their prostomia, that of Opheliids is a single conical outgrowth; in their parapodia and setæ. The Scalibregmidæ have little in common with any other family of Polychætes.

We may therefore say that the Scalibregmidæ agree in several respects with the Arenicolidæ and Opheliidæ, and it is difficult to say that they are more related to one of these than to the other, though, on the whole, there are rather more features in which the Scalibregmidæ agree with the Arenicolidæ (e. g. shape, secondary annulation, sculpturing of skin, character of the gills when present, prostomium, brain, and nerve-cord) than with the Opheliidæ. The Scalibregmidæ, however, are clearly distinguished from these families by the presence of the peculiar furcate setæ in the parapodia, and by their numerous delicate nephridia, among other characters.

21. Summary of Results.

1. Specimens of Scalibregma inflatum from the northern seas of Europe and America are not distinguishable by any essential and constant character from those obtained by the "Challenger" in southern seas.

2. The parapodia of the segments posterior to the fifteenth or sixteenth bear dorsal and ventral cirri which contain large unicellular glands, the secretion of which is in the form of elongate fusiform rods. The fine-pointed tips of the glands pass between the epidermal cells and open on the free surface. The notopodium, its cirrus, and some of its setæ are formed in advance of the neuropodium and its corresponding parts.

3. The setæ of each ramus of the parapodium are of two kinds: (1) simple capillary bristles, the distal third of which bears (in unworn examples) a large number of minute hair-like processes; (2) rather stouter, shorter setæ, furcate distally, the two unequal pointed limbs bearing on their inner faces a number of curved barbules. Both these kinds of setæ are found in the earliest recognisable parapodia. Furcate setæ of this type are practically restricted to the family Scalibregmidæ.

4. The dorsal vessel is dilated at two points to form the blood-reservoir and the heart. There is no cardiac body in the heart.

5. The brain consists of an anterior lobe in relation to the prostomial epithelium, and two posterior lobes, each applied to the inner side of the corresponding nuchal organ. The ganglion cells are found chiefly on the dorsal and ventro-lateral faces of the brain. The anterior lobe gives off a pair of nerves to the tentacles; the œsophageal connectives arise from the middle region of the brain; the posterior lobes give off nerves which run along the sensory epithelium of the nuchal organs. In old specimens the fibrous part of the brain becomes proportionately larger and more complex, and the ganglion cells become aggregated into groups.

6. The nerve-cord is situated close to the epidermis, and is non-ganglionated. The ganglion cells are distributed along the whole length of the cord on its lateral and ventral faces. The cord gives off in each segment a pair of nerves lying in each interannular groove, and a pair lying in the chætigerous segment. The latter supplies the cirri, sense organs, and setal sacs.

7. A pair of lateral sense organs is present in each chætigerous segment. Each sense organ is a small eminence rising from the base of a shallow depression bordered by prominent lips of epidermis. From a darker area in the centre of the papilla the delicate sense hairs arise. They are implanted in exceedingly slender columnar cells, closely and regularly arranged. These cells are in connection at their inner ends with pyriform or fusiform ganglion cells, which occupy the axis of the sensory papilla. Around and below these are numerous deeply-staining nuclei, which are probably, as Eisig showed, the nuclei of multipolar ganglion cells, the protoplasm of which forms the fine network upon which the nuclei are situated. The sense organ receives a moderately stout branch from the spinal nerve, which runs along the middle of the chætigerous annulus. The sense organ may be withdrawn into the depression in the epidermis by the contraction of a retractor muscle attached to its base. In very young sense organs, such as are found in the last two or three segments of a specimen about 15 mm. long, the rods which occupy the space of only one or two epidermal cells are exceedingly small, and do not bear sense hairs. There are only two or three small ganglion cells at their bases, accompanied by about twenty of the deeply staining nuclei mentioned above. In the next segment anterior to this the rods are more obvious, and one segment further forward the sense hairs may be seen on their distal ends. In old sense organs the axial part of the organ is more fibrous, and the deeply staining nuclei are very numerous.

8. Similar sense organs are present in Eumenia crassa and Lipobranchius jeffreysii.

9. These organs are similar to those described by Eisig in the Capitellidæ, except that in the latter there are no large ganglion cells beneath the rods. The sense organ is not, as Eisig supposed, morphologically equivalent to a neuropodial dorsal cirrus. It does not form part of the neuropodium; it occupies a position between the two parapodial rami, but it may be connected by means of its retractor muscle to the base of the notopodial setal sac. Eisig believes that the sense organ is homologous with the dorsal cirrus of the Glyceridæ, and that the parapodium of Gycerids is a neuropodium only (the notopodium being absent) equivalent to the neuropodium of Capitellidæ. This view cannot be supported; the parapodium of the Glyceridæ is essentially biramous, its division into notopodium and neuropodium being less obvious than in many Polychætes, owing to the close approximation of the two rami. (For further details of the discussion see p. 276.)

10. Each nephridium is a delicate ciliated tube opening into the cœlom by a minute simple nephrostome. The excretory part of the tube is bent once upon itself. There is a pair of nephridia in each chætigerous segment except the first three.

11. Scalibregma inflatum is diœcious, and not hermaphrodite, as described by Danielssen. The gonads are formed by proliferation of the cells covering the septum by which the nephrostome is attached to the body-wall. The genital cells fall from the gonad at a very early stage, and complete their growth in the cœlomic fluid. In their structure and stages of growth the ova and spermatozoa closely resemble those of Arenicola. Eumenia crassa and Lipobranchius jeffreysii are also diœcious, and their genital products are similar to those of Scalibregma.

12. The prostomium is an important character in the classification of the Scalibregmidæ. It affords, along with the nature of the parapodia, the most reliable means of determining whether a given specimen belongs to the Scal bregma—or to the Eumenia—section of the family.

13. The Scalibregmidæ resemble the Arenicolidæ and Opheliidæ in several respects, but several of these characters may be largely due to the limnivorous mode of life of the members of these three families. The following characters are common to them :—the spacious cœlom non-septate in the middle region of the body; the eversible pharynx followed by an œsophagus bearing a pair of glandular outgrowths; a dilated stomach with glandular walls and a straight intestine with a ciliated ventral groove; the blood-vessels of the middle region of the gut are arranged so as to allow the swinging movement of the stomach.

The Scalibregmidæ agree with the Arenicolidæ also in the annulation and sculpturing of the body-wall, the prostomium, the brain, and non-ganglionated nerve-cord. They differ in their parapodia, setæ, the position of the gills, the heart, and the nephridia.

The Scalibregmidæ resemble the Opheliidæ in their musculature, the non-ganglionated nerve-cord, and the circulatory system; but they differ in their prostomia, nephridia, parapodia, and setæ.

The Scalibregmidæ, although allied to some extent to the Arenicolidæ, and to a less degree to the Opheliidæ, form a separate and compact family, one of the most characteristic features of which is the presence of the peculiar furcate setæ in the parapodia.

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EXPLANATION OF PLATES 13—15,

Illustrating Dr. J. H. Ashworth's memoir on "The Anatomy of Scalibregma inflatum, Rathke.

List of Reference Letters.

An. Anus. *Ant. Cr.* Anterior cornu of brain. *Bl. R.* Blood reservoir. *Br.* Gill. *Br. Aff.* Branchial afferent vessel. *Br. Eff.* Branchial efferent vessel. *Cirr. An.* Anal cirri. *Cirr. D.* Dorsal cirrus of parapodium. *Cirr. Gl.* Gland situated in the cirrus. *Cirr. V.* Ventral cirrus of parapodium. *Cœl.* Cœlom. *Cœl. Epith.* Cœlomic epithelium. *Cut.* Cuticle. *Dphm.*$^{1-4}$. Diaphragms. *D. V.* Dorsal blood-vessel. *Ep.* Epidermis. *Ep. Gl.* Gland-cells of epidermis. *Ep. Pap.* Epidermal papillæ. *F.* Fibrous part of nerve-cord. *Gang. C.* Ganglion cells. *Gen. C.* Genital cells. *Gr. V.* Ventral groove of intestine. *Ht.* Heart. *Int.* Intestine. *Int. N.* Nerves (? see p. 268) of intestine. *Int. S.* Intestinal sinus. *Mo.* Mouth. *M. Long.* Longitudinal muscles of body-wall. *M. Obl.* Oblique muscles. *M. Ph.* Retractor muscles of pharynx. *M. Protr.* Protractor muscles of the setal sacs. *N.* Nucleus. *N. Annul.* Annular nerve situated in the interannular groove. *N. C.* Nerve-cord. *N. Chæt. Annul.* Annular nerve of chætigerous annulus. *Neur. S.* Neuropodial seta. *Ngl.* Neuroglia. *Ngl. Sh.* Neuroglial sheath. *Nllm.* Neurilemma. *Nm.* Neuropodium. *N. M. C.* Nucleus of multipolar ganglion cell. *N. Nuc.* Nerve to nuchal organ. *N. O.* External opening of nephridium. *Notm.* Notopodium. *Not. S.* Notopodial setæ. *Nph.* Nephridium. *Nphs.* Nephrostome. *N. Tent.* Nerve to prostomial tentacle. *Nuc. Gr.* Nuchal groove. *Nuc. Retr.* Retractor muscle of nuchal organ. *Œ.* Œsophagus. *Œ. Gl.* Œsophageal glands or pouches. *Per.* Peristomium. *Ph.* Pharynx. *Post. Cr.* Posterior cornu of brain. *Prost.* Prostomium. *Prost. Tent.* Prostomial tentacle. *R.* Rods of lateral sense organ. *S. Aff. V.* Segmental afferent vessel (from ventral vessel). *S. Cap.* Capillary seta. *S. Eff. V.* Segmental efferent vessel (to subintestinal vessel). *Sept.* Septum. *S. Furc.* Furcate seta. *S. H.* Sense hairs. *S. O.* Lateral sense organ. *S. O. Retr.* Retractor muscle of sense organ. *Sp. N.* Spinal nerve. *Stom.* Stomach. *Subint. V.* Subintestinal vessel (sinus). *T.* Tail segment. *V. Mes.* Ventral mesentery (imperfect). *V. V.* Ventral blood-vessel. *I, II, III, IV . . . LX.* Somites beginning with the first chætigerous.

PLATE 13.

All figures, except Fig. 13, are drawn from specimens of Scalibregma inflatum.

Fig. 1.—The large Norwegian specimen, 56 mm. long, seen from the left side to show the external features, prostomium, parapodia, cirri, setæ, gills, segmentation and annulation, the sense organs, etc. The nephridiopores (*N. O.*), the first of which opens on the fourth chætigerous annulus, are very small, and are not well seen in this drawing (see Fig. 5). There are sixty-one segments in the specimen. × 4½.

Fig. 2.—Ventral view of a very regular American specimen which, if complete, would have been about 20 mm. long. The prostomium, peristomium and first seven chætigerous segments are seen. The mouth (*Mo.*), bordered by epidermal papillæ, and the secondary annulation of the skin are seen. The nerve-cord runs along the middle line of the median depressed area. × 22.

Fig. 3.—Dorsal view of the anterior end of the same specimen to show the prostomium, nuchal grooves, peristomium, and the first and second chætigerous segments, the latter bearing the first pair of gills. × 22.

Fig. 4.—The first gill of the specimen drawn in Fig. 1, along with a portion of the second chætigerous and succeeding annuli. Only the dorsal half of the gill is fully drawn; the ventral half is cut down to the bases of the two main branches. × 16.

Fig. 5.—A portion of the tenth chætigerous segment of the left side of the same specimen. Note the four annuli, the skin of which is subdivided into squarish elevations, the epidermal papillæ, the prominent lips of the setal sacs, the sense organ, and the nephridiopore (*N. O.*). × 16.

Fig. 6.—Ventral view of the posterior end of a specimen 13 mm. long, showing the pygidium or tail segment (*T.*), the newly formed body segments

anterior to this, and the cirri and secondary annulation of the older segments. The dorsal cirri are formed earlier than, and are larger than, the ventral cirri. The slightly raised area in the median line marks the position of the nerve-cord (which is non-ganglionated; the appearance of ganglionation presented by the specimen is due to the contraction of the body-wall). The anal cirri on one side have been cut off close to their bases. × 80.

Fig. 7.—Posterior aspect of a parapodium from the specimen drawn on the preceding figure. The parapodium was situated three segments in front of the oldest segment shown in Fig. 6. × 80.

Fig. 8.—The thirty-fifth parapodium of the specimen drawn in Fig. 1. The dark area (*Cirr. Gl.*) in each cirrus marks the position of the gland, which is seen by transparency through the epidermis of the cirrus. The sense organ is situated in and hidden by the small papilla seen between the bases of the notopodium and neuropodium. × 20.

Fig. 9.—The thirtieth parapodium of a specimen 14 mm. long, which was stained, cleared, and compressed in order to bring the muscles into the same plane as the other structures. The typical parts of a parapodium are shown —the dorsal and ventral cirri with their large gland-cells, the notopodium and neuropodium each with simple and furcate setæ, the sense organ and its retractor muscle, and the protractor muscles of the setal sacs. × 80.

Fig. 10.—Five gland-cells from one of the glands shown in the preceding figure. The pointed ends of these unicellular glands pierce the epidermis and open on the free surface. Each gland contains a large number of rod-like bodies. The nucleus of one of the cells is seen near its inner end. × 500.

Fig. 11.—Rods from the parapodial glands of the specimen shown in Fig. 1. Compare their size with that of the rods from a much younger specimen shown in the preceding figure. × 500.

Fig. 12.—A thick longitudinal section (25 μ thick) through an annulus of a specimen 14 mm. long, to show the unicellular glands of the skin, the circular and longitudinal muscles, and the annular nerves. *N. Chæt. Annul.* is a section of the nerve of the chætigerous annulus, which is larger than the nerve (*N. Annul.*) supplying the following annulus. × 270.

Fig. 13.—Dorsal view of the anterior end of a specimen of Eumenia crassa 29 mm. long, to show the prostomium, nuchal grooves, peristomium, and the first and second chætigerous segments, the latter bearing two small gills. × 9.

PLATE 14.

All the figures relate to Scalibregma inflatum.

Fig. 14.—Dissection of the anterior portion of the specimen drawn in Fig. 1, to show the general arrangement of the internal organs. The principal features shown are the four anterior diaphragms, the alimentary canal, and

œsophageal pouches, the vascular system and the nephridia (see also p. 254). The neuropodia and the afferent nephridial vessels are drawn only in the five segments immediately behind the last diaphragm, and the oblique muscles, which are present in all the chætigerous segments, are shown only in the last three segments drawn on the right side. The incomplete ventral mesentery, which binds the ventral wall of the stomach to the body-wall near the nerve-cord, is omitted. In order to prevent confusion, the course of the blood-vessels running on the left side of the body-wall is not fully shown behind segment 15. Some of the folds in the wall of the stomach are probably artificial. × 3.

Fig. 15.—A section passing almost horizontally through the head, prostomium, and first and second chætigerous somites, to show the brain with its anterior and posterior cornua lying in the prostomium, the nuchal organ, and its retractor muscle, etc. The ganglion cells which cover the brain are in close relation to the epithelium of the prostomium and of the nuchal organ. The section has not passed through the whole length of the anterior lobe of the brain, only its posterior portion is seen here. × 80.

Fig. 16.—Transverse section of the specimen shown in Fig. 1 passing through the twenty-fifth chætigerous annulus. The various parts of the parapodium and the sense organ are seen on the right (cf. Fig. 9). In the ventral divisions of the cœlom sections of the small tubular nephridia are seen; on the left a nephrostome has been cut through. At the base of the ventral groove in the intestine are two cords (*Int. N.*) seen in section. From their structure and general appearance they appear to be nervous. × 24.

Fig. 17.—Transverse section of the nerve-cord and surrounding structures from a specimen 14 mm. long. The fibrous part of the cord is partially subdivided by a neuroglial ingrowth. The ganglion cells are situated chiefly on the ventral side of the cord. The origin of a spinal nerve is seen on the right. Note also the nuclei of the longitudinal muscle-fibres. × 200.

Fig. 18.—A nephridium from the twentieth segment of the specimen seen in Fig. 1. The lumen of the nephridium is shown, as seen in optical section Attached to the nephrostome is the rudimentary septum bearing the genital cells. × 40.

Fig. 19.—Section of a nephrostome from the thirtieth segment of the same specimen. The dorsal lip is seen on the right, it is more strongly ciliated than the ventral lip. On the left is the septum bearing the genital cells. The blood-vessel lies between the cœlomic and the ciliated epithelium. × 250.

Fig. 20.—Section of a small nephridium at the junction of the excretory and terminal portions. The latter is on the right; its cells are cubical or even slightly flattened, while those of the excretory portion are columnar, and have vacuoles which in life probably contained excretory products. × 250.

Fig. 21.—A very small nephridium drawn in situ on the body-wall after the preparation had been stained and cleared. Note the septum accompanying the blood-vessel to the nephrostome. On the right of the nephrostome the nuclei of genital cells are seen. The excretory part of the nephridium—the loop—is at this stage very short. The nephridium is closely invested by a delicate cœlomic epithelium, the nuclei of which are seen at intervals. × 300.

Fig. 22.—Section of an ovum from a specimen 35 mm. long. The peripheral layer of protoplasm is almost free from yolk granules. × 150.

Fig. 23.—Section of a portion of the wall of the œsophageal pouches, to show the blood-sinus enclosed between two epithelial lamellæ. × 50.

Fig. 24.—Some of the cells of the wall, showing the cavities in which the granules of secretion are usually found. They have been dissolved from these cells leaving the cavities empty. × 300.

PLATE 15.

Fig. 25.—Two furcate setæ. A in full view; B in profile. The portion shown in the figure represents only the distal twelfth of each seta. × 800.

Fig. 26.—The tip of a capillary seta, to show the hair-like processes. The portion figured is only $\frac{1}{25}$ of the seta. × 800.

Fig. 27.—Section of a very young sense organ. The organ was situated ·25 mm. from the posterior end of a specimen 13 mm. long. There was only one chætigerous segment behind this one, and in both these segments the notopodial setæ only were formed, as shown. This is the earliest recognisable sense organ in the specimen. Note the minute rods (*R.*), the three ganglion cells, and the nuclei of the multipolar ganglion cells (*N. M. C.*). For further explanation see p. 274. × 600.

Fig. 28.—A rather thick longitudinal section of a sense organ about 3 mm. from the posterior end of the specimen 13 mm. long. The sense-hairs are now seen. This sense organ contains an exceptional number of large ganglion cells. × 500.

Fig. 29.—Transverse section of a parapodium of the same specimen situated 2 mm. from the posterior end. The retractor muscle of the sense organ is seen. See also p. 272. × 500.

Fig. 30.—Transverse section of an old sense organ from the twenty-fifth segment of a specimen 35 mm. long. The fibrous part of the organ is proportionately larger. The ganglion cells are situated nearer to the rods in this organ than in most others. Note the stout nerve supplying the organ entering on the ventral side, and turning almost through a right angle into the axis of the organ. See p. 274. × 200.

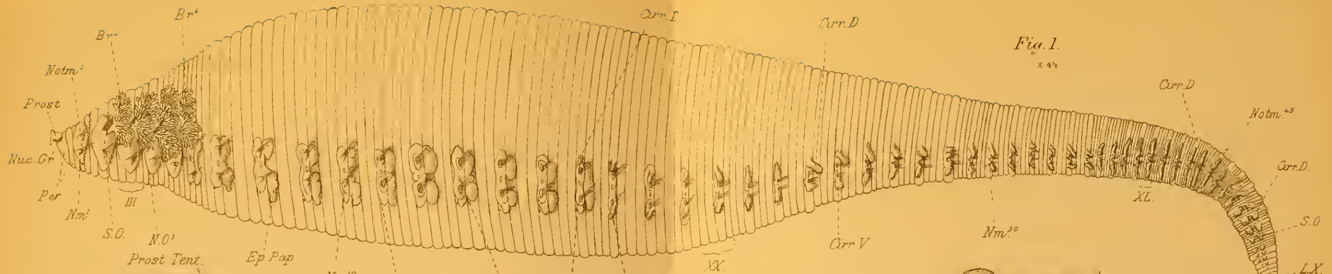

Fig. 1.
× 4½

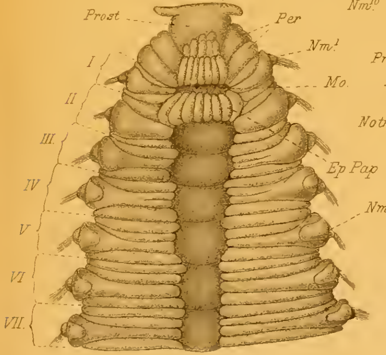

Fig. 2.
× 22

Fig. 3.
× 22

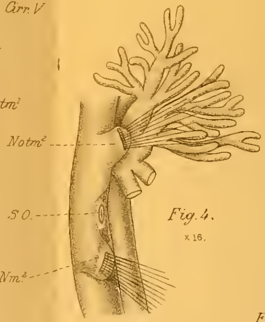

Fig. 4.
× 16.

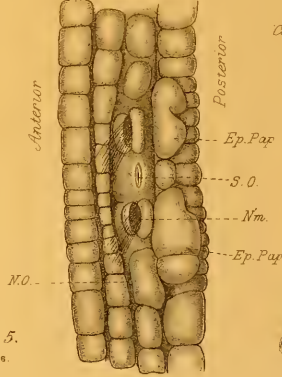

Fig. 5.
× 16.

Fig. 10.
× 500.

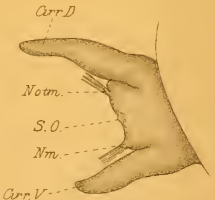

Fig. 7.
× 80

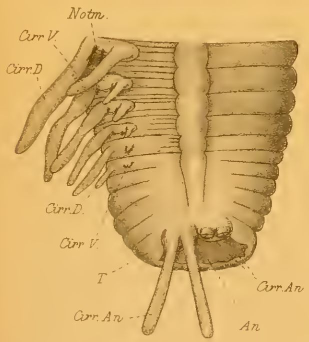

Fig. 6.
× 60

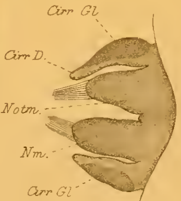

Fig. 8.
× 20

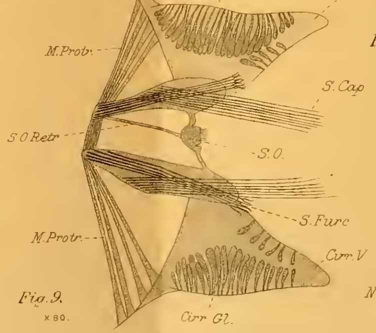

Fig. 9.
× 80.

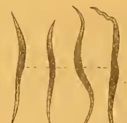

Fig. 11.
× 500.

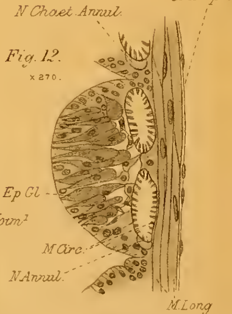

Fig. 12.
× 270.

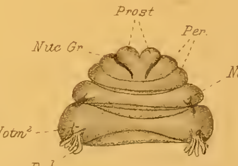

Fig. 13.
× 9.

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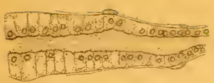

Fig. 20.
x 250

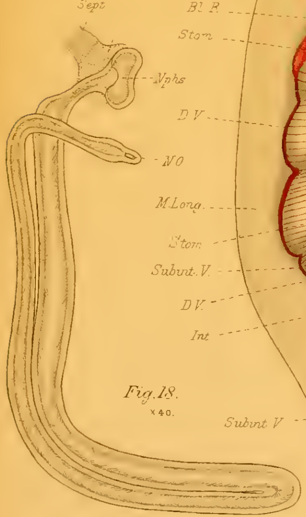

Fig. 18.
x 40.

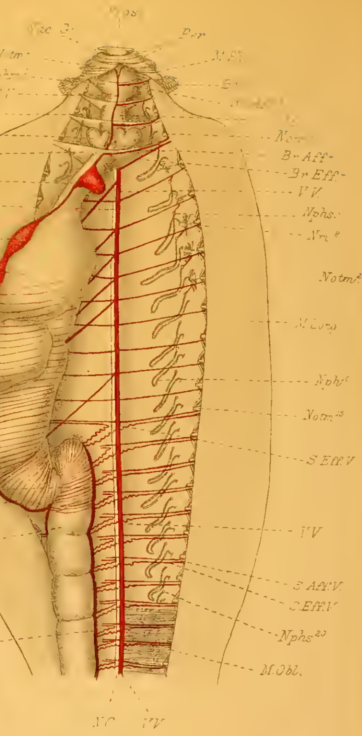

Fig. 14.
x 3

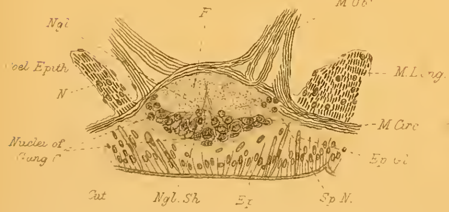

Fig. 17.
x 200

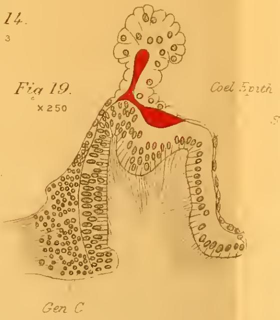

Fig 19.
x 250

Fig 15.
x 80

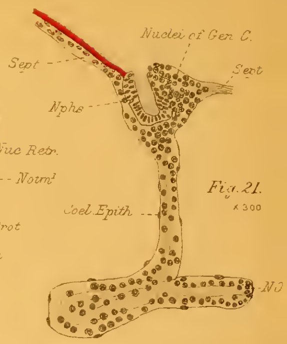

Fig. 21.
x 300

Fig. 22.
x 150.

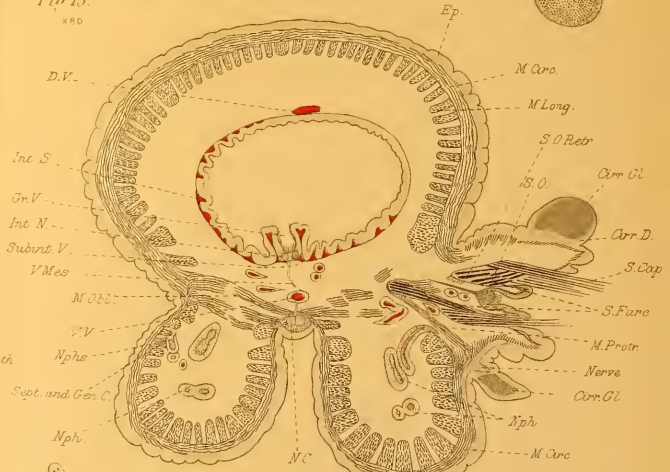

Fig 16.
x 24.

Fig. 23.
x 50

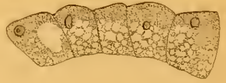

Fig. 24.
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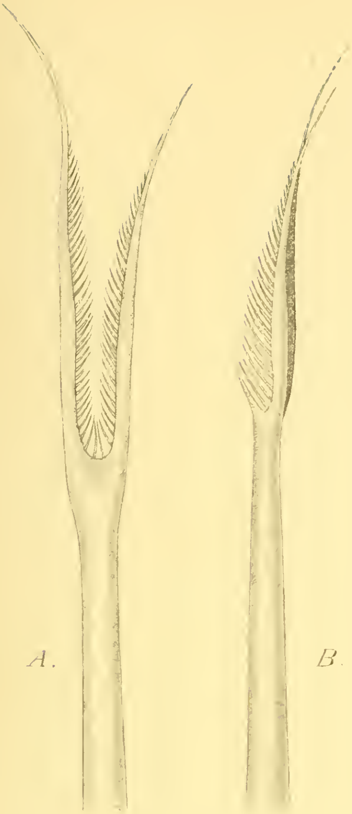

Fig. 25.
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Fig. 26.
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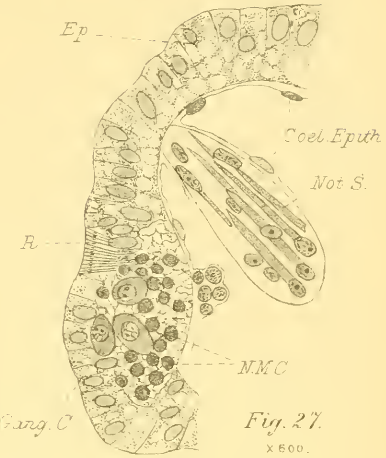

Fig. 27.
× 600.

Fig. 30.
× 200

Fig. 28.
× 500

Fig. 29.
× 500

On the Pelvic Girdle and Fin of Eusthenopteron.

By

Edwin S. Goodrich, M.A.,
Fellow of Merton College, Oxford.

With Plate 16.

Through the kindness of Mr. A. Smith Woodward,[1] I have recently had the opportunity of looking through the fossil fish acquired by the British Museum since the Catalogue was published. Amongst these was found a specimen of Eusthenopteron foordi, Whit., showing the endoskeleton of the pelvic girdle and fin, of which I here give a description. The interest attaching to this fossil is considerable, since, of all the numerous extinct fish usually included in the group "Crossopterygii," it is the first and only one in which the parts of the skeleton of the pelvic girdle and its fin have been found complete and in their natural relations.[2]

The specimen (P. 6794) of which both the slab and the counterslab have been preserved, comes from the Upper Devonian of Canada. In it can be made out the skeleton of the pelvic girdle and fin of the right side, in a fairly complete and well-preserved condition, as represented in Pl. 16, fig. 1, natural size.

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[1] To Mr. Smith Woodward I am also indebted for constant help when working in his Department.

[2] The skeleton of the pelvic fin of Megalichthys has to some extent been made known by Cope, Miall, and Wellburn (**2**, **5**, and **9**), and the essential structure of that of Eusthenopteron has been briefly described by Traquair (**7**).

It will be seen at once that the skeleton of this fin closely resembles that of the pectoral fin of the same species already described and figured by Whiteaves and Smith Woodward (**10** and **12**).[1] In the pelvic fin (figs. 1 and F) we find an axis consisting of three segments or mesomeres, and three pre-axial endo-skeletal rays or parameres. Of these the first two and largest are borne by the first and second mesomeres respectively, whilst the last is in a rudimentary condition, being represented by a small rounded piece at the distal end of the outer branch of the slightly bifurcated terminal mesomere. A similar semi-lunar piece fits on to the axial branch of the third mesomere. The whole skeleton of the fin is formed, then, of an axis consisting of three large segments, and a small terminal piece, and of two well-

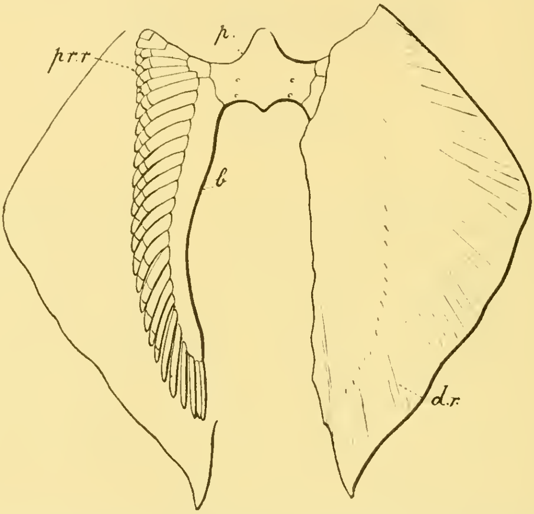

FIG. A.—Ventral view of the pelvic girdle and fins of Heptanchus cinereus, Gm.; in this and the succeeding figures the complete skeleton is exposed on one side only. For the lettering see the Explanation of Plate 16.

---

[1] This resemblance was pointed out by Traquair (7), who writes "A very similar arrangement is found in the pelvic fin . . . ; here I find at least two mesomeres, each bearing a paramere, there being, I think, also a probability of the presence of a third or distal mesomere."

defined pre-axial rays, and probably a vestigial third ray.

The chief difference between the pectoral and the pelvic fin is, that whereas in the former there are post-axial expansions on the first, third, and fourth axial segments, in the pelvic fin no such post-axial process is visible in our specimen (figs. 1 and 2).

The pelvic fin projects from the body as a free lobe of considerable size, and is covered with scales similar to those on the trunk. Round this lobe the extensive web of the fin is supported by jointed bony dermal fin rays. On the pre-axial side the dermal rays are, as usual, stronger than on the post-axial side. The pre-axial edge of the fin is straighter and considerably longer than the post-axial, so that the fin is not symmetrical about its skeletal axis either internally or externally.

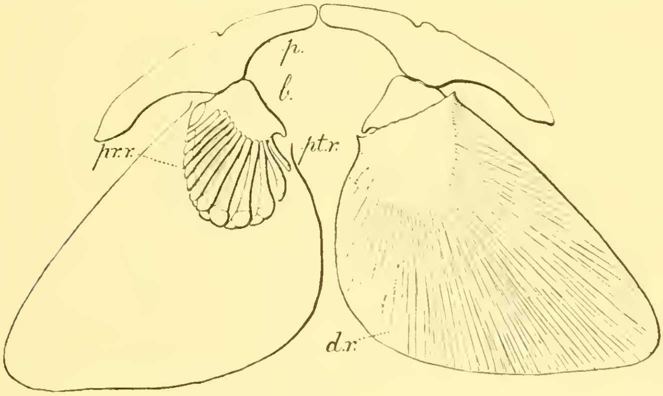

Fig. B.—Ventral view of the pelvic girdle and fins of Chimæra monstrosa, L.

The pelvic girdle is represented on the right side by a somewhat triangular elongated bone. It is pointed in front, and widens out behind into a broad plate. The outer edge is almost straight, whilst the inner edge is sharply curved where the bone widens out. To the posterior edge is articulated the axis of the pelvic fin. The whole girdle consists of two such bones, which in the living animal no doubt lay parallel to the ventral surface, with their sharp ends pointing forwards and converging towards the middle line. The posterior expansions would also extend towards the mid-ventral line (fig. F).

The structure of the skeleton of the pelvic girdle and fin is of great importance as a taxonomic character. But before attempting to discuss the value of these organs in deciding the position occupied by Eusthenopteron in the scheme of classification, it will be well to briefly compare the various types of pelvic supports in the Fish series.

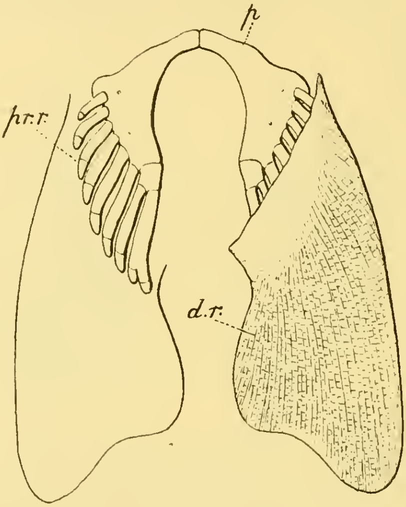

Fig. C.—Ventral view of the pelvic girdle and fins of Acipenser sturio, L.

Amongst the Elasmobranchs we find embedded in the body-wall a median-ventral cartilaginous plate, to which the pelvic fins are attached by a moveable joint (Fig. A). In the Holocephali there is on each side an elongated cartilage supporting the pelvic fin; these cartilages are joined together in the middle line by a ligament (Fig. B). A somewhat similar, but shorter, pair of cartilages is found in the extinct Pleuracanthidæ (Fig. D). A specimen in the Oxford Museum (Fig. E) shows particularly well their ligamentous union in the middle line. Coming now to the Teleostomi, we find in the Chondrostei somewhat ill-defined, more or less triangular, cartilaginous plates stretching from the base of the pelvic fins towards the middle line (Fig. C). Amia lepidosteus and all the "Teleostei," in fact all the Actinopterygii, possess paired bony ventral plates supporting the pelvic fins. These plates may be joined together in front by a median cartilage, as in Gadus (Fig. J), or they may be merely united by ligament (Figs. H, I). In the Dipnoi, on the contrary, the pelvic support is represented by a median cartilage with two diverging branches, to which are articulated the fins (Fig. K). Of the so-called Crossopterygii,

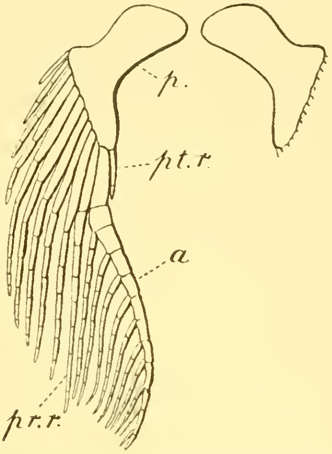

Fig. D.—Ventral view of the pelvic girdle and fin of a female Pleuracanthus Oelbergensis, Fr. (from Fritsch).

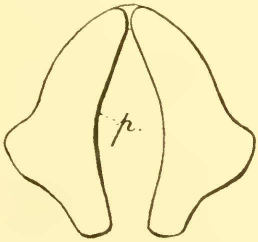

Fig. E.—Ventral view of the pelvic girdle of Pleuracanthus Gandryi, Brogn.

the only forms in which the pelvic girdles are thoroughly well known are the Cœlacanthidæ and the Polypteridæ.[1] In both these families the pelvic bones closely resemble those of the Actinopterygii (Figs. G, L).

Concerning the morphology of these pelvic supports there is considerable confusion. Whilst the older anatomists believed them, I think quite rightly, to be homologous, and the representatives of the pelvic girdle of other fish, some modern authors would have us believe that they are of quite different nature in the various orders of Pisces. They hold that whilst, for instance, in the Selachii, Holocephali, and Dipnoi, a true pelvic girdle is present, the supports in the Crossopterygii and Actinopterygii are, on the contrary, derived from the fin skeleton itself.

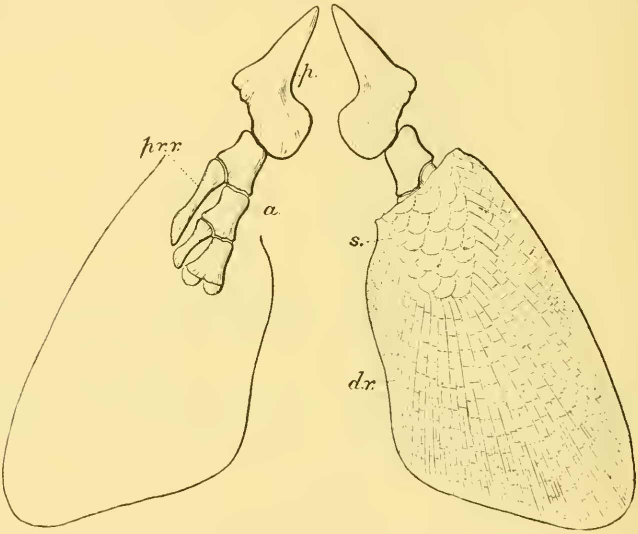

Fig. F.—Ventral view of the pelvic girdle and fins of Eusthenopteron Foordi, Whit., restored.

Let us see what difficulties such views lead us into. Whether we hold, with the advocates of the fin-fold theory,

---

[1] Paired bony plates seem to have been present in Megalichthys (**5**, **9**), and Specimens 21,547 and P. 6513 of the British Museum Collection show traces of similar structures in Osteolepis and Glyptolepis.

that the pelvic girdle originated as an ingrowth of the base of the primitive fin skeleton, or whether, following Gegenbaur, we consider it to have been derived from a gill arch, it will be admitted that the girdle was primarily differentiated as a right and a left support and fulcrum for the fin, and as a point of attachment for the muscles whereby the fin is moved. The girdle plate must have been from the first embedded in the ventral body-wall from which sprang the free lobe of the pelvic fin.

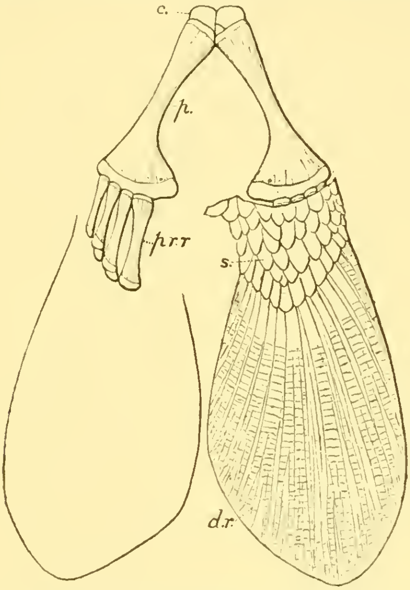

Fig. G.—Ventral view of the pelvic girdle and fins of Polypterus bichir, Geoffr.

Such appears to have been the structure of the paired pelvic girdle of the Pleuracanthidæ (Fritsch [3] and Figs. D and E), and such it is essentially at the present day in the Holocephali (Fig. B). The development of the pelvic girdle in the Selachii (Balfour [1], Mollier [6]) warrants the view that the median cartilage there found has been formed by the fusion of two originally separate halves. Presumably in this way has also originated the median cartilage of the Dipnoi.

It is not until we reach the Teleostomes that difficulties arise. Davidoff[1] held that the girdle proper is represented in the Bony Ganoids and Teleosts by the cartilage at the anterior ends of the long pelvic bones, which themselves would be homologous with the metapterygium (basipterygium) of the Selachian fin.

Weidersheim (**11**), considering the bones as metapterygial, believes the girdle to be appearing in Polypterus as small paired or median cartilages (Fig. G) at the tip of the pelvic bones. A somewhat similar little piece of cartilage, occasionally found at the anterior extremity of the pelvic supports of the Chondrostei, is supposed to have the same significance. Rautenfeld (**8**), on the other hand, compares the basal support in the Ganoids to the propterygium of the Selachii. Wiedersheim's view, that the minute paired or median

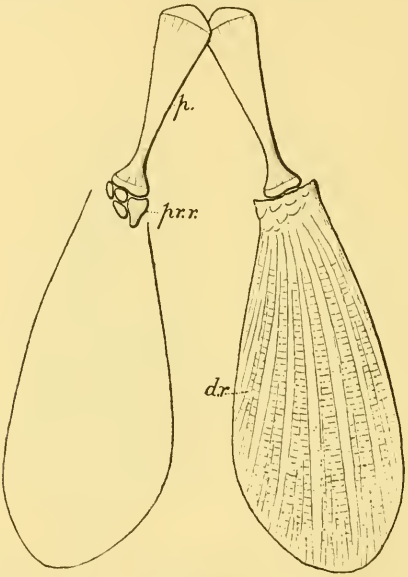

Fig. H.—Ventral view of the pelvic girdle and fins of Amia calva, Bon. (Partly from Davidoff.)

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[1] Davidoff, "Beiträge z. vergl. Anat. der Hinteren Gliedmasse der Fische." 'Morph. Jahrb..' vols. v, vi, and ix.

cartilages often found in front of basal supports, represent the first origin of the girdle, has not met with much favour for many reasons. More especially the obvious objection may be urged against it, that the pelvic girdle is already fully developed in more primitive forms (Elasmobranchs). Gegenbaur (**4**), whilst adopting the theory of the homology of the basal supports with the metapterygium of the Selachian fin, considers that the small anterior cartilages of the Ganoids represent the last vestiges of the pelvic girdle, which has undergone degeneration, and may have entirely disappeared in other Teleostomes.

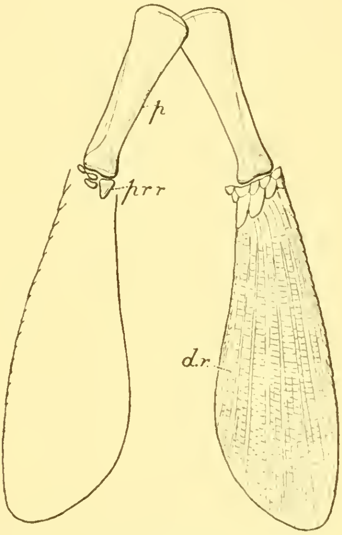

Fig. I.—Ventral view of the pelvic girdle and fins of Lepidosteus osseus, L. (Partly from Davidoff.)

Now Gegenbaur's view seems to be no less open to objection than Wiedersheim's. For if we are to believe that the girdle has disappeared and been functionally replaced by bones derived from an ingrowth of the already differentiated fin skeleton, we may well ask, what plausible reason can be given for the substitution in the place of the girdle supports of these new structures of very similar shape, and of perhaps even larger size? During this important change what has become of the muscles attached to the girdle for the moving of the fin? Have they disappeared also, and been replaced by others, or have they shifted their base of attachment on to the basals? What evidence is there that the moveable joint, where the base of the fin skeleton articulates with the girdle, firmly embedded in the body-wall, has not always been where it now is, but has been carried forwards at the tip of the basal bones and lost its primitive function? What evidence is there that this primary articulation between the moveable fin skeleton and the fixed pelvic girdle, has been replaced by a new joint between two different regions of the fin skeleton itself?

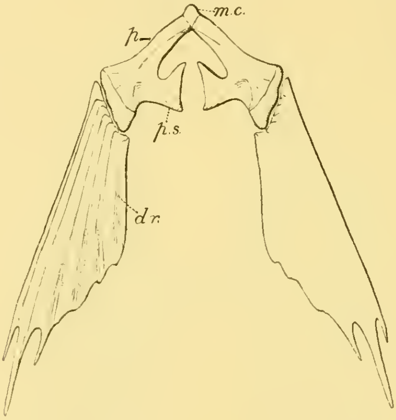

Fig. J.—Ventral view of the pelvic girdle and fins of Gadus morrhua, L.

Moreover, is it credible that such a fundamental alteration in the relations of the internal skeleton should have taken place without a corresponding change in external shape? Here the evidence afforded by the structure of Eusthenopteron may be called in. On the one hand there seems to be no reasonable doubt that the pelvic bones of this fish are homologous with those (so-called basals) of Polypterus, Cœlacanthus, or Amia (Figs. G, L, and H). On the other hand, it will, I think, be allowed that the moveable joint whereby the segmented axis of the fin of Eusthenopteron articulates with the pelvic bone is strictly homologous with the corresponding articulation at the base of the pelvic fin of Ceratodus or Pleuracanthus.[1] We are, then, inevitably led to the conclusion that the pelvic supports, whether paired or unpaired, are homologous throughout the fish series. These structures are similarly situated, fulfil the same functions, and are, as far as we know, developed in the same way in all fish. In

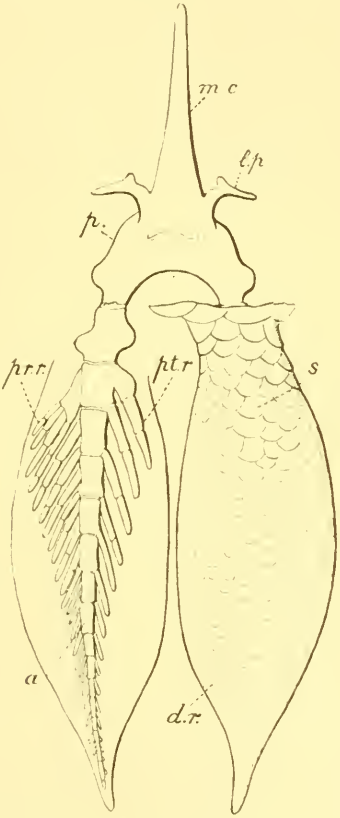

Fig. K.—Ventral view of the pelvic girdle and fins of Ceratodus Forsteri, Kr. (Partly from Davidoff.)

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[1] The persistence of the same articulation between the girdle and fin skeleton is obvious in the case of the pectoral limb of fishes.

some cases, however, as in Dipnoi and Teleosts, they are well differentiated; in other cases, as in the Chondostrei, they are ill-defined, and probably in a more or less degenerate condition, not clearly marked off from the true fin skeleton.

To conclude, we may briefly mention the evidence afforded by the structure of the skeleton of the pelvic fin as to the systematic position of Eusthenopteron. Unfortunately we know hardly anything about the structure of the fin skeleton of other extinct "Crossopterygii." But from our knowledge of the Dipnoi, it may be inferred with some degree of certainty that the skeleton of the elongated lobed fins of such forms as Glyptolepis and Osteolepis was built on the biserial archipterygial plan (distichopterygia). It is therefore of considerable interest to note that although in the shape of the outline of the fin-web, and in the disposition and structure of the dermal rays, the pelvic limb of Eusthenopteron approximates to that of the more highly specialised Teleostomes (Actinopterygii); yet its internal skeleton is probably to be interpreted as a modification of the biserial archipterygium, with a distinct axis, in which the post-axial endo-skeletal rays have been lost. Further, the skeleton of the pectoral and of the pelvic fin of Eusthenopteron still exhibit that close resemblance to each other which is so marked a characteristic of the Dipnoan fins, and presumably also of the more primitive forms from which they have been derived.

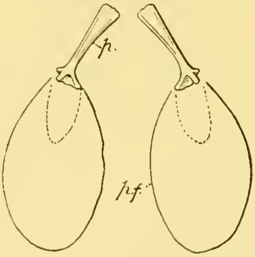

FIG. L.—Ventral view of the pelvic girdle and fins of Holophagus gulo, Huxley.

In contrast to this we find in Polypterus and the Actinopterygii a great and increasing modification in structure of the fins. All trace of an axis is soon lost in the pelvic limb, whilst at the same time the pelvic girdle bones in these fish and the Cœlacanthidæ, assume that peculiar elongated and flattened shape, widening out in front, which is so characteristic.

Finally it may be pointed out that, whilst Eusthenopteron is undoubtedly closely allied to the Rhizodontidæ, judging from the skeleton of the pelvic fin, it appears to be very far removed from Polypterus, which probably belongs to the Actinopterygian line of development.

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EXPLANATION OF PLATE 16,

Illustrating Mr. Edwin S. Goodrich's paper "On the Pelvic Girdle and Fin of Eusthenopteron."

List of Reference Letters in Plate 16 and Text-figures A—L.

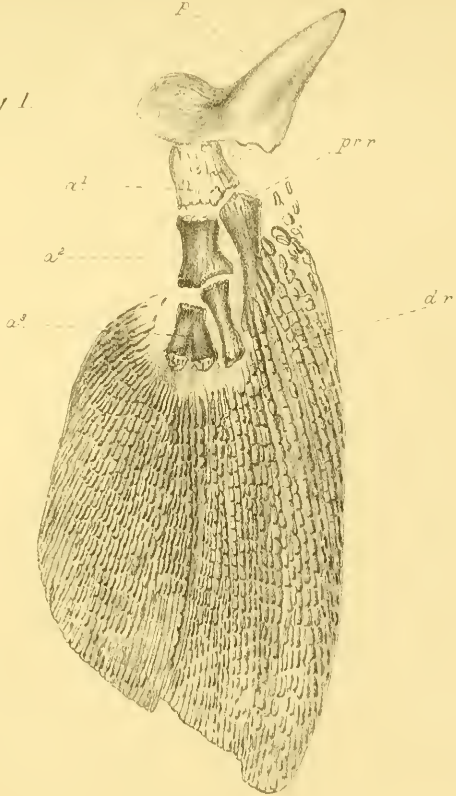
a. Axial mesomere. *b.* Basipterygium; basal mesomere in fig. 2. *c.* Cartilage. *d.r.* Dermal fin ray. *l.p.* Lateral process. *m.c.* Median cartilage. *p.* Pelvic cartilage. *p.f.* Pelvic fin. *pr.r.* Preaxial endoskeletal ray. *p.s.* Posterior expansion. *pt.r.* Postaxial endoskeletal ray. *s.* Scale. *x.* Postaxial process.

Fig. 1.—Outer view of the right half of the pelvic girdle and of the right fin of Eusthenopteron Foordi (Brit. Museum, No. P. 6794).

Fig. 2.—Outer view of the left pectoral fin of Eusthenopteron Foordi (Brit. Museum, 6796), copied from A. Smith Woodward.

Fig. 2.

Fig 1.



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Dendrocometes paradoxus.

Part I.—Conjugation.

By

Sydney J. Hickson, M.A., D.Sc., F.R.S.,
Beyer Professor of Zoology in the Owens College, Manchester

Assisted by

Mr. J. T. Wadsworth.

With Plates 17 and 18.

INTRODUCTION.

THERE is no species of the class Acinetaria that can be obtained with greater facility at all times of the year than Dendrocometes paradoxus (Stein). This is due to the fact that it is found with unfailing regularity on the gills of our commonest fresh-water Crustacean, Gammarus pulex.

In addition to the fact that it is readily obtained, however, it presents us with the further advantage of being attached to a soft and tolerably transparent gill, which can be easily seen with the naked eye, and manipulated without difficulty on the slide and in the paraffin bath. The difficulties that have usually to be overcome in preserving and staining the Infusoria whole or in sections are, in this form, largely obviated, and it is not very difficult, after the preliminary examination of the specimens attached to any one gill, to imbed and cut them into a series of sections in any plane that may be desired. Possessing these advantages, it was obvious that a careful examination of the changes of the nuclei during conjugation and gemmation might yield results of interest and importance.

I have had preparations of Dendrocometes under observation for a considerable number of years, but it was not until 1899 that I obtained specimens which clearly showed the mitotic figures of the division of the micronuclei, and then I determined to investigate the matter with greater thoroughness. I may explain that during the last two years I have entrusted the mounting of the preparations, as well as the staining and cutting of the sections, to Mr. J. T. Wadsworth, and that he has saved me an immense amount of time and labour in pointing out to me the slides that exhibited interesting features, and in keeping a catalogue of the preparations. The discoveries therefore that are here recorded were, in the first instance, made by him, and I have to acknowledge here his unfailing assistance and perseverance in the investigation.

The structure of Dendrocometes has been investigated by Bütschli (**1**), Wrzesniewski (**27**), Plate (**21**), Maupas (**19**), Schneider (**24**), and Sand (**23**); but, notwithstanding their excellent work, many points of interest and importance remain to be illustrated and described.

Dendrocometes paradoxus is found attached to the gills of Gammarus at all times of the year, but in the summer months there are usually fewer specimens on each gill than in the spring and autumn. We have found that by keeping about twelve or fourteen Gammarus in a shallow pie-dish containing an inch or two of water, with a little mud and waterweed at the bottom of it, the number of Dendrocometes on the gills increases, and that in a fortnight's time a considerable number of pairs may usually be found in a state of conjugation.

Dendrocometes appears to have a wide geographical distribution. I have found it myself on Gammarus at Oxford, Cambridge, in the neighbourhood of Manchester, and on specimens of Gammarus sent to me by Mr. Bolton from Birmingham. It was observed by Prof. Lankester on Gammarus in the ponds at Hampstead. On the continent of

Europe it also appears to be generally distributed. It certainly occurs in Belgium (Sand), France (Maupas), Germany (Butschli, Plate, etc.), Russia (Wrz.). It also occurs in North America (Bütschli). It is probable that the Dendrocometes which occur on the gills of Gammarus putaneus (Lachmann) may be a distinct species, but, apart from this, Dendrocometes only occurs on the gills of Gammarus pulex, although exceptionally a few specimens may be found attached to the hairs on the legs of the same host (Sand).

Dendrocometes paradoxus has a planoconvex-shaped body, and is provided with three, four, or five arms (Pl. 17, fig. 1). The morphology of these arms is a matter of some dispute, but it is not an unreasonable view to regard them as homologous with a bundle of Acinetarian tentacles. They capture, kill, and partially digest the prey in the same manner as the tentacles and suckers of other Acinetaria. The body contains a single large meganucleus, and a variable number, but usually three, micronuclei. There is a single large contractile vacuole. Reproduction is effected by an interesting process of internal gemmation, first described by Bütschli (**1**). The single planoconvex bud that is formed is frequently called the "embryo," but I think it is more appropriate to call it the "gemmula." It escapes from the parents without arms, but provided with a girdle of three bands of cilia, and swims away.

From time to time, or perhaps, under certain conditions only, nearly the whole substance of an individual escapes from the pellicullar sheath and swims away from the gill in a form which cannot be readily distinguished from a gemmula.

With this brief introductory account of the structure and reproduction of the animal I pass on to the phenomena of conjugation, to which I have paid special attention.

Part I.—Conjugation.

The phenomena of conjugation in Dendrocometes may be briefly stated as follows :

Two individuals in proximity on a gill of Gammarus send out simultaneously blunt lobe-like processes, which may be called the conjugative processes. These meet but do not completely fuse, a distinct membrane delimiting the process of each individual throughout the conjugation. This membrane does not prevent the fusion of the meganuclei nor of the conjugative micronuclei in the latter stages, nor does it prevent a certain amount of mixture of the cytoplasm of the conjugating individuals.

Stage A (Pl. 17, fig. 2).—In the initial stage one or both the meganuclei may exhibit pseudopodial processes indicating that they have some power of amœboid movement. The micronuclei are a little but sometimes very little larger than they were before conjugation. (In this respect, as in so many others, there is considerable variability. The reader will notice that the individuals drawn in fig. 1, in which the conjugative processes have not yet met the micronuclei, are actually larger than they are in the individuals drawn in fig. 2, which are actually conjugating.)

Stage B (fig. 3).—The micronuclei increase considerably in size during this stage, the chromatin being resolved into a delicate skein. The meganuclei also increase in size, become spindle-shaped, and show an arrangement of the chromatin into roughly parallel lines. From this stage onwards until Stage K (fig. 13) is reached, the meganuclei increase in size without showing any material change in structure; and as the interest of the phenomena now centres in the micronuclei, further reference to the behaviour of the meganuclei will be for the present omitted.

Stage C (figs. 4, 5).—When the micronuclei have reached their full size the chromatin collects in the form of numerous minute chromosomes in an equatorial plane. At the same time extremely delicate, faintly staining threads (linin threads) roughly parallel with one another, forming a tub-shaped spindle, make their appearance. Neither in this nor in any other stage of mitosis is there any sign of the presence of centrosomes or similar bodies. I have found it impossible to count the number of chromosomes with any degree of accuracy in this or in any other stage of division. The mode of division of the chromosomes is also very difficult to determine, but I have seen V-shaped appearances, Pl. 18, fig. 13, very similar to those figured by Prowazek (22) in Bursaria. I believe with him that these appearances point to longitudinal division.

The chromosomes separate into two parties, which travel to the opposite poles of the spindle (fig. 5), where they apparently fuse to form a solid irregular lump of chromatin. The spindle then elongates enormously, so that the two chromatin bodies are sometimes separated from each other by a distance equal to three fourths of the full diameter of the Dendrocometes. The spindle then becomes detached from the chromatin and dissolves in the cytoplasm (fig. 6). The stages in the division of the micronuclei are usually synchronous in the two individuals, but sometimes one set of figures is a little in advance of the other, as shown in fig. 5.

By this division six micronuclei are formed in those individuals which began the process with three.

Stage D (fig. 7).—One of the five micronuclei of each individual passes down the conjugative process to a position very close to the membrane, where it enlarges and again forms a mitotic figure. The other micronuclei degenerate and disappear.

The nuclei which are found close to the membrane give rise by their division to the germ nuclei, to use the term employed by Wilson (26). The division is always in a plane parallel with the membrane (fig. 8).

Stage E (fig. 9).—The germ nuclei take up such a position in contact with the membrane that each germ nucleus of an individual is exactly opposite one of the other individual. These nuclei consist of a clear vacuole containing a single coarse skein of chromatin. The spindle entirely disappears.

Stage F.—The germ nuclei then fuse in a manner shown in Pl. 17, fig. 10, and Pl. 18, fig. 12, giving rise to the cleavage nuclei of the two individuals.

Attention may here be directed to two important points of comparison with ciliate Infusoria. The difference between the migratory or male germ nucleus and the stationary or female germ nucleus is in Dendrocometes reduced to a minimum. It is possible that in all cases one germ nucleus traverses the membrane and the other does not, so that the distinction remains, but the two nuclei are as nearly neuters as can be. In the second place, the fusion of the germ nuclei takes place during a resting and not in a mitotic state. According to the researches of Maupas, Hertwig, and others, the germ nuclei of the ciliate Infusoria fuse when in the form of spindles or mitotic figures.

Stage G (Pl. 17, fig. 11).—One of the cleavage nuclei passes into each of the conjugating individuals and prepares to divide again by mitosis. The early stages of this division probably occur very soon after the fusion of the germ nuclei, as the figures may be seen sometimes quite close to the membrane (cf. Pl. 18, fig. 13). This stage may be distinguished from Stage D, which it somewhat resembles, by the fact that the axes of the spindles are not parallel.

Stage H (Pl. 17, fig. 12).—The cleavage nucleus divides into two nuclei which take up a position in close proximity to the meganucleus.

Stage J (Pl. 18, fig. 1).—The nuclei formed by the division of the cleavage nucleus again divide, and almost immediately one of the four becomes a little larger than the other three.

Stage K (Pl. 17, fig. 13).—The largest of the four nuclei of the last stage becomes the new meganucleus, the other three the new micronuclei. There is some evidence to show that occasionally two of the three smaller nuclei again divide in this stage, giving rise to a condition in which there are six nuclei in all, as seen in the preparations from which Pl. 18, fig. 8, was drawn. In some cases, too, it appears that two nuclei enlarge to give rise to new meganuclear structures, as seen in Pl. 18, fig. 19. Variations of this kind at these stages have added very much to the ordinary difficulties of the investigation, but the establishment of the fact that variations of such an important character do occur is, in my opinion, a result of considerable interest.

At some time during the last three stages (H, J, K) the old meganucleus becomes very large, and is bent on itself in the form of a loop or horseshoe. One extremity of this figure passes into the conjugative process, and approaching the limiting membrane traverses it and fuses with the corresponding extremity of the meganucleus of the other individual. The exact phase at which this meganuclear conjugation takes place seems to vary considerably; all that can be said at present is that, so far as my experience goes, it usually occurs between Stages J and K. The number of cases of actual contact of meganuclei observed by Mr. Wadsworth and me is small, and this may be interpreted to mean either that the period of meganuclear conjugation is very short or that it does not always occur. Until some satisfactory method is invented of watching the nuclear phenomena of the conjugation of living Dendrocometes, it is impossible to prove that the meganuclear conjugation never fails. I am inclined to believe that it always occurs. Similarly I have no proof to offer of the length of time occupied by this process; but I am inclined to believe, on the circumstantial evidence at my disposal, that it is very brief.

Soon after the meganuclei have conjugated they separate and begin to degenerate.

The usual phenomena of nuclear change during conjugation in Dendrocometes may be represented by the following diagram, in which the circles above M represent the stages in the meganucleus, and the black dots above m, m, m, the stages in the history of the micronuclei. Conjugation of the meganuclei usually occurs in Stage J, as explained above, and in Stage K these bodies disintegrate.

In the following diagrams I have endeavoured to interpret certain phenomena which appear to be variations of the more usual stages. In Diagram B, which starts with Stage G, the important variation is that two of the micronuclei formed by the second division of the cleavage nucleus divide again (see p. 330).

In Diagram C we have the same variation as in Diagram B,

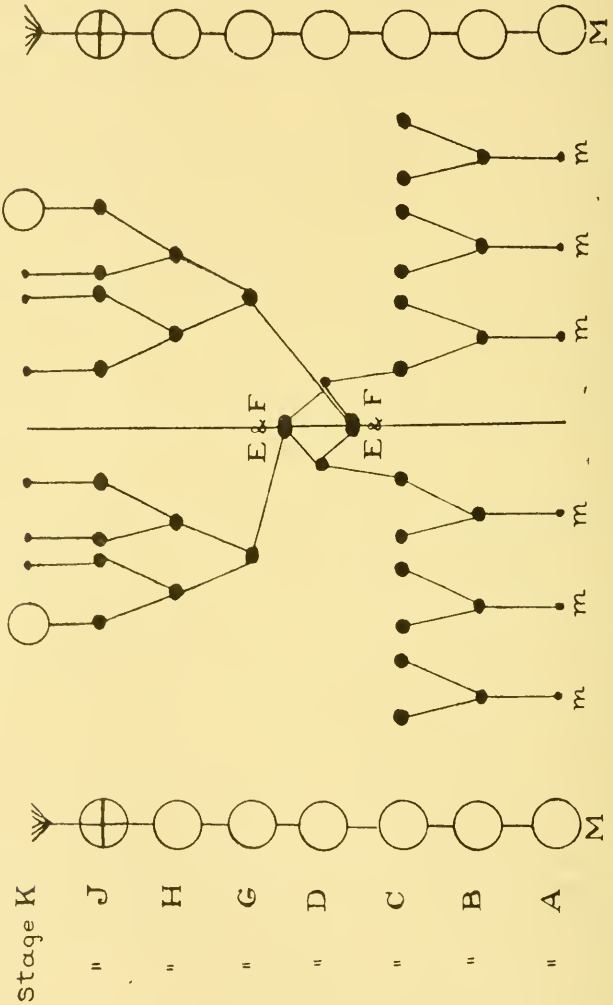


Diagram A.

with the additional peculiarity that two of the nuclei give rise to new meganuclei in Stage K, and I have added in Stage L the suggestion that these two new meganuclei fuse together to form the single meganucleus of the new individual.

The phenomenon of conjugation in the Acinetaria has been known for a great many years. It has been observed in several species of Acineta by Claparède and Lachmann (4), Fraipont, D'Udekem, Keppen (15), and others; in Metacineta (Claparède and Lachmann and Lieberkühn), in Podophrya, Tokophrya, Stylocometes, and in Dendrocometes. In Dendrocometes it was observed by Wrzesniowski (27), but more fully described by Plate (21).

Diagram B.

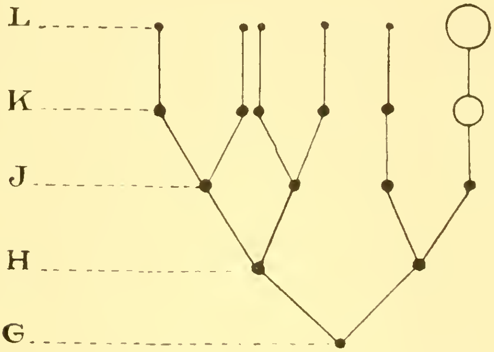
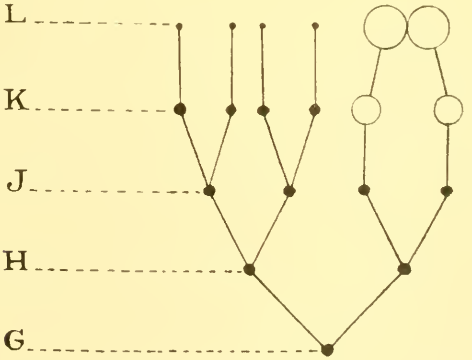


Diagram C.



As regards the external features very little can be added to Plate's description. As he observes, conjugation usually occurs when the gill of the host is unusually crowded with the Dendrocometes. The two conjugating individuals are in most cases similar in all essential respects. Occasionally, however, a difference may be observed between the two conjugates. Plate states that sometimes one of the individuals which is clearer than the other withdraws its tentacles during the process. Sand (23) says, "Chez Dendrocometes la conjugaison a lieu souvent entre un individu amaigre et un animalcule bien nourri." Mr. Wadsworth and I have frequently observed differences between the conjugating individuals, and Mr. Wadsworth has observed the retraction of the arms of certain individuals during conjugation.

Plate observed occasionally a conjugation of three individuals. This I am able to confirm, but the occurrence is so rare that no series of nuclear changes in them have been followed.

As Plate denied the existence of micronuclei, he failed to see any of the stages of their division and conjugation which are described in this paper. In one of his figures he shows the points of the meganuclei in the bases of the conjugative processes, but he did not observe the fusion of these bodies. He gives a good figure to illustrate the fragmentation of the meganucleus at the close of conjugation. In Schneider's (24) figures of Dendrocometes in the act of conjugating the meganuclei are shown to be approaching much more closely than in Plate's figure, and in the same author's figures of the closely allied genus Stylocometes the meganuclei are actually shown to be in contact. The statement made by Plate and Schneider that the new meganucleus is formed by a regeneration of the fragments of the old is not correct.

The mixing of the cytoplasm in the conjugative process is affirmed, and I believe correctly, by Plate, Sand, and others. I have myself observed a flow of protoplasm passing backwards and forwards through the membrane with each contraction of the vacuole for several hours in one pair, but the period during which this occurs is limited, and during the greater part of the forty-eight or more hours during which the pair remain in conjugation no interchange of particles can be seen.

An important feature of the conjugation of this genus is that the ordinary vital processes of the individuals are not materially affected during the act. The arms remain fully extended—they catch and swallow particles of food, which are digested in the ordinary course. The contractile vacuoles continue their pulsations for some time after the process has commenced.

Conjugative Processes.—These processes are formed specially for conjugative purposes in Dendrocometes. In development and in structure they differ from ordinary arms, and I do not consider that they are rightly considered to be homologous with arms. This view does not agree with that expressed by Bütschli (2), who, on the strength of the observations of A. Schneider on Stylocometes, regards them as rudimentary arms. In Stylocometes, according to that author, an arm of each of two neighbouring individuals becomes abnormally thick and elongated to form the conjugative process, and that it is a true arm is proved by the fact that it contains a canal. I have had no opportunity of examining Stylocometes, but I do not feel that Schneider's account of it is convincing. Until his account is confirmed, therefore, I must agree with Plate that the conjugative processes in Dendrocometes are not homologous with the arms.

Bütschli (2) states that in Dendrocometes one individual sends out a process which fuses with the body-wall of another, but that such an occurrence is rare. I have never seen such a phenomenon. In nearly all cases the conjugative processes begin and grow simultaneously, so that they are throughout approximately equal. In the preparation from which fig. 1 was drawn, the individual to the left has a decidedly longer process than the individual on the right, but such a difference as this is exceptional. It is impossible to state what stimulus there is that causes two individuals to begin the sexual proceeding. It may be that some excitement may be caused by the touching or brushing of the arms, but nothing of the kind has been observed. Judging from the development of the conjugative processes alone, which is all that we have to guide us in the initial stages, it seems probable that the sexual stimulus affects the two individuals simultaneously, and that there is no differentiation of sex.

The Micronuclei.

It is an interesting fact that, notwithstanding the careful and elaborate investigations made by several observers on the micronuclei of the Ciliata, there is at present no satisfactory account of these structures in the Acinetaria.

That micronuclei do occur in all Acinetaria is not yet proved, but nevertheless it is extremely probable that they are as constant a feature of the anatomy of this group of animals as they appear to be of the Ciliata.

In Bütschli's great work on the Infusoria (p. 1873) the following notes will be found on the subject. Bütschli himself in 1867 discovered a micronucleus in a species of Sphærophrya. Maupas proved with certainty the existence of a micronucleus in Tokophrya limbata, Acineta tuberosa, Podophrya fixa, and Podophrya cyclopum. He probably, but not with certainty, found them also in Acineta Jolyi, whilst certain bodies which may have been micronuclei were seen in Ephelota gemmipara. In Tokophrya limbata Möbius also proved the existence of micronuclei.

In a recent paper on the anatomy of a new species of Ephelota, Ishikawa writes with some uncertainty about the existence of micronuclei. The most satisfactory figures of the micronuclei of Acinetaria are those given by Keppen (**15**), but as his monograph is written in the Russian language I am unable to read it.

The authors of the 'Traité technique de Zoologie' (**5**) accept the view that there is a micronucleus in the body of the Acinetarian.

In the recently published monograph of the Acinetaria, however, Sand (**23**) denies the existence of true micronuclei. He believes, however, in the existence of a body lying close to the meganucleus, which he calls the "centrosome."

"Un corps un peu plus colorable que le noyau, creusée exprès pour le recevoir. . . . Quand ce corps est vu au centre du noyau, il paraît entouré d'une petite zone claire formée par le cytoplasma qui le sépare du noyau." He further states that no Acinetarian ever contains two of these bodies, and that it is absolutely homogeneous, both in a state of rest and of division. He has proved the existence of this body in sixteen species. I have very little doubt that the "centrosome" of Sand is not a "pseudo-micronucleus," but a true micronucleus. Maupas (**20**) says that his series of stages of the micronuclei of Podophrya fixa is incomplete, and he would probably himself admit that the figures he has published of them are not satisfactory. To account for his unsatisfactory results in the Acinetaria, Maupas ventures upon the statement that the micronuclei of these Infusoria are smaller than they are in the Ciliata, and stain very lightly. He adds that the study of the nuclear phenomena of the Acinetaria is beset with so many difficulties that he considers it to be "une des recherches les plus pénibles qu'un micrographe puisse entreprendre."

In Dendrocometes, however, these excuses cannot be put forward, as the micronuclei are even larger than they are in many Ciliata, and their affinities for certain stains are exceedingly powerful.

The presence of micronuclei in this genus has, nevertheless, been denied.

Plate (**21**) described a number of small bodies in the cytoplasm which, on account of their affinities for safranin, he called the "Tinktinkörnchen," but he denied the existence of "Nebenkerne." Maupas replied to Plate's paper by stating emphatically that micronuclei do occur in Dendrocometes and referring to Plate's own figure, pl. vi, fig. 17, as affording a convincing proof of it. Neither Butschli (**1**), Wrzesniowski (**27**), nor Schneider (**24**) appear to have observed them, and Sand (**23**) only mentions one "centrosome" as being present in this genus.

The number of micronuclei in Dendrocometes varies, but, as stated above, the usual number is three. In individuals that are neither conjugating nor preparing for gemmation it is sometimes difficult to count the micronuclei, as they are very small, and are difficult to distinguish from other bodies in the cytoplasm which have affinities for the stains that are used. However, a certain number of individuals with moderately clear cytoplasm can nearly always be found, and in these it is not difficult to recognise the micronuclei in sections stained by the iron-hæmatoxylin and iron-brazilin methods (**13**). There are sometimes two micronuclei, and sometimes four, and but rarely five. I do not believe that there are ever more than five or less than two.

In the state of rest the micronucleus consists of a small, irregular granule of chromatin, enclosed in a clear zone, which is invariably perfectly spherical in shape. There is no evidence of a definite membrane surrounding the clear zone. The zone is from 2—4 μ in diameter. It is very difficult to form an opinion of the nature of the substance composing the clear zone. When the nucleus is in a state of rest this zone resists the action of all the stains I have tried, and no lines nor granules of any kind or description can be seen in it. It is possible that it may be a mere artefact, due to the shrinkage of the chromatin during the process of preservation, but the regularity of its shape and its relation to the chromatin granule do not support this view. In my opinion it really represents the "achromatin" elements of the nucleus.

When preparing for division the micronuclei increase considerably in size, the solid granule of chromatin becoming converted into a coarse skein (Pl. 18, fig. 14 *m*). Later the skein breaks up into a much finer tangle (Pl. 17, fig. 3), which gradually fills up nearly the whole of the clear zone. In the next stage there is a differentiation of the skein into a number of lines, which stain very faintly in iron-hæmatoxylin, but a little more deeply with iron-brazilin, and a band of deeply staining rods and granules having the usual chromatin reactions. At this stage the micronucleus is frequently 10 μ in diameter (Pl. 17, figs. 4, 11, 12). The exact determination of the nature of the equatorial band of chromatin granules is a matter of considerable difficulty. With the highest powers of the microscope the granules or minute rods appear to be connected together in the manner shown in Pl. 18, fig. 13, but still I do not feel so far convinced of this connection as to deny the proposition that they are isolated chromosomes. With lower powers of the microscope they have every appearance of being a band of rod-shaped chromosomes (Pl. 17, fig. 12). Whatever the future may reveal regarding these bodies, I think it is clear that the chromosome elements are numerous,—too numerous, in fact, to count with any degree of accuracy.

The micronucleus next becomes somewhat oval in shape (Pl. 18, fig. 16), and the band divides into two bands. The faintly staining lines, which we may call the linin threads, are arranged in a roughly parallel manner forming a somewhat tub-shaped spindle. They do not come to a point at each end of the figure, and there is never any dot or granule that can suggest the presence of a centrosome. In the next stage (Pl. 18, fig. 17) the two bands of chromosomes have passed to the extremities of the figure, and soon become aggregated together to form a single irregular lump. In some cases there is a clear vacuole present at one of the poles (the right pole in Pl. 18, fig. 17), but I have seen it so rarely that I am at a loss to understand its meaning. In the next stage (Pl. 18, fig. 18) the spindle becomes very much more elongated, so that the whole figure may be 25—30 μ in length; the chromatin is in the form of a single spherical lump surrounded by a clear zone at the points o the spindle. The spindle next becomes detached from the new micronuclei (Pl. 17, fig. 6), and gradually dissolves in the cytoplasm. Throughout this mitosis the clear outline (membrana limitans ?) is never lost.

The mitosis of the micronuclei of Dendrocometes has considerable resemblance to the mitosis of the micronuclei of Paramœcium, as described by Hertwig (8), of Bursaria, as described by Prowazek (22), and of other Ciliata.

The Meganucleus.

In specimens of Dendrocometes that are neither conjugating nor preparing for gemmation, the meganucleus is usually a spherical body 0·02 mm. in diameter. It is not, however, constant in shape, many examples being found that are oval or even spindle-shaped.

It is usually situated in the centre of the animal's body, but it is often more or less excentric. On examination in section with an oil immersion lens, there may be seen a distinct meshwork of darkly staining lines which appear to support a series of minute rounded chromatin granules (Pl. 18, fig. 14). In many cases the lines connecting these granules cannot be easily seen when the appearance is as shown in Pl. 18, fig. 10. In the meshes of the darkly staining chromatin there is a homogeneous substance, which in many iron-hæmatoxylin preparations is quite colourless, but stains faintly yellow with brazilin.

Plate states that in the nucleus there are a number of nucleoli: "Bei einem Thier meiner Präparate ist der ganze Kern dicht erfüllt von solchen Binnenkörperchen deren jedes von einem hellen Hof umgeben ist." I have frequently seen in my preparations appearances similar to this described and figured by Plate, but my interpretation of them is different. In the first place I must state very emphatically that in my opinion there is never in the meganucleus of Dendrocometes any body or bodies which correspond with the nucleoli of Metazoan cells. The clear space round the "Binnenkörperchen" of Plate is in my opinion due entirely to the refraction of the light in passing through the preparation; and this opinion has been thoroughly tested by comparison of whole mount preparations such as Plate studied, with the thinnest sections of the meganucleus. My opinion is that the substance in the meshes of the chromatin is quite homogeneous. The periphery of the meganucleus is not in my opinion surrounded by a definite membrana limitans, notwithstanding Plate's statement that "ein Kernmembran ist deutlich erkennbar."

When the meganucleus is spherical or oval in shape and situated at the centre of the body, or in other words, when it is at rest, no definite membrana limitans can be seen (Pl. 18 fig. 10); but in the elongated and dividing meganuclei the chromatin network at the periphery is so arranged that a limiting membrane seems to surround the whole nucleus. The limiting membrane is not a definite and peculiar structure of the nucleus, but a temporary arrangement of the substance of the chromatin-bearing network at the periphery during the nuclear movements.

During gemmation the meganucleus undergoes a simple constriction, and is divided into two parts, one of which is retained by the parent, and the other by the young bud (Pl. 18, fig. 14). There is no reason to believe that these two parts are exactly equal in size. In many preparations the part retained by the bud is apparently smaller than that retained by the parent, but, as I have no means of measuring the capacity of these bodies, I cannot make any positive statement on the subject. There is, however, no arrangement of the chromatin in rods or bars during this division which would suggest equivalent chromatin division. Nor have I been able to find after very careful search anything of the nature of anterior fibres, centrosomes, asters, or other characteristic features of karyokinesis. There can be no doubt whatever that when the maganucleus divides the process is purely amitotic.

The Fusion of the Meganuclei during Conjugaion.—Whatever difficulties there may be in finding an explanation of the fact, there can be no doubt that the meganuclei do, during .conjugation, meet and become continuous. The statement of this fact was made in my preliminary communication (Hickson, 1900, **12**). I am not the first, however, to maintain that the meganuclei of the Infusoria fuse. In 1867 Stein made the following statement concerning the Acinetaria (Stein, 'Der Organismus,' vol. ii, p. 139), 1867:

"Die conjugation verläuft auch bei denjenigen Acineten, bei welchen sie bisher genauer studirt wurde, im Wesentlichen auf dieselbe Weise, wie bei der gleichartigen Conjugation der Vorticellen; es verschmelzen zuerst die Körper der beiden Acineten zu einem einzigen, und dann fliessen auch deren Nuclei in einem gemeinsamen Nucleus zusammen."

Bütschli (**2**) gives a figure (pl. lxxiii, 96) of two attached Vorticellids in which the meganuclei are in junction, but considers that this is doubtfully a case of conjugation. Schneider (**24**), in Stylocometes, figures the junction of the meganuclei in two individuals that are conjugating, but suggests that this also may be a case of fission. Bütschli may have been right as regards his Vorticellids, but such a method of fission as Schneider suggests for Stylocometes is extremely improbable. In a recent paper by Prowazek (**22**) a number of new and excellent figures are given of the nuclear phenomena during the conjugation of Bursaria, and it seems probable from these that in this ciliate Infusorian there is a junction of the meganuclei before they disintegrate. Unfortunately Prowazek's description is not very clear, and he does not attach much importance to the phenomenon.

In my preparations of Dendrocometes I have at least three cases in which the meganuclei actually touch, but a considerable number in which they approach one another very closely in the conjugative processes. That the junction is not merely casual contact, but actual organic connection, is proved by the preparation which is represented in Pl. 18, fig. 11. Here there is no sign of any boundary between the two nuclei, and the chromatin granules are fixed in such a manner as to suggest very forcibly that during life they were flowing from one side into the other. Apart from this evidence, however, attention may be called to the fact, which is evident not only from my own preparations (Pl. 18, figs. 6—8), but also from Schneider's figure of Stylocometes, that when the points of the meganuclei pass down the conjugative processes they converge to the same spot on the membrane. This shows, I think, that there is some force at work which is bringing them together. Sand refers to this in Stylocometes when he says, "Les deux noyaux s'approchent et se placent dans le bras dilaté vis-à-vis l'un de l'autre séparés par une couche de plasma." But he adds, "Pourquoi, dira-t-on, les noyaux vont-ils se placer dans le pont qui réunit les deux Stylocometes ou les deux Dendrocometes? C'est peut-être pour diriger les échanges et les mouvements qui ont lieu dans ce pont."

The organic junction of the two meganuclei lasts a very little while, I believe, and it is probably followed immediately by their disintegration. Each meganucleus breaks up into a number of irregular lumps, in each of which there are at first several granules of unaltered chromatin. A large piece of darkly staining substance is frequently present in these lumps, but in many of them the central parts are simply vacuolated (Pl. 18, figs. 15 and 19).

In the next stage the cytoplasm is filled with numberless vacuoles, granules, and lumps (Pl. 18, fig. 19) of endless forms, sizes, and colourable property. In such a preparation as that from which the figure was drawn, it is almost impossible to distinguish the various remnants of the old meganuclei from food bodies and micronuclei.

The mode of formation of the new meganucleus at the close of conjugation is of great importance and interest.

I must confess that in the earlier stages of this investigation I had some hesitation in believing that the new meganucleus is formed from a product of the segmentation nucleus. The descriptions, and more particularly the figures, of the nuclei of conjugation in Ciliata by Maupas (**20**), Hertwig (**8**), Hoyer (**14**), and others, although unanimous are not convincing. In none of these papers are the stages of the enlargement of the micronuclear element to form the characteristic meganuclear body very complete, and it seemed to me that there was just a possibility that these authorities were mistaken, and that the new meganucleus arises independently in the cytoplasm, or from one or more of the old meganuclear fragments. This hesitation in accepting the orthodox view was due to the fact, that in the earliest stages I had then found of the formation of the new meganucleus there was no chromatin in its centre. It was, moreover, very much larger than any of the other micronuclei, and the connection between it and a micronucleus could not be traced.

The subsequent discovery of the intermediate stages, however, removed my doubts, and now I feel that it is quite an established fact that the new meganucleus is formed from one of the four nuclei produced by the second division of the germ nucleus. Plate, Schneider, and Sand, who maintain that the new meganucleus is formed by the reconstitution of one or more fragments of the old meganucleus, are in error, and I believe that the views expressed by Maupas and Hertwig as to the origin of the new meganucleus in Ciliata are correct.

The principal stages in the formation of the new meganucleus are shown in Pl. 18, figs. 2—5. In the first stage one of the four micronuclei (figs. 1 and 2) increases in size in a manner very similar to that in which the micronuclei swell up just before mitosis in bud formation, or in the earlier stages of conjugation. In the preparation, the enlarged micronucleus was 5 μ in diameter, and the others 4 μ. This enlargement is caused by a considerable increase in the clear substance, and by the resolution of the chromatin into a coarse skein. In the next stage (fig. 3) the nucleus has still further increased in size to about 8 μ in diameter; the chromatin has become more diffused, and does not stain so deeply. It is probable that the change in staining power indicates some slight change in constitution, but there is no evidence as to the nature of this change. The greater part of this modified chromatin is arranged in the form of a thick ring at the periphery. There are, however, some strands stretching across the nucleus, and a considerable number of rows of granules extending from the edge into the cytoplasm. I think there can be little doubt that at this stage either the whole or the greater part of the chromatin, in its modified form, passes into the surrounding cytoplasm, leaving the new meganucleus perfectly clear and homogeneous.

The elimination of chromatin from nuclei is a phenomenon of rare occurrence in animal and vegetable cells. In the maturation of the ovum of many animals a considerable amount of chromatin is ejected into the cytoplasm. Wilson (**26**) says, "In these cases (Asterias, Polychærus, Thalassema, Nereis) only a small fraction of the chromatin substance is preserved to form the chromosomes, the remainder degenerating in the cytoplasm. Some years ago I described the fragmentation of the germinal vesicle of the Stylasterid Allopora (this Journal, vol. xxix) and the distribution of its chromatin in the cytoplasm. A similar phenomenon occurs in Distichopora (**10**). I have recently devoted a considerable amount of attention to the ovum of Alcyonium, and in this case, too, the whole of the chromatin appears to be ejected into the cytoplasm before fertilisation takes place. In certain insects, judging from the figures given by Henking (**9**) and others, the amount of chromatin that takes part in the formation of the first polar figure is a very small fraction of the chromatin originally present in the germinal vesicle (cf. Cuenot, **3a**).

That the elimination of chromatin is not confined to the nuclei of egg cells is clear from the discovery of Boveri's, that in those blastomeres in the early stages of development of Ascaris which are destined to produce somatic cells, "a portion of the chromatin is cast out into the cytoplasm, where it degenerates, and only in the germ cells is the sum total of the chromatin retained" (quoted from Wilson, **26**). In all these cases of the elimination of chromatin from the nuclei of ova and blastomeres there appears to be no recovery in the amount of chromatin before the next division occurs. In the history of the formation of the new meganucleus of Dendrocometes, however numerous, granules of chromatin subsequently appear at the periphery (Pl. 18, figs. 4, 7, 8), and later they invade the clearer central parts (Pl. 18, figs. 5, 15), to build up the characteristic chromatin network of the functional meganucleus. The exact meaning of this elimination and recovery of chromatin at this stage is a mystery, but taken in conjunction with the other phenomena of conjugation, it may be regarded as a part of the general process of protoplasmic reconstitution of the organism, which is the essential feature of the sexual act.

General Considerations.

Maupas, in his famous work on the conjugation of the Infusoria, expressed the opinion that conjugation is essentially an affair of the micronuclei; and I think that the prevailing opinion held by zoologists who have taken a special interest in this matter, is in general agreement with this view. Bütschli's opinion, as expressed in 'Infusoria' (p. 1643), is that the meganucleus is of the nature of a somatic nucleus (Gewebekerne), which becomes gradually exhausted (allmählich abgenutzt wird) during somatic life, whilst the micronucleus is of the nature of the sexual nuclei of Metazoa, and does not become exhausted by the vital processes (keine solche Abnutzung erfahrt). Wilson (**26**) expresses very fairly the prevalent view in this sentence: "During conjugation the macronucleus degenerates and disappears, and the micronucleus alone is concerned in the essential part of the process."

With the general proposition that the meganucleus is of the same essential nature as the nucleus of the somatic cells of the Metazoa, and that the micronucleus is essentially a sexual nucleus, I am in agreement; but there are serious objections to be raised to the further proposition, that the only essential process in connection with conjugation is that in which the micronuclei are concerned.

Plate expressed a view that during conjugation there is a recovery of some essential substance of the nucleus from the cytoplasm (see Bütschli, 2); but, as Bütschli rightly points out, it is difficult to understand upon what grounds Plate's view is based.

Without going further into a review of the opinions of various writers on conjugation, it may be sufficient to state here the problem which is still in need of solution. Is the interchange of molecules of the cytoplasm of the two conjugates during conjugation an essential part of the process?

This question cannot be answered by direct evidence at present. Whatever interchange of molecules of the cytoplasm there may be during conjugation, no method of observation has yet been discovered by which the course of the molecules of one individual can be traced into the body of the other. It is otherwise with the micronuclear nucleoplasm, the peculiar structure and staining properties of which enable us to trace with certainty the course of one micronucleus (or germ nucleus) into the body of the other. The direct evidence which we have in the case of the micronuclear fusion is absent in the case of the cytoplasm. It is not reasonable to conclude from this alone that the cytoplasm plays no part in the process of conjugation, nor that conjugation is simply "une affaire de micronucleus." It appears to me that there is some indirect evidence, however, on this point which is worthy of considerable attention. If the micronuclei alone were concerned in the process, the act of conjugation need be of very short duration. In fact, if the germ nuclei were prepared for their transposition a mere momentary contact would be sufficient. It might also be conceived that such a momentary conjugation would be of advantage to the species in lessening the disadvantageous conditions of the conjugating phase, particularly in the free-swimming Ciliata. In all cases, however, the conjugation is a lengthy process, lasting from twelve to forty-eight hours or more. It is inconceivable that the state of insensate, helpless, defenceless syzygy would remain so long if there were nothing else of essential importance done but the interchange of germ nuclei. The fact suggests that there is during the process some interchange of the molecules of the cytoplasm, and, indeed, that the interchange or mixing of the molecules is thorough, and not partial or local in character. If there is during conjugation an interchange of the molecules of the cytoplasm such as has been suggested, it is probable that some protoplasmic streaming movement would be noticed between the two individuals. The observations on the changes or movements of the cytoplasm during the process are, however, very limited. Maupas observed that numerous granules (zooamylum) appear in the cytoplasm during the conjugation of certain Ciliata, which he supposed to be connected in some way with the active metabolism that is going on; but I cannot find in his writings any reference to a streaming movement taking place between the two individuals. But Maupas, like Bütschli and many others,[1] it must be remembered, regarded the micronuclear phenomena as the only essential phenomena of the process, and did not expect to find any such flow of cytoplasm.

In Dendrocometes a flow of cytoplasm between the two conjugates does certainly take place. This was observed by Plate and is confirmed by my own observations. Sand (**23**, p. 100) goes so far as to say that conjugation is essentially a process of plastogamy, and that there is not the least mixing of the nucleoplasm of the two individuals. But Sand's view is, I believe, as far wrong in the one extreme as the older view is in the other.

Whether a similar streaming movement of the cytoplasm between the conjugates can actually be observed in the group of the Ciliata or not, is a question upon which I have no evidence to offer. But whether it can or cannot be observed under the microscope, the intimate contact of the two cytoplasms renders an invisible interchange of molecules

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[1] Delage and Hérouard say, "Les phénomènes intérieurs de la conjugaison sont SURTOUT nucléaires."

possible, and the "onus probandi" really rests upon those who maintain that two globules of protoplasm, such as these, can remain in junction for twenty-four hours without becoming intimately mixed.

A third point of indirect evidence bearing upon this question is afforded by the behaviour of the meganucleus of Dendrocometes during conjugation. If we regard the meganucleus as a somatic nucleus—that is to say, as a nucleus which is functionally connected with all the vital functions except the sexual functions of the body, and as a nucleus therefore which controls or is controlled by the greater part of the cytoplasm of an animal cell such as Dendrocometes is,—then the presence of the meganuclei in the conjugative processes during the interchange of the molecules of the cytoplasm is not a matter for surprise. "Pourquoi, dira-t-on," says Sand, "les noyaux vont-ils se placer dans le pont qui réunit les deux Stylocometes et les deux Dendrocometes? C'est peut-être pour diriger les échanges et les mouvements qui ont lieu dans ce pont." I am prepared, however, to go further than Sand, and regard the presence of the meganuclei in the conjugative processes (le pont) not only as evidence of their relation to the interchanges taking place in the cytoplasm, but as evidence of the necessity of the interchange of molecules of the substance of the meganucleus itself. During conjugation there is, in my opinion, a mixing or a shuffling of the molecules of all the essential plasms of the body, namely, of the micro-nucleoplasm, of the meganucleoplasm, and of the cytoplasm.

Concerning the conjugation of the meganuclear elements two or three obvious objections appear. It might be urged that the rarity of recorded observations of the fusion of the meganuclei in the Heterokaryota, the disintegration of the meganucleus during conjugation, and the origin of the new meganucleus from the micronuclei, are facts which prove that the junction of the meganuclei during conjugation in Dendrocometes is a matter of no essential importance.

It may be pointed out that in the majority of the Ciliata the meganucleus undergoes fragmentation at an earlier stage than it does in Dendrocometes, and consequently any conjugation that takes place between meganuclear fragments might be very easily overlooked. The fact that in his most recent publication Prowazek figures (figs. 27 and 30) the extension of a fragment of the meganucleus of one conjugating Stylonychia into the body of the other, supports the suggestion that it may occur elsewhere. The second objection is fatal to the view I am putting forward, if it is true, that the meganucleus dies when it fragments. It is, however, really of the nature of an assumption to say that the meganucleus dies at the close of conjugation.

Entz, Balbiani, Gruber, Maupas, Hoyer, and Prowazek are agreed in the statement that the fragments of the meganucleus are absorbed by the cytoplasm. In some species (Chilodon cucullulus, Colpidium colpoda, etc.) the meganucleus does not even fragment, it simply gradually diminishes in volume and disappears. On the other hand, Bütschli (2, p. 1617) is of opinion that in Colpidium and Stylonychia the fragments of the meganucleus areejected by the anus after conjugation. Having very carefully examined the process in Dendrocometes, and found no evidence of the rejection of any part of the meganucleus during or after conjugation, I am disposed to agree with those who believe that the old meganucleus is, as a rule, absorbed by the protoplasm. It is quite possible, however, that with the absorption of the greater part of the meganucleus there may be a rejection, in some species, of the remainder.

The expression "absorption" or "solution," as applied to the meganucleus at this stage, is very liable to mislead. We may hold the view that the meganucleoplasm is killed, converted into some proteid food substance, and then assimilated by the surrounding cytoplasm, and we may use the word "absorption" to express this meaning. Or we may hold the view that the meganucleoplasm becomes more fluid in consistency, and is diffused in a chemically unaltered, or very slightly altered, condition through the cytoplasm, and we may use the word "solution" to express this meaning; but we have no evidence that it is either of these processes that actually takes place. All the information we have is that at a certain stage in conjugation certain structures, which by their form and reactions to certain stains we recognise to be meganucleoplasm, become indistinguishable from ordinary living cytoplasm. There is evidence of a certain change in chemical constitution, and perhaps this is only a very slight change, and there is evidence of a certain change in consistency. There is really no evidence that any substance actually dies. Theoretically, there is no inconsistency in the view that after the disappearance of the old meganucleus, its nucleoplasm is still living in a modified form diffused through the cytoplasm. The new meganucleus of the Dendrocometes individual is an enlarged and modified nucleus derived from one of the four micronuclei which are produced by the second division of the segmentation nucleus, as described above, or, to put the matter in few words, the meganucleus is derived from a micronucleus. The important changes which occur during the transition from a structure we call a micronucleus to a structure we call a meganucleus are these:—1st. A considerable increase in size (from 4 μ in diameter to over 12 μ in diameter in Dendrocometes). 2nd. A considerable increase in the amount of chromatin. From whence is this increase in substance derived? It must come either directly as formed nucleoplasm, or indirectly as food material from which nucleoplasm can be formed, from the surrounding cytoplasm. The evidence as to which of these two alternatives is correct is not conclusive, but there is no sign of such metabolic activity as might be expected if the material brought to the new meganucleus is unformed food material, and consequently it is very probable that the increase in size is due to formed nucleoplasm transfused from the cytoplasm to the new meganucleus. If this is the case, then the phenomenon of the conjugation of the meganuclei receives an explanation.

This view appears to me to receive considerable support from the observation made by Bütschli that the posterior fragment of the meganucleus of Euplotes charon does not die, but fuses with the new meganucleus. A similar observation was made by Maupas on Euplotes patella.

The investigation of the conjugation of Dendrocometes described in this paper throws no new light on the important question of the initial stimulus to syzygy. It is well known that Maupas was able to induce conjugation in several species of Ciliata by a judicious withdrawal of food material after a certain number of binary fissions; that he was of opinion that in natural conditions it is the exhaustion of the food supply which affords the main stimulus to the epidemics of conjugation. The views of Maupas have recently received some support from the experiments of Prowazek (22), who was able to induce conjugation by hunger in Stylonychia pustulata. On the other hand, Joukowsky (17) failed to induce conjugation by hunger in Pleurotricha after experimenting for eight months and reaching the four-hundred-and-fifty-eighth generation.

I tried the experiment several times of isolating a number of Gammarus bearing the Dendrocometes in filtered water for six days or a week, and obtained in some cases sufficient evidence that the Acinetarians were affected by hunger; but there were on an average neither more nor less pairs in conjugation than in the Dendrocometes of the control experiment. Starvation cannot be extended for more than a week in this case, as the hosts soon die in the filtered water, and their macerating bodies afford ample food again for the epizoites.

Dendrocometes itself is peculiar among Infusoria in that it appears to be capable of feeding all through the process of conjugation. Mr. Wadsworth and I have observed the arms of conjugates catch food and pass it down into the body protoplasm. Judging from the food granules as seen in sections, the onset and progress of conjugation appear quite indifferent to the condition of hunger or satiety.

The following notes will illustrate this point:

(The letter F in the third and fourth columns signifies that the conjugate contains food vacuoles, and the letter S that its cytoplasm is clear or moderately clear.)

Number of Slide.	Stage of Conjugation.	Conjugate A.	Conjugate B.
146	B	F.	F.
83, 84	B	F.	S.
10	C	F.	S.
129	C	S.	S.
127	C	S.	S.
126	E	S.	S.
122	E	F.	S.
121	E	F.	F.
25	J	S.	S.
127	J	S.	S.
120	J	F.	S.
119	J	F.	F.

The General Morphology of the Heterokaryote Body.—The investigations of Maupas (**20**), Bütschli (**2**) and Keppen (**15**), notwithstanding the writings of Plate (**21**), and more recently of Sand (**23**), have placed beyond all reasonable doubt the zoological affinity of the classes Acinetaria and Ciliata. In these two classes alone there are two kinds of nuclei in each independent organism. In all other Protozoa, with the exception perhaps of a few forms like Pelomyxa, in which there are only scattered granules of chromatin, there is only one kind of nucleus.[1] This fundamental distinction of the Ciliata and Acinetaria justifies us in placing them together in a subdivision of the Protozoa, which may be called the Heterokaryota (Hickson, **11**).

There may be some difficulty in giving an absolute definition of what is a nucleus. It will be agreed, however, that every structure in a protoplasmic mass that contains

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[1] Cuenot (**3**) has recently discovered that in a Gregarine belonging to the genus Diplocystis, which is parasitic in the common cricket, the two forms of nuclei occur. The micronucleus, however, does not become visible until the onset of sporulation, but it then divides by a mitotic process to give rise to the nuclei of the spores, while the meganucleus disappears.

chromatin and that divides by mitosis is a nucleus. It is frequently very difficult, however, to distinguish true nuclear chromatin from substances in the cytoplasm that are not chromatin, and there are many examples of nuclei known to science that do not divide by mitosis. It may be taken, however, as a further axiom of histology that every structure originating as a daughter nucleus by mitosis of a pre-existing nucleus is itself a nucleus.

Both the meganucleus and the micronucleus of the Heterokaryote body, therefore, are true nuclei; the former on the ground that it originates from the nucleus formed by the mitotic division of a micronucleus, notwithstanding the fact that it always divides amitotically,[1] and the latter on the ground that it divides by mitosis. These two nuclei, however, differ from each other in several important particulars. The meganucleus is very much larger in bulk during the somatic life of the individual than the micronucleus. In fission or gemmation it divides amitotically. It does not divide during conjugation, but during or at the close of this process it ceases to exist as a definite entity.

The micronucleus, on the other hand, is very much smaller than the meganucleus during somatic life. In fission and gemmation it divides by mitosis. It does divide, again by mitosis, during conjugation, and one of the products of its division gives rise to the germ-nuclei. It is not necessary to discuss further in this place the relations of these two nuclei. The reasons set forth by Bütschli with masterly ability in his great work on the Infusoria, for considering the meganucleus to be the "somatic" nucleus, and the micronucleus as the "sexual" nucleus, are sufficient for my purpose. If, however, we accept the view that in the body of the Heterokaryote there is one (or occasionally more than one) somatic nucleus and one or more than one sexual nuclei, we are led to the further inquiry whether there is also a distinction between the somatic cytoplasm and the sexual cytoplasm.

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[1] Apparent exceptions to this rule are afforded by the meganuclei of Opalina and Kentrochona.

There is no evidence of a positive character to show that this is the case, but the absence of any visible boundary line between the sexual cytoplasm and the surrounding somatic cytoplasm is not a definite proof that the distinction does not occur. Many instances could be quoted, both from animal and vegetable tissues, in which each nucleus of a plasmodium has its own sphere of influence in the surrounding protoplasm, even when no cell boundaries can be distinguished. It is, indeed, contrary to our general knowledge and usual conceptions of cell structures that any nucleus should be entirely independent of the cytoplasm that immediately surrounds it, just as it is that any nucleus should exist entirely free from any cell protoplasm.

There is one feature of the sexual cells of the Metazoa which at this point in the argument I should like to call attention to. When ova and spermatozoa are ripe, that is to say, when they are ready to perform the only function they possess, they are entirely free from surrounding cell structures. There is no reason to believe that in any case I can call to mind the individual ovum or spermatozoon is in protoplasmic continuity or even contact with other cells. There are no other cells of the animal body, except the white blood-corpuscles, of which the same statement can be made, and it is a feature of some interest and importance that in the Metazoa these cells are in their mature condition independent entities. Now in the Heterokaryota the sexual cytoplasm must be in contact with, and in all probability is in continuity with, the somatic cytoplasm at the time of maturity, and even after the fertilisation has been effected. In this respect then, there is an essential difference between the Metazoa and the Heterokaryota. In the Metazoa a conjugation of the somatic cells and of the somatic nuclei could have no possible effect upon the sexual cells, either before or after fertilisation. In the Heterokaryota, on the other hand, whatever effect the conjugation of the meganuclei and the somatic cytoplasm may have, it must be felt by the sexual nuclei and the sexual cytoplasm with which they are in contact. This consideration throws some light on the phenomenon of the conjugation of the meganuclei in the Infusoria, a phenomenon which has no parallel in the Metazoa.

In the recent discovery of the phenomenon called "Xenia" by the botanists in plants, we find a parallel although not strictly homologous case. The ripe ovum of the angiosperm is not an isolated cell. Its germinal cytoplasm is continuous with the general cytoplasm of the embryo sac, in just the same way as, according to my views, the germinal cytoplasm of a Dendrocometes is in continuity with the somatic cytoplasm. It is quite possible, therefore, that anything which influences the polar nuclei or the general cytoplasm of the embryo sac would influence also the ovum (oosphere) before or after fertilisation is effected. Nawaschin and Guignard (7) have shown that in Lilium and some other Angiosperms the second nucleus of the pollen grain does pass down the tube, and conjugates with one of the polar nuclei to form the mother nucleus of the endosperm nuclei. The second nucleus of the pollen grain and the polar nuclei of the embryo may be compared with the meganuclei of the Heterokaryote body. Like these nuclei they conjugate at the time of the true sexual conjugation of the germinal nuclei, and, moreover, they do not by subsequent division give rise to the nuclei of the new individual. It is true that there are important differences between the two cases. In the plant the conjugation of these nuclei is not temporary as it is in Dendrocometes, but permanent, and the product of the conjugation gives rise to a considerable progeny of well-defined nuclei in the endosperm before their history is closed. But such differences as these are not surprising in organisms so widely separated as the Infusorian and the Angiosperm plant. Detailed comparison of the two phenomena would probably not be profitable, and might, indeed, be misleading. All that the comparison can do for us at present is to confirm the impression that the temporary fusion of the meganuclei of Dendrocometes that has just been described is an important and essential part of the process of conjugation, and not an exceptional or accidental juxtaposition of the nuclei in the individual cases examined. It may also lead to the discovery of other cases of the conjugation of meganuclei in the Acinetaria and in the Ciliata.

As a general result of these considerations, it seems to me that we must either abandon the use of the expression "unicellular organisms" in our definition of the Protozoa, or else very largely extend the meaning of the term "cell." In the recent text-books published by Sedgwick and by Shipley and Macbride, the former course is adopted; but Lang, in his 'Lehrbuch der vergleichenden Anatomie,' 2nd edition, 1901, says, "Die einfachsten Organismen, die einfachsten Thiere (Protozoa), und die einfachsten Pflanzen (Protophyta) sind weiter nichts als selbständig und unabhängig lebende Zellen."

The body of a Paramœcium or of a Dendrocometes is no more a single independent cell than is the embryo sac of an Angiosperm plant.

If we are prepared to extend the use of the term cell so as to include all structures that are bounded by an undivided cell wall or cell boundary, then the expression "unicellular" may still be applied to the Protozoa; but, in my opinion, the inconvenience of such a course would far exceed the advantages it might present.

LIST OF THE PRINCIPAL PAPERS REFERRED TO IN THIS MEMOIR.

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2. O. Bütschli.—"Infusoria" in Bronn's 'Thierreich,' 1889.
3. L. Cuenot.—'Évolution des Grégarines célomique du Grillon domestique," 'C. R.,' cxxv, p. 52.
3a. L. Cuenot.—'L'Épuration nucléaire au début de l'Ontogenèse,' t. c., p. 190.
4. E. Claparède et J. Lachmann.—'Études sur les Infusoires,' Geneva, 1857—1860.

5. Yves Delage et E. Hérouard.—'Traité de Zoologie concrète,' tome i, Paris, 1896.

6. Y. Delage.—"Embryons sans noyau maternel," 'C. R.,' cxxvii, p. 528.

7. L. Guignard.—"Sur les Anthérozoides et la double Copulation sexuelle chez les Végétaux angiospermes," 'C. R.,' cxxviii, p. 864.

8. R. Hertwig.—"Ueber die Konjugation der Infusorien," 'Abh. der bayr. Akad. der Wiss.,' Cl. II, Bd. xvii.

9. O. Henking.—"Untersuchungen über die ersten Entwickelungsvorgänge in der Eiern der Insekten," 'Zeits. f. w. Zool.,' liv, 1.

10. S. J. Hickson.—"The Early Stages in the Development of Distichopora, with a short essay on the Fragmentation of the Nucleus," 'Q. J. Micr. Sci.,' 1893, vol. xxxv, 1.

11. S. J. Hickson.—"The Reproduction and Life History of the Protozoa," 'Trans. Manch. Microscop. Soc.,' 1900.

12. S. J. Hickson.—"The Nuclei of Dendrocometes," 'Reports of the British Assoc.,' 1900.

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14. H. Hoyer.—"Ueber des Verhalten der Kerne bei der Conjugation des Infusors Colpidium Colpoda," 'Arch. mikr. Anat.,' 54.

15. — Keppen.—"Remarks on the Infusoria Tentaculifera," 'Mem. Soc. Nat.,' Odessa, 1888, xiii, 2 (in the Russian language).

16. C. Ishikawa.—"Ueber eine in Misaki vorkommende Art von Ephelota und über ihre Sporenbildung," 'Japan Coll. Sci. Imp. Univ.,' vol. x, p. 119 (1896–8).

17. D. Joukowsky.—"Beiträge zur Frage nach den Bedeutungen der Vermehrung und des Eintritts des Conjugation bei den Ciliaten," 'Verh. naturh. med. Ver. Heidelberg,' n. F., vi.

18. E. Maupas.—"Sur la Podophrya fixa," 'Arch. Zool. expér.,' vol. v. 1876, p. 401.

19. E. Maupas.—"Contribution a l'étude des Acinétiens," 'Arch. Zool. expér.,' vol. ix, 1881, p. 299.

20. E. Maupas.—"La Rajeunissement karyogamique chez les Ciliés," 'Arch. Zool. expér.,' II série, vol. vii, 1889.

21. L. Plate.—"Untersuchungen einiger an den Kiemenblättern des Gammarus pulex, lebenden Ektoparasiten," 'Zeits. f. w. Zool.,' vol. xliii, p. 175, 1886.

22. S. Prowazek.—"Protozoenstudien," 'Arb. aus Zool. Instit. Wien,' tom. xi, 3, 1899.

23. R. Sand.—'Étude monographique sur le groupe des Infusoires tentaculifères,' Brussels, 1901.

24. A. Schneider.—'Fragments sur les Infusoires. Tablettes zoologiques,' vol. i.

25. H. J. Webber.—"Xenia," 'U.S. Dept. of Agriculture,' Bulletin 22.

26. E. B. Wilson.—'The Cell in Development and Inheritance,' 2nd edition, 1900.

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EXPLANATION OF PLATES 17 & 18,

Illustrating Mr. Sydney J. Hickson's paper on "Dendrocometes paradoxus."

PLATE 17.

The figures in this plate, with the exception of 1, 2, and 5, are constructed from a series of drawings of the actual sections of the Dendrocometes. The micronuclei do not all occur in the same plane as represented, and it is very rarely that the whole of the meganucleus can be seen in one section. The structures have been represented as nearly as possible in their true relative positions. Throughout, M. refers to the meganucleus; m., the micronuclei; A., the arms; P., the conjugating process; L. M., limiting membrane. The number at the end of the description of each figure refers to the permanent preparation from which the figure was drawn. These preparations are preserved in the Zoological Laboratory at the Owens College, and may be inspected by qualified zoologists.

Fig. 1.—Two individuals of Dendrocometes about to conjugate. Each one is protruding a conjugating process (P. P.) and these ultimately meet. In these two individuals the arms are of approximately the same size and degree of branching. Whole mount, No. 14.

Fig. 2.—Two individuals which have just joined together in conjugation (Stage A). One of them (to the right) has one short arm and two very rudimentary arms (A. 2, A. 3). The other has one large branched arm and two shorter simple arms (see p. 328). The micronuclei are very small, and the meganuclei have undergone very little change (see p. 331). Whole mount, No. 29.

Fig. 3. Stage B.—The meganuclei have become spindle-shaped and are slightly enlarged. The micronuclei (three in each individual) are considerably enlarged, the chromatin forming a loose meshwork. Section No. 139.

In this and the following figures details of the arms are omitted.

Fig. 4. Stage B (later).—The micronuclei now show chromosomes arranged in equatorial planes and linin fibrils running through them to the poles. In this preparation only two micronuclei can be seen in each individual. Sections No. 129.

Fig. 5. Stage B (close).—The micronuclei are in later stages of their mitosis. In the individual on the right the chromosomes of the micronuclei have separated into two parties travelling toward the poles. In the individuals on the left the chromosomes have reached the poles and fused into a compact mass. Whole mount, No. 14.

Fig. 6. Stage C.—There are now six micronuclei in each individual, and the undissolved remnants of some of the spindles (Sp.) may be seen in the cytoplasm. The meganuclei have been omitted from the drawings to render the positions of the nuclei clear. Section No. 139.

Fig. 7. Stage D.—Five of the micronuclei in each individual are now undergoing degeneration, but one in each (m.c.) travels down the conjugative process and approaches the membrane of separation. The meganucleus is omitted in the figure from the individual on the right. Sections No. 126.

Fig. 8. Stage D.—The conjugative micronuclei (mc., mc.) are now dividing by mitosis in the conjugative process of each individual. Sections No. 134.

Fig. 9. Stage E.—The conjugative micronuclei have now divided into two separate nuclei.—the "germ nuclei." Sections No. 138.

Fig. 10. Stage F.—The germ nuclei of the two individuals have now fused or are fusing (upper one). Sections No. 140.

Fig. 11. Stage G.—The cleavage nuclei (S.m.) formed by the fusion of the halves of the conjugative nucleus in the last stage now travel towards the centre of each individual and again show mitosis. During the preceding stages the meganuclei have been gradually enlarging and have now reached a considerable size. Degenerate remnants of the other micronuclei may still be seen in the cytoplasm. Sections No. 141.

Fig. 12. Stage H.—The segmentation nuclei having divided once more show mitosis. Sections No. 107.

For illustrations of Stage J see Plate 17, figs. 1, 7, 8.

Fig. 13. Stage K.—The segmentation nuclei have now divided into four nuclei in each individual, three of which become reduced in size and the chromatin concentrated into a single granule, and one in each becomes enlarged to form the new meganucleus (n. M.). The old meganucleus is beginning to disintegrate. Sections No. 25.

PLATE 18.

1. Section through one of a pair of conjugates after the second division of the segmentation nuclei (Stage J), showing one nucleus (n. M.) slightly larger (5 μ) than the other three (4 μ). This larger nucleus becomes the new meganucleus. No. 122.

2. The new meganucleus from the last figure enlarged to show that the chromatin is at this stage in the form of a coarse skein lying in the centre of a clear space.

3. The new meganucleus at a later stage. It is now about 8 μ in diameter. A considerable quantity of the chromatin has now collected at the periphery, and some of it appears to be escaping into the cytoplasm. No. 145.

4. New meganucleus at a still later stage, 10 μ in diameter. Darkly staining granules of chromatin are now seen at the periphery, one or two within the periphery, but the central parts stain very faintly indeed. Series 131.

5. New meganucleus at a still later stage, 12 μ in diameter, containing numerous evenly distributed granules of chromatin. Slide 131.

6. Section through a pair of conjugates showing the approach of the old meganuclei (M.) to each other at the bar of junction. No. 52. (The micronuclei were not clearly stained in this preparation, and are consequently entirely omitted from the drawing.)

7. Section through a pair of conjugates (Stage J), showing one meganucleus at the limiting membrane, the other pointing towards it but not reaching it. There is one new meganucleus and three micronuclei represented in each. (In the preparation, owing to an unfortunate tear, only one micronucleus can be actually seen in the lower conjugate.) No. 141.

8. Section through a pair of conjugates (Stage J), showing the approach of the old meganuclei to each other at the limiting membrane. In each of these there is one new meganucleus and five micronuclei (an exceptional condition). In the cytoplasm of the lower conjugate there may be seen three granules of chromatin (?). These may be the remnants of the polar nuclei. Slide 131.

9. A small portion of the old meganucleus of one of the conjugates of the last preparation more highly magnified, showing the chromatin arranged in irregular parallel lines with thickened nodes and lumps.

10. Section through a resting meganucleus, stained by iron-hæmatoxylin. No membrana limitans can be seen. No. 255.

11. Section through the conjugative processes of a pair of Dendrocometes, showing the organic fusion of the two meganuclei in Stage J. No. 98 S.

12. Section through the conjugative processes of a pair of Dendrocometes

(Stage F), showing the fusion of the germ nuclei (G. m.). On the left the two nuclei have not completely joined; the chromatin is in the form of a coarse skein with thickened nodes. On the right the pair have fused, and the chromatin has assumed an irregular asterid form. No. 140.

13. Section through the conjugative processes after the fusion of the germ nuclei to form the segmentation nuclei (S. m.). The segmentation nuclei become mitotic soon after their formation, but the axes of the figures are not parallel with the membrane nor with one another. In this case the upper figure is seen in longitudinal section and the lower in transverse section. No. 117.

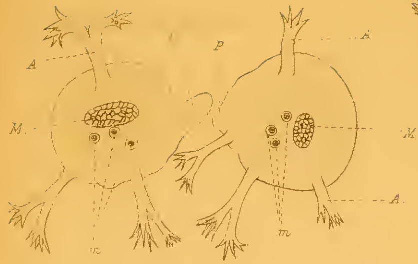
14. Section through a Dendrocometes at an early stage in the formation of a gemmula to show the normal mode of division of the meganucleus. B. B. Bands of concentric modified cytoplasm which form the peritrichous bands of cilia of the gemmula. No. 34 s.

15. Section through one of a pair of conjugates in Stage K, showing the fragments of the old meganucleus and the new meganucleus. m., One of the micronuclei? No. 92.

16—18. Three stages in the division of the micronuclei. 16. Immediately after the division of the chromosomes. 17. The chromosomes separated to the poles of the figure. 18. The chromosomes collected into a granule of chromatin at each of the poles, and the achromatin in the form of an elongated spindle. 16 and 17, No. 129. 18, composition drawing from several preparations.

19. Section through a Dendrocometes at the close of conjugation. It shows the rare condition of two new meganuclei. The old meganucleus has almost completely disintegrated. No. 74 E.

NOTE.—In Stage K, when the old meganucleus has fragmented, it is extremely difficult to distinguish the micronuclei from fragments of the old meganucleus. I have therefore made no attempt to reconstruct Fig. 15 and Fig. 19, so as to show all the micronuclei in their correct relative positions. These two figures were drawn with the assistance of the camera lucida from one section only of each series of sections.



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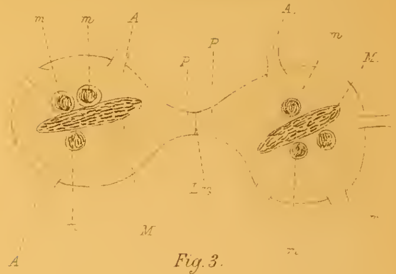

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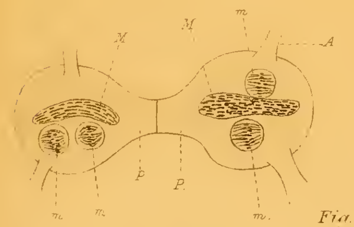

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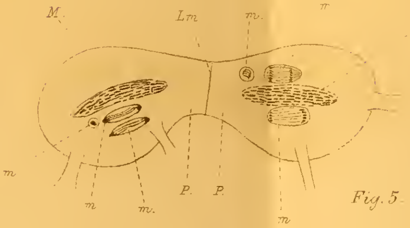

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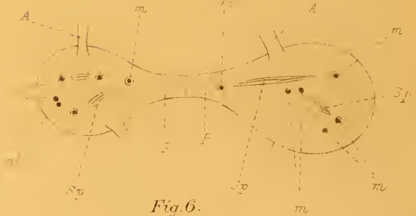

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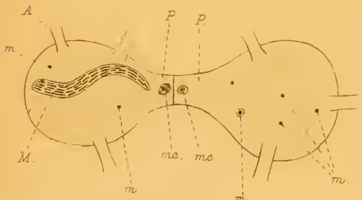

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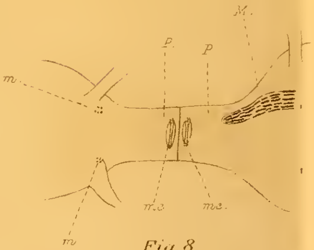

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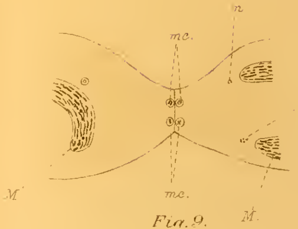

Fig. 9.

Fig. 10.

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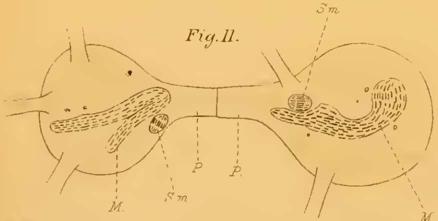

Fig. 12.

Fig. 13.

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A. Huth, Lith^r London

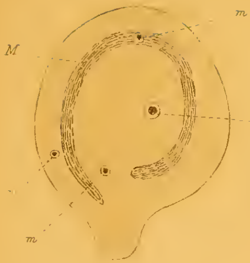
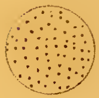


Fig. 1.


Fig. 2.


Fig. 3.


Fig 4.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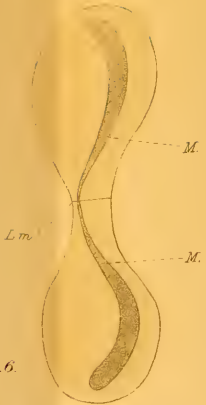

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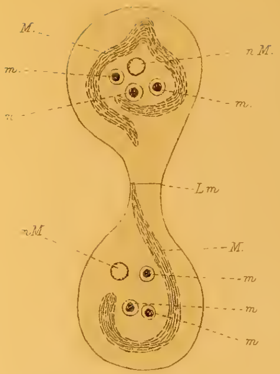

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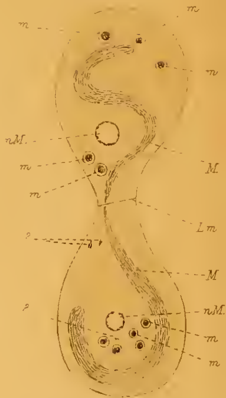

Fig 8.


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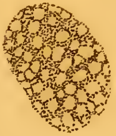
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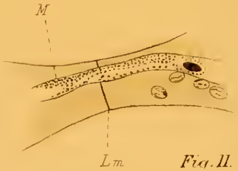

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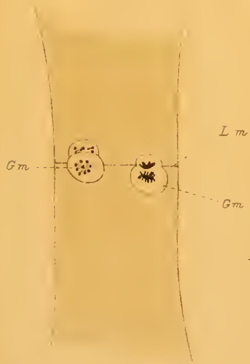

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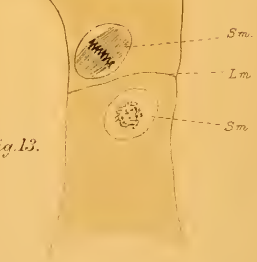

Fig. 13.

Fig. 14.

Fig 15.

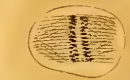
Fig. 16.


Fig. 17.


Fig 18.

Fig. 19.

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A.S. Huth, Lith^r London.

On the Oviparous Species of Onychophora.

By

Arthur Dendy, D.Sc., F.L.S.,
Professor of Biology in the Canterbury College, University of New Zealand.

With Plates 19—22.

CONTENTS.

I. INTRODUCTION.

THE present memoir is an attempt to bring together and extend our information with regard to a very remarkable group of Onychophora, the species of which are characterised by their egg-laying habit and by a corresponding change in the structure of the female organs. The subject is one upon which I have been engaged at intervals for more than twelve years, and our knowledge of which for various reasons has progressed very slowly. Owing in part, at any rate, to an unfortunate confusion in nomenclature, for which I can scarcely hold myself entirely responsible, my earlier observations were at first met with scepticism[1] and hostile criticism, (Fletcher, **6**) and the scarcity of material and difficult nature of the investigation were equally discouraging. The recent discovery of a new egg-laying species in New Zealand has, however, stimulated further inquiry, and though I cannot even now make the work anything like complete, I think the time has come when a general account of the subject with the necessary illustrations may be found useful. As previous observations on these species have been published in scattered periodicals, I prefix to this memoir a short historical notice.

In December, 1888, I found two specimens of Peripatus in a fern-tree gully at Warburton, on the Upper Yarra, Victoria. These specimens I described in a letter to 'Nature' (**1**), published on February 14th, 1889.[2] Peripatus had previously been known from Victoria only by a single specimen discovered at Warragul by Mr. R. T. Baker, and exhibited by Mr. J. J. Fletcher at a meeting of the Linnæan Society of New South Wales on July 27th, 1887. Mr. Fletcher (**1**) considered the specimen to be "in all probability an example of P. Leuckartii, Sänger." Owing, however, to the peculiar colour-markings of the Warburton specimens, I came to the conclusion that these belonged to a new species, which I, however, refrained from naming.

In reply to my letter to 'Nature' Mr. Sedgwick (**3**) wrote to the same journal (February 28th, 1889), and expressed a doubt as to the distinctness of the Victorian species.

The examination of additional specimens unfortunately

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[1] Compare Sedgwick (**4**, p. 10). "All species are viviparous. It has lately been stated that one of the Australian species is normally oviparous, but this has not been proved."

[2] Also in 'The Victorian Naturalist,' January, 18 9

convinced me that Messrs. Fletcher and Sedgwick's suggestions as to the specific identity of the Victorian species with P. Leuckartii were correct, and on several subsequent occasions (**2**, **3**, **4**, **5**, **6**, **7**, **8**, **9**) I referred to the Victorian species under that name.

In 1891 I made the somewhat surprising discovery that the Victorian Peripatus, unlike all other known species, lays eggs, and I therefore announced that P. Leuckartii was oviparous (**6**, **7**, **8**, **9**). For making this statement I was very severely criticised by Mr. J. J. Fletcher (**6**), who certainly showed conclusively that the common New South Wales Peripatus is viviparous, like the great majority of species, a fact which, through the kindness of my friend Mr. T. Steel, I was subsequently enabled to verify for myself. The unfortunate controversy on this subject, which has probably done much towards preventing zoologists from appreciating the true facts of the case, was really due to the confusion between two species (the nomenclature of one of which is not yet by any means definitely settled), so that perhaps it was hardly worth while to say so much about it. As, however, I replied fully (**11**) to Mr. Fletcher's criticisms at the time, I need say no more about them in this place.

Meanwhile, in 1890, I had described (**5**), under the name Peripatus insignis, a second Victorian species, distinguished by the presence of only fourteen pairs of walking legs, and this species was afterwards found by Professor Baldwin Spencer (**2**) in Tasmania, which would appear to be its headquarters.

In my Presidential Address to the Biological Section of the Australasian Association for the Advancement of Science, at Brisbane in January, 1895, I pointed out a further element of doubt which enters into the nomenclature of the Australian species of Peripatus. Professor Baldwin Spencer had obtained in London a translation of Sänger's original diagnosis of Peripatus Leuckartii, of which he had kindly given me a copy. Concerning this I made the following remarks in my address :

"The diagnosis commences: 'Found in New Holland, north-west from Sydney. Fifteen pairs of legs—one pair without claws, fourteen with.' If this be correct, then the common Australian species usually accepted as P. Leuckartii is certainly not the species described by Sänger under that name, for I can certify that it has fifteen pairs of legs, all of which bear claws. There appear to me to be two possibilities in the case: (1) Sänger has failed to observe the claws on one of the pairs of legs, or (2) there were really only fourteen pairs of claw-bearing legs in his specimen, and he counted the oral papillæ as a pair without claws. It is difficult to say which of these alternatives is more likely to be correct, but it seems just possible that my P. insignis may be the real Leuckartii, with only fourteen pairs of claw-bearing legs. The only way to settle the question definitely would be by an appeal to Sänger's original specimen, which is stated to have been in the possession of Professor Leuckart."

Up to the present time no such appeal to Sänger's original specimen has, so far as I am aware, been made.

After my address was written, when passing through Sydney I called upon Mr. Fletcher and discussed the question of nomenclature with him, and found that he had independently arrived at conclusions similar to those contained in my manuscript. It was then arranged that we should each contribute a paper on the subject at the next meeting of the Linnean Society of New South Wales, and that in my contribution I should confine myself to the egg-laying species of Victoria, which we agreed should receive a name. My description of P. oviparus (**16**) was published in accordance with the above arrangement.

Before finishing his paper on the subject (**7**), however, Mr. Fletcher received specimens from Western Australia which caused him to modify his views; and, after a lengthy discussion, he comes to the conclusion that the most satisfactory arrangement would be to consider all known Australian specimens of Peripatus as referable to one comprehensive species with four varieties, viz.:

1. P. Leuckartii, var. typica = P. insignis, Dendy.

2. P. Leuckartii, var. occidentalis, var. nov. (for the West Australian specimens).

3. P. Leuckartii, var. orientalis, for the New South Wales and presumably the Queensland specimens (the P. Leuckartii, auctorum).

4. "The Victorian Peripatus to be dealt with by Dr. Dendy," referring to Peripatus oviparus, my description of which is placed after Mr. Fletcher's paper.

Although I myself pointed out that P. insignis might be identical with P. Leuckartii, the latter possibly having only fourteen pairs of claw-bearing legs, instead of fifteen, as usually believed, yet I do not by any means consider that the evidence is sufficient to justify the rearrangement proposed by Mr. Fletcher. Indeed, it seems to me very improbable that Sänger should ever have had Peripatus insignis in his possession. In any case the original accounts by Leuckart and Sänger are so inadequate and apparently contradictory that the species (without re-examination of the type) cannot be certainly identified, and therefore we are fully justified in following the usual custom, and applying the specific name Leuckartii to the common New South Wales species, while retaining the name insignis for the very different southern species with fourteen pairs of legs. This question will be more fully discussed later on.

So far, however, from agreeing with Mr. Fletcher that all the Australian forms are varieties of the same species, I maintain that there are in Australia two genera of Onychophora each with at least two species. I consider, in fact, that P. oviparus may be regarded as the type of a new genus, for which I have **(19)** proposed the name Ooperipatus, and in which I also include P. insignis and the species from New Zealand lately **(17)** described by me under the name P. viridimaculatus. All these three species differ from the common Australian Peripatus (P. Leuckartii, auctorum) in the possession by the female of a prominent ovipositor.[1] P. oviparus and viridimaculatus certainly lay eggs with thick sculptured shells. In P. insignis the same habit may be inferred from the presence of the ovipositor.

It is this extremely interesting group of egg-laying species which forms the subject of the present memoir. So far as I know no figures have yet been published of any of these three species, and it is this deficiency in particular which I wish to make good. Inasmuch as they all three agree very closely as regards internal anatomy with one another, and, with the exception of the reproductive organs, with the already well-known species of Peripatus, I have not felt it necessary to enter into details which would be merely repetition. It is the female reproductive organs which are of chief interest, and upon these attention has been mainly concentrated.

I have to thank many kind correspondents both in Australia and New Zealand for assistance in collecting material, and I am especially indebted to my friends Miss Ferrar, of Christchurch, New Zealand, and Mr. C. C. Brittlebank, of Myrniong, Victoria, for the large amount of trouble which they have taken in order to satisfy my desire to have coloured drawings of the three species.

II. THE GENUS OOPERIPATUS, DENDY (**19**).

a. Diagnosis.

Oviparous Onychophora. Eggs with thick sculptured chorion. Genital aperture in the female at the end of a prominent ovipositor which lies between the legs of the last pair; in the male the aperture is only slightly prominent between the legs of the last pair. Male with crural glands. Legs with three spinous pads. Transverse ridges of the

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[1] It seems probable that the female from Queensland described by Sedgwick (**2**) as P. Leuckartii was really a specimen of Ooperipatus oviparus, for Sedgwick says "the genital papilla of the female is remarkably prominent, and bears at its free end a longitudinally disposed slit."

integument interrupted in the mid-dorsal line by a narrow longitudinal groove, from the floor of which pigment is absent. Papillæ in an approximately single row on each transverse ridge.

b. External Characters.

Shape and Size.—In shape all three species do not differ conspicuously either amongst themselves or from other Australasian Onychophora. It must be remembered that we have in Australasia species of Onychophora with fourteen [O. insignis, O. viridimaculatus], fifteen [P. Leuckartii, P. occidentalis, P. novæ-zealandiæ, O. oviparus], and sixteen [P. Suteri] pairs of walking legs respectively, and, as might be expected, the size of the adult appears to be proportional to the number of pairs of legs, O. insignis and O. viridimaculatus being, so far as my experience extends, usually somewhat smaller than P. Leuckartii, P. novæ-zealandiæ, and O. oviparus; while P. Suteri[1] is considerably larger than any of the others. The "anal cone" (figs. 10, 31) is only about as long as the legs of the last pair. It is less well developed than represented by Sedgwick (**2**, fig. 23) in P. novæ-zealandiæ, upon which Bouvier's (**2**) diagram of the genus Peripatoides appears to be founded.

Appendages.—The number of claw-bearing walking legs is, as has just been stated, either fourteen or fifteen in the species of Ooperipatus hitherto described, but in view of past experience it would be unwise to generalise from these three species, and it is quite possible that species with more or even fewer pairs of legs may be forthcoming. Each leg is provided with three spinous pads, of which the middle one is the broadest, while the proximal one is very narrow. The foot is provided with the usual pair of horny claws and dorsally with three conspicuous primary papillæ—anterior, posterior, and median.

The oral papillæ have the usual structure, consisting each

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[1] Dendy (**13**).

of a proximal portion with little pigment and no papillæ, but pleated transversely and capable of extension, like an accordion; and a distal pigmented portion, almost hemispherical in form, and bearing papillæ.

The jaws, also, are quite normal in structure. The outer blade has an accessory tooth at the base in O. oviparus (figs. 7, 8), but this tooth is extremely small and irregular, while in O. insignis and O. viridimaculatus (figs. 29, 34) there is no accessory tooth. The inner blade (figs. 7, 30, 35) has from about five to about eight accessory teeth.

The ringed antennæ have no special characteristics as compared with other species. They are broadly rounded, or even perhaps slightly club-shaped at the extremity, and very similar, as is the case also with the oral papillæ, to those which Sedgwick has figured for P. novæ-zealandiæ.

External Apertures.—The mouth with its tumid lips, tongue, and jaws; the terminal anus; the apertures of the slime-glands and the nephridial apertures (fig. 28) resemble closely the corresponding parts in other Onychophora. In the fourth and fifth pairs of legs the nephridial aperture is shifted outwards into about the middle of the narrow proximal spinous pad, which is thus divided transversely into two parts, separated by the nephridial papilla.

The genital aperture of the female is a longitudinal slit at the extremity of a very protrusible ovipositor (figs. 9, 10, 27, 31) placed between the legs of the last pair. The ovipositor when retracted is still a conspicuous organ; its shape is subcylindrical, bluntly rounded, and may be slightly enlarged at the extremity, and covered, at any rate distally, with small spinose papillæ of a yellowish colour. It is capable of being extended until two or three times the length of the legs, and in this condition I have seen it in a drowned specimen (fig. 10) of O. oviparus, in which it was 4 mm. long. It is of about the same size and shape in all three species.

The male genital aperture lies between the legs of the last pair, and is only slightly prominent.

Crural glands are apparently developed in the male only, and their apertures are more or less conspicuous on the under surfaces of more or fewer of the legs in all three species (fig. 28). They are present in most if not all of the legs, and I include under this name the glands of the last pair of legs, whose apertures lie at either side of the genital orifice. The apertures of the crural glands are borne on white papillæ which are retractile, and may be considerably protruded in the form of thin-walled vesicles. Behind the male orifice is yet another pair of white papillæ, probably bearing the apertures of accessory glands.

Tracheal pits occur scattered over the surface of the body, as seen in sections of P. oviparus (fig. 5, *Tr. P.*). In this species (and probably in the others) there is a tracheal pit immediately in front of the mouth, and a pair of very large ones opening in the buccal cavity just behind and close to the base of the inner jaw on each side, and running backwards for some distance, at first just outside the lateral nerve-cords (fig. 5, *B. Tr.*) and then above them and just inside the salivary glands. These buccal tracheal pits have a thick chitinous lining, and may be traced back in a series of transverse sections very nearly to the level of the second pair of walking legs. They give off along their course and from their extremities an immense number of very fine tracheal tubes. When the jaws are removed, these enormously elongated tracheal pits may be pulled out in connection with them, and the chitinous lining of the pit appears to pass over into the chitinous covering of the smallest accessory tooth of the inner jaw.

Integument.—The structure of the integument closely resembles that described by Gaffron (1) for P. Edwardsii. As usual, it is furrowed by narrow transverse grooves, and produced into papillæ of varying size on the intervening ridges. There is approximately a single row of papillæ on each ridge. The pigment is lodged in the polygonal, nucleated, epidermic cells, outside each of which the cuticle forms a small, transparent, sharp-pointed, scale-like spine.

These small spines are prominent upon the papillæ, each of which may bear in addition a single spine at its apex.

On the spinous pads of the feet the spines are long and slender, and covered near the base with numerous minute secondary spines.

Along the mid-dorsal line there runs a very narrow longitudinal groove (figs. 5, 6, *D. F.*), from the floor of which pigment is absent, giving rise to a narrow white line which may be concealed by overarching of the lips of the groove in contracted specimens.

The predominant colour of the pigmented epidermic cells, when seen by transmitted light, is a beautiful indigo-blue, which may be replaced by green, tawny orange, brown, or nearly black, giving rise to a variety of patterns, which will be described when dealing with the specific characters.

The eyes appear externally as a pair of small, pearl-like, hemispherical protuberances in the usual situation, one just behind and on the outer side of the base of each antenna. In one specimen of O. oviparus the eyes appeared of a bright red colour.

c. Internal Anatomy.

General.—The internal anatomy of Ooperipatus (as exemplified by O. oviparus and O. viridimaculatus) agrees so closely in most respects with the well-known Peripatus type, that it seems almost superfluous to do more than refer to the general dissections shown in figs. 4 and 27.

The slime-glands are enormously developed, so that when unravelled they are much longer than the entire animal. When the animal is starved for some time, the tubular slime-reservoir becomes greatly distended by the accumulation of the secretion, which the animal has been unable to make use of in capturing its prey (fig. 27). I have elsewhere (**4**) pointed out that in O. insignis the secretion of the slime-glands contains very numerous corpuscles, but as the liquid rapidly hardens into an enamel-like mass on exposure to the air, it is difficult to say whether or not they are amœboid, as is the case with the similar corpuscles found in the liquid discharged from the nephridia (in O. oviparus).

Reproductive Organs of the Male.—The male organs of reproduction are, owing to the small size of the animal and the brittle nature of the organs themselves, extremely difficult to dissect in spirit-preserved material. I have, however, made some observations on the subject in the case of O. viridimaculatus, and the following notes are perhaps worth recording.

The unpaired portion of the male duct (vas deferens) is extremely long, considerably exceeding the entire length of the animal when at rest. It has very much the same structure as described by Gaffron (**1**) in the case of P. Edwardsii. Its middle portion contains a long spermatophore, while the terminal portion forms a long muscular ductus ejaculatorius. The spermatophore is in general similar to that of P. Edwardsii. It appears to contain no ripe spermatozoa, but numerous spherical sperm mother-cells. It is irregularly swollen out at intervals, but the sperm mother-cells occur throughout almost the entire length. The outer cover of the spermatophore is a thick, homogeneous, transparent, apparently chitinous sheath, and there appear to be no spherical globules, such as occur on the surface of the spermatophore in P. Edwardsii.

Reproductive Organs of the Female.—Of greater interest are the internal reproductive organs of the female, which I have been able to study in freshly-killed specimens, and of which I have already (**15**) given a short account in the case of O. oviparus. The ovary (O. oviparus and O. viridimaculatus) is as usual placed far back in the body cavity above the alimentary canal (figs. 4, 6, 12, 27, 31). It consists of right and left halves united with one another in front and behind (fig. 12), and attached by a mesoarium to the pericardial septum in the mid-dorsal line. It contains a large number of eggs, varying enormously in size according to the amount of yolk which they have received, the structure of which will be considered in the next section. The wall of the ovarian tubes is extremely thin and delicate, and in such a state of collapse that the tubular character is extremely difficult to demonstrate. The eggs project into the body-cavity from the outer surface of the ovary in all stages of intra-ovarian development, the larger ones being attached by short epithelial pedicles (fig. 13) and containing much food yolk, and the entire structure, when exposed by dissection, appears as a mass of eggs held together by a thin, transparent membrane, but readily separable into right and left halves except in front and behind.

The oviducts, owing to their great length, are in their natural position much convoluted in the hinder part of the body-cavity (fig. 31), but do not extend forwards much, if at all, beyond the ovary itself. They have a common origin from the posterior end of the ovary (figs. 4, 12, 27), with which they are directly continuous. There are no receptacula ovorum, but the receptacula seminis (figs. 4, 11, 12, 27) are well developed, and each opens as usual by two short ducts (fig. 11) into the oviduct of its own side at only a very short distance from the ovary. The receptacula seminis may contain spermatozoa, and it is difficult to believe that the latter enter the body of the female through the integument, as has been suggested for P. capensis.[1] Both the extreme toughness of the integument and the presence of receptacula seminis seem to argue against such a hypothesis.

In O. oviparus (fig. 4) I was able to recognise a division of the oviduct into three parts, though by no means sharply defined. All three parts are narrow, except where swollen out by the contained eggs. The first is very short, and extends from the commencement of the oviduct in front to the receptaculum seminis behind. Its wall is much folded, and provided with little irregular protuberances (figs. 11, 12, *Pr. O.*) on the side opposite to the receptaculum. The middle and last portions of the oviduct are of about equal length; the former has very thick glandular walls and the latter very thin

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[1] Compare Sedgwick (4).

membranous walls, though whether the difference is simply due to stretching by the contained eggs may be regarded as an open question. At their hinder ends the oviducts unite in a thick-walled, muscular, triangular sac (figs. 4, 9, 10, *Tr. S.*), whose posterior angle is continued into the ovipositor. Over this sac the nerve-cords pass, enlarging upon its dorsal surface to form a pair of especially large ganglia. The ovipositor is a thick-walled muscular organ, with an outer layer of more or less longitudinally and an inner layer of more or less circularly or obliquely arranged muscle-fibres. Eggs were found in the middle and last portions of the oviducts, but much more abundantly in the last. Their number, of course, varies; thus in one specimen there were three eggs in each oviduct; in a second, six in one and seven in the other; in a third, eight in one and nine in the other.

In O. viridimaculatus the structure of the female reproductive organs (figs. 27, 31) is closely similar, but I have not detected any differentiation corresponding to that between the second and third parts of the oviduct in O. oviparus, while the short proximal division of the oviduct in front of the receptaculum seminis is devoid of distinct protuberances, though its wall is folded. The number of eggs produced in this species appears to be smaller than in O. oviparus, for of the two freshly killed specimens dissected, one (fig. 31) contained only a single egg in the right oviduct and none in the left, while the second (fig. 27) contained only two in the right and one in the left oviduct; the former specimen, however, had two very large ovarian eggs, apparently almost ready to enter the oviducts (fig. 31).

d. Eggs and Development.

The Question of Oviparity.—Notwithstanding the scepticism of certain writers, who have apparently never thoroughly investigated the species in question, I do not think that any impartial observer could hesitate for long in pronouncing both O. oviparus and O. viridimaculatus to be genuinely oviparous, and, by analogy, O. insignis may pretty safely be included in the same category. As, however, the eggs have not yet been actually observed in the case of the latter species, it will be as well to reserve our final judgment in this case, and the following remarks, of course, apply only to the two former.

In the case of O. oviparus, I have already (**6**, **7**, **8**, **9**, **10**, **11**, **12**, **15**) entered pretty fully into the question of the egg-laying habit; some years ago eggs were laid by this species in my vivarium at Melbourne, one of which, after an extraordinarily long period of development (seventeen months), finally hatched out. In the case of O. viridimaculatus, only one deposited egg has yet been observed, and that was found by me last autumn in rotten wood in which a specimen of O. viridimaculatus had been packed for transmission, the animal itself having unfortunately died on the journey.

Equally strong evidence is afforded by the fact that no specimen of either species has yet been found to contain recognisably developed embryos, while nearly all the females that have been dissected have contained large thick-shelled eggs. In other species, such as P. Leuckartii (the common New South Wales species), as is well known, the adult females invariably contain developing embryos enclosed only in very thin transparent membranes.

The idea that the deposition of the eggs by Ooperipatus is merely an abnormal phenomenon, such as occasionally occurs in Peripatus, has been practically refuted by Steel (**1**), who observes of P. Leuckartii (New South Wales) that "pregnant females somewhat readily extrude the young when distressed by close confinement or uncomfortable conditions. Frequently soft adventitious eggs are laid. These bear no resemblance to those described by Dendy from P. oviparus, but are quite smooth and have a very flaccid thin envelope. They very soon break up into a drop of turbid liquid. My supposition is that they are merely ova which have escaped fertilisation, and are thus making their natural exit from the body."

The presence of the ovipositor in Ooperipatus alone amongst Onychophora is in itself strongly indicative of the oviparous habit, while the elaborate and closely similar structure of the egg-shell in both species in which it has been observed also indicates that the habit is constant and normal.

The Eggs.—The ovarian eggs (O. oviparus), formed presumably from the epithelial cells of the ovarian tubes, range in size from about 0·037 mm. to about 1·4 in diameter. In the young ovarian egg (fig. 14), as seen in sections stained with borax carmine, the vitelline membrane, if present, is very thin, the cytoplasm uniformly and very finely granular, and the nucleus very large in proportion to the entire egg. There is a very distinct nuclear membrane, and a single large and remarkably well-defined spherical nucleolus, with finely granular, darkly-staining contents. The nucleolus is placed excentrically, and around it the nucleoplasm stains very lightly, and sometimes at any rate has the appearance of being vacuolated (fig. 14). Outside this light area the nucleoplasm stains fairly darkly with borax carmine. In older ovarian eggs (fig. 15) the vitelline membrane is much thicker and the cell-body has increased in size much more rapidly than the nucleus, owing to the deposition in the former of large quantities of food-yolk, which appears first in the form of minute highly refringent granules thickly scattered through the cytoplasm (fig. 15). In still older ovarian eggs these granules appear to be arranged around spherical globules of some clear transparent substance (fig. 16). Some of these globules occupy the interior of irregular polygonal corpuscles slightly larger than themselves (fig. 16).

In order to study further the structure of the yolk, a quantity was removed from an egg which had passed into the oviduct. This material, which was obtained from a specimen of O. oviparus which had been preserved for a long time in alcohol, was partly treated with osmic acid, and partly stained with eosin and examined in oil of cloves. The yolk (fig. 17) was found to consist chiefly of the clear, transparent globules above mentioned, each enclosed in a polygonal corpuscle of almost homogeneous structure. The polygonal shape of the corpuscles is apparently due to mutual pressure. Their diameter is about 0·016 mm. Both the globular body and the enclosing corpuscle appear to be stained fairly darkly by alcoholic solution of eosin, but osmic acid (2 per cent. solution) has little effect on either, and in sections treated by the borax-carmine and acid-alcohol method they appear quite unstained. Whether the highly refractive yolk granules observed in the ovarian eggs and shown in fig. 15 have any relation to the corpuscles and their contained globules, it is impossible at present to say with any degree of certainty, but it seems not unlikely that the yolk is first deposited in the finely granular form, and subsequently converted into the comparatively large globules with their enveloping corpuscles. The appearances shown in fig. 16 support this hypothesis.

The Egg Envelopes.—The ovarian egg, as we have already seen, is enclosed in a distinct, transparent, apparently structureless vitelline membrane, which attains only a moderate thickness, and persists inside the chorion or egg-shell for a very long time, probably throughout the entire development, for I found it around an embryo in an egg which had been laid for at least eight and a half months. This vitelline membrane is, I believe, homologous with the thin membrane which alone surrounds the embryo of Peripatus Leuckartii (New South Wales), and which Steel (1) has shown to persist until birth. Willey (1) considers this membrane in the New South Wales species to be a chorion and not a vitelline membrane, but I can see no reason for maintaining this view. The "shell" described by Miss Sheldon (2) in the ovarian eggs of P. novæ-zealandiæ, P. Balfouri and P. capensis, is also probably a vitelline membrane, but the shell which the same writer [Sheldon (1)] describes as lying outside the vitelline membrane in the uterine egg of P. novæ-zealandiæ is no doubt correctly regarded as a chorion.

In Ooperipatus oviparus and O. viridimaculatus the chorion is very strongly developed and has an elaborate structure. It is formed while the egg is passing down the oviduct, evidently partly, if not entirely, by a secretion of the walls of the latter, and is, I believe, homologous with the coating of the spermatophore in the male and with the chorion of the uterine egg in P. novæ-zealandiæ.

The structure and mode of formation of the chorion are, however, extremely difficult to understand, and I propose to describe it separately in the two species in which it has been observed.

In O. oviparus I have observed three well-marked stages in the development of the chorion, which we may term A, B, and C, respectively.

Stage A.—This stage I have observed only in a specimen from Cooran, Queensland, collected by Professor W. Baldwin Spencer, in October, 1891. In surface view the chorion exhibits a finely and uniformly punctate appearance, except over certain areas which appear clear and transparent (fig. 18). These clear areas are rounded in outline, and distributed at fairly regular intervals over the chorion. In a specimen stained with eosin the clear areas seem to be crossed by very irregular networks of darkly stained threads, and in many of them a darkly stained nucleus-like body is visible (fig. 18). Possibly each of the clear areas marks the position of an epithelial cell, derived either from the ovarian follicle or from the wall of the oviduct, but the scanty material at my disposal has not enabled me to decide this question. In optical section (fig. 19) the chorion is seen to be very thick (about 0·02 mm.), except in places corresponding to the clear areas, where it thins out very greatly. It is also seen to be marked by fine vertical striæ, possibly canaliculi, whose cross sections undoubtedly give rise to the punctate appearance seen in surface view. The fact that this specimen was collected in the spring probably accounts for the incomplete development of the chorion; the eggs would probably not be deposited till much later in the season, as I shall show subsequently.

Stage B.—This stage was found in an animal which had lain for a long time in spirit previous to dissection, and the chorion had assumed a brown colour. Where thin places occurred in the Queensland specimen we now find thick ones, forming rounded protuberances very regularly scattered over the surface (figs. 20, 21, 22). The chorion now consists of two distinct layers, an inner much thicker one exhibiting radial striation and evidently corresponding to the chorion as already described in Stage A, and an outer one which is a new formation—or at any rate was only beginning to be formed in the preceding stage. This outer layer is developed chiefly, if not entirely, over the thin clear areas in the inner layer, which thus come to protrude externally in the form of low, rounded knobs. The outer layer is for the most part clear and structureless, and has a chitinoid appearance, but in this particular specimen a group of highly refringent granules is very conspicuous in the middle of each protuberance. This clear outer layer of the chorion probably increases in thickness as the egg passes down the oviduct.[1]

Stage C.—This stage occurs in eggs which have been deposited, and may be regarded as the mature condition. The two layers are still clearly recognisable (figs. 25, 26). The inner one exhibits the usual radial striation, but it no longer shows the thin areas of the first stage, which seems to indicate that unequal thickening has taken place in it. The outer layer is clear and transparent, and the refringent granules of the preceding stage are no longer visible. The extent to which it has become thickened varies in different cases; fig. 26 shows, in optical section, a specimen in which the protuberances remain comparatively low, though the outer layer is clearly recognisable even between them. Fig. 25, on the other hand, is drawn from a specimen in which the protuberances were remarkably strongly developed. After the deposition of the egg, the outer layer of the chorion

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[1] It seems possible that the nucleus-like bodies observed in Stage A may belong to cells which are concerned in the formation of the outer layer of the chorion.

undergoes a certain amount of wrinkling, probably in drying, and the wrinkling gives rise to the extremely characteristic surface pattern or sculpture to which I called attention (cf. 7) long ago, and samples of which are shown in figs. 23 and 24. It will be seen that the pattern is not quite identical in all cases, the differences, doubtless, depending upon the thickness of the outer layer and the particular conditions under which drying takes place.

The views expressed above as to the formation of the chorion in Ooperipatus oviparus differ to some extent from my previously expressed ideas on the subject, but the question is an extremely difficult one, and cannot even yet be regarded as by any means finally settled. We may, however, now regard it as certain that the chorion consists of two layers, an inner thick and radially striated layer, and an outer clear layer which is thickened over certain areas to form mound-like protuberances. The fully formed chorion is a tough, flexible membrane, varying in thickness up to about 0·04 mm. (exclusive of protuberances). When newly laid it has a pale yellow colour, but preserved specimens may become much darker, and the deposited eggs darkened greatly in course of time.

In Ooperipatus viridimaculatus the chorion certainly has a structure very similar to that exhibited by O. oviparus. I have observed stages corresponding to B and C of the former, B in the oviduct and C after deposition. In the former I was unable to detect the radial striation in the very thick inner portion, but the rounded protuberances on the outside were quite distinct. In the latter (figs. 32, 33) the radial structure was indicated by the strong tendency to split up radially which the chorion manifested on compression. The rounded protuberances on the outer surface had become to some extent wrinkled (fig. 32), but not to the same degree as seems to be usual in O. oviparus. It must be borne in mind, however, that only a single egg of O. viridimaculatus was observed after deposition, and that may possibly have been prematurely laid, owing to the unfavourable conditions which resulted in the death of the parent.

Number of Eggs produced; Size and Shape.—The number of eggs produced by the different species of Onychophora appears, as in other animals, to be inversely proportional to the amount of yolk, and consequently to the size of the egg. Thus in the viviparous P. Leukartii (New South Wales) the ovarian egg is comparatively small and with little yolk, the largest ovarian egg which I have seen measuring only about 0·37 mm. in greatest diameter,[1] while I have myself found as many as thirty embryos in the uteri of one female, and Mr. Fletcher (**7**) has found as many as fifty-three. In P. novæ-zealandiæ the egg, according to Miss Sheldon, measures as much as 1·5 mm. in greatest diameter, and in this species, which is also viviparous, Captain Hutton (**1**) found from four to twenty-six embryos in each female, and Miss Sheldon from seven to eighteen. In O. oviparus the eggs are a little larger, measuring (in the oviduct and when laid) about 1·9 by 1·5 mm., while the number found in the two oviducts varied from six to seventeen. In O. viridimaculatus the eggs are perhaps a shade longer and somewhat narrower in proportion to their length, and the number produced appears to be still smaller, the three females dissected containing respectively only one, three, and seven eggs in the two oviducts.

The eggs are deposited in the winter or in the late autumn, which perhaps accounts for the fact that in the only specimen of O. oviparus captured and dissected at the end of July, the oviducts were found to be empty.

Only one batch of deposited eggs of O. oviparus and a single deposited egg of O. viridimaculatus have, as yet, so far as I am aware, been obtained. The former was laid (at any rate fourteen of them) between May 18th and July 31st, 1891, in a vivarium in Melbourne, in which there were three females and one male animal. Fourteen eggs

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[1] As I have carefully examined the ovarian eggs in only one specimen, killed in January, this result needs confirmation.

were found beneath and in the crevices of bits of rotten wood placed in the vivarium, and a fifteenth, though perhaps laid about the same time, was not found till the vivarium was completely turned out on September 16th.

The single deposited egg of O. viridimaculatus was found on April 18th, 1900, amongst rotten wood in which an adult animal had been forwarded to me from Lake Te Anau, New Zealand. The package was unfortunately delayed in transit, and the animal itself was dead when it arrived, so that the deposition of the egg may have been hastened by abnormal conditions.

Development.—Owing to the great scarcity of material, it is impossible to say much under this head, and the remarks which I have to offer, except as regards the newly laid egg, are based exclusively upon O. oviparus. Two facts, however, stand out clearly, the first being that the newly deposited egg contains no embryo recognisable by ordinary means, and the second that the development progresses extremely slowly, and may occupy as much as seventeen months from the time of laying to the time of hatching.

The recently laid egg is filled with a milky fluid containing very many yolk granules, the structure of which has already been described (fig. 17).

The first embryo, already far advanced in development, was removed on November 30th from the egg found on September 16th, so that it was at least ten weeks old from the time of oviposition, and probably a good deal older. Within the chorion the embryo was surrounded by the thin, transparent, vitelline membrane, which fitted closely on to it and was very difficult to remove. The total length of the embryo, exclusive of the antennæ, is about 4 mm. It is spirally coiled, making rather more than one complete turn of the spiral, so that the posterior extremity lies against the side of the neck, pointing in an opposite direction from the head, and the ventral surface occupies the inside of the curve. The form of the body is already very like that of the adult, except that the head is larger in proportion.

The head when viewed from above appears broadly and squarely truncated between the bases of the antennæ, one of which has been accidentally broken off, the other pointing forwards. The two cerebral ganglia and the eyes (with pigment) are clearly recognisable. The antennæ are well-developed and annulated. Owing to the position of the embryo (which is now mounted in Canada balsam) it is possible to see only one of the oral papillæ, and the jaws are completely hidden from view. There are perhaps nine pairs of walking legs, but it is impossible to count the exact number. They appear as blunt outgrowths of the body, ventro-lateral in position. No claws are yet visible, and little or no pigment is yet developed in the integument.

The second embryo obtained was at least eight and a half months old from the time of egg-laying, and was already a perfect young animal, differing externally from the adult only in its smaller size and less deeply pigmented skin. It was removed from the egg on April 14th, 1892, when only three eggs remained in the hatching box, the others having been taken away, as they showed signs of going bad.[1] One of the remaining three had been showing dark pigment inside for some days past. This egg I removed and dissected. I found the shell of a much darker (yellow) colour than when laid, a good deal crumpled on the surface, and very soft, as though beginning to decay away. The contained embryo was removed and found to be in excellent condition. It was enclosed in the usual vitelline membrane within the chorion. As in the previous case it was tightly coiled up. When uncoiled it measured about 5 mm. in length (exclusive of the antennæ) and 1 mm. in breadth. All the appendages were developed, namely, antennæ, oral papillæ, jaws, and fifteen pairs of claw-bearing legs. The eyes were conspicuous at the bases of the antennæ, and the antennæ themselves showed each about twenty deeply pigmented annuli. The

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[1] The majority of the eggs unfortunately perished, shrivelling up and being attacked by a mould; which is hardly to be wondered at when we consider the difficulty of keeping the conditions suitable for so long a period.

remainder of the body was nearly white, but very distinct isolated pigment patches (chiefly indigo-blue, with a few specks of orange) appeared scattered pretty abundantly over the legs and back. The mouth was surrounded by the very characteristic, thick, transversely furrowed lip. The dermal papillæ were very obvious, and exhibited the characteristic spines, the cuticle being very strongly developed. The claws on the feet were very distinct. The alimentary canal was full of granular food-yolk.

The embryo just described was between eight and a half and eleven months old from the time of egg-laying, and was apparently just about ready to hatch. It is therefore very remarkable that another embryo of the same batch remained in the egg for another eight and a half months (or thereabouts) before hatching.

About the end of 1892 only a single egg remained in the hatching box, all the others having either gone bad or been used for investigation. On January 3rd, 1893, not having opened the box for some days, I found this egg, so far as I could tell, in its former position, lying on a small piece of rotten wood, which rested on the glass bottom of the hatching box. The shell, however, was split on one side, and the young animal had made its escape. It was found lying dead on the glass, 25 mm. from the egg-shell. The animal was itself only about 5 mm. in length, so that, even assuming that it had moved in a perfectly straight line, it must have crawled for a distance of five times its own length, off the rotten wood and along the glass to the position in which it was found.

To the naked eye the young animal appeared of a pale greenish colour. It cannot have been dead for very many days, but decomposition had already set in, and the body adhered to the glass upon which it lay, so that it could not be removed without considerable injury. I mounted it in Canada balsam, however, and even in its present condition it shows under the microscope such characteristic features as claws and jaw-blades and indigo-coloured pigment. The ruptured chorion also still shows a portion of the characteristic pattern on the outside.

It appears, therefore, that the only egg yet known to hatch out, did so after being laid for about seventeen months. There is no reason, however, to believe that under natural conditions the process of development takes as long as this, and the apparently fully-formed embryo obtained at about eight and a half months indicates a normally shorter period. Development was possibly retarded by the eggs being kept in a room which was unusually cool in summer; probably, also, conditions of moisture and the softening by decay of the tough chorion, have a good deal to do with the date at which the young animal escapes.

e. Distribution and Œcology.

The genus Ooperipatus, so far as we know at present, is confined to the eastern portion of Australia (including Tasmania for O. insignis) and New Zealand, so that its distribution forms a striking parallel to that of many vegetable types, and may be similarly accounted for by supposing it to have spread southwards at a time when New Zealand was connected with North-eastern Australia, probably not later than the cretaceous period. O. oviparus has been found in Victoria, New South Wales, and Queensland, O. viridimaculatus in the South and possibly also the North Island of New Zealand, and O. insignis in Victoria and Tasmania.

Like other members of the group, the species are all thoroughly cryptozoic, hiding away beneath stones or logs, or in the crevices of decaying tree trunks. O. oviparus is usually found beneath stones or fallen logs, either on the ground, or attached to the under surface of the stone or log which covers it. O. viridimaculatus, on the other hand, is, according to my experience, found in the interior of rotten tree trunks, which have to be broken to pieces in order to obtain specimens, and I think the same will usually be found to be true of O. insignis. All species seem to be very rare, though pretty widely distributed. Thus I have never heard of O. oviparus or O. insignis being found in anything like the quantity in which Steel (1) has found Peripatus Leuckartii in New South Wales, nor is O. viridimaculatus anything like so common in New Zealand as is P. novæ-zealandiæ.

The nature of the locality in which the logs or stones used as cover may occur varies greatly. Thus O. oviparus may be found under logs in a fern-tree gully, or under stones on a bare hill-side,[1] while probably the largest collection of this species[2] yet made was obtained at an altitude of 5000 feet or more, on Mount Kosciusko,[3] and amounted to thirty-five specimens.

f. Phylogeny.

The genus Ooperipatus evidently stands in the closest phylogenetic relationship to the other Australasian genus of Onychophora—Peripatoides, which occurs side by side with it both in Australia and New Zealand. The genus Peripatoides was founded by Pocock (1) in 1894, for the reception of the Australasian species of Onychophora, and characterised as having the legs furnished with only three spinous pads, and the generative aperture between the legs of the last pair and well in advance of the anus. These characters are also found in Ooperipatus, which is distinguished from Peripatoides, however, by its egg-laying habit and the presence of the ovipositor in the female.

Of Peripatoides I distinguish four species, as follows:

1. P. Leuckartii, auctorum,[4] with 15 (fifteen) pairs of claw-bearing legs and an accessory tooth on the outer blade of the jaw. Male with crural glands. Characteristic of New South Wales.

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[1] Compare Dendy (2).

[2] Steel (2) has identified the Kosciusko specimens as P. oviparus; they were described by Fletcher (3) as P. Leuckartii.

[3] Compare Fletcher (3).

[4] = P. Leuckartii, var. orientalis, Fletcher (7).

2. P. occidentalis,[1] Fletcher, with 15 (fifteen) pairs of claw-bearing legs and no accessory tooth on the outer blade of the jaw. Male with crural glands. Characteristic of Western Australia.

3. P. novæ-zealandiæ, Hutton, with 15 (fifteen) pairs of claw-bearing legs and no accessory tooth on the outer blade of the jaw. Male without crural glands. Characteristic of New Zealand.

4. P. Suteri,[2] Dendy, with 16 (sixteen) pairs of claw-bearing legs and no accessory tooth on the outer blade of the jaw. North Island of New Zealand.

In the presence of crural glands in the male, Ooperipatus is most closely related to the Australian species of Peripatoides, but in the structure of its eggs it stands nearer to P. novæ-zealandiæ. We may take P. Leuckartii and P. novæ-zealandiæ as typical of the Australian and New Zealand sections of their genus respectively. P. Leuckartii is viviparous. The ovarian eggs, so far as my experience goes, are comparatively small, and I can find no trace of a chorion, but only a vitelline membrane. P. novæ-zealandiæ, though viviparous, has eggs nearly as large as those of Ooperipatus, and according to Miss Sheldon, there is a second membrane (chorion) outside the vitelline membrane. Thus P. novæ-zealandiæ in the structure of its eggs to some extent resembles Ooperipatus, and this fact may help us to solve the vexed question whether the oviparous or viviparous habit is the more primitive.

This question has been recently discussed by Willey (**1**), and he has come to the conclusion that "the oviparity of P. oviparus, Dendy, is an acquired habit, and not in any way to be confused with the primitive deposition of alecithal ova." This may be very true, but I am inclined to think that even if the structure of the eggs is secondary, yet the viviparous habit must be regarded as still more recently acquired.

P. novæ-zealandiæ, with its large, heavily yolked eggs

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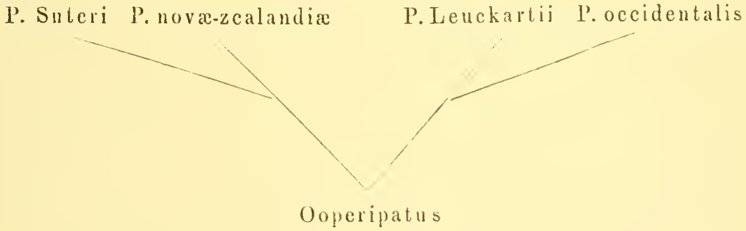
[1] = P. Leuckartii, var. occidentalis, Fletcher (**7**).

[2] = P. novæ-zealandiæ, var. Suteri, Dendy (**13**).

and chorion, may be either progressing towards a condition of oviparity or away from it. Organs are not usually developed ahead of their uses, and the chorion may be regarded as a vestigial structure inherited from oviparous ancestors, in which a chorion formed an essential protection to the deposited egg during the lengthy period of development. In P. Leuckartii and other viviparous species the chorion may have completely disappeared.

It is hardly likely that the oviparous habit should have been independently acquired by two or more different species in Australasia, but in no other part of the world. Yet, unless we regard P. novæ-zealandiæ as representing an ancestral form of Ooperipatus, which is hardly admissible, if only on account of the absence of the crural glands, this is the conclusion to which we should be forced if we accept the viviparous as being more primitive than the oviparous habit. If, on the contrary, we regard the oviparous habit as being the more primitive, it is not difficult to arrange the Australasian Onychophora in a phylogenetic series, which may be tentatively represented as follows :



Of the three species of Ooperipatus, two (O. insignis and O. viridimaculatus) are very nearly related to one another. Each has only fourteen pairs of walking legs and no accessory tooth on the outer blade of the jaw. O. oviparus, on the other hand, has fifteen pairs of walking legs and an accessory tooth, and is evidently very closely related to the New South Wales P. Leuckartii, though by no means far removed systematically from its congeners.

The occurrence of such closely allied species in Eastern

Australia and New Zealand respectively is very remarkable. They must have had a common origin, and the question arises, "Did the ancestral form enter Australasia from the north or from the south ?" Either view might be maintained. It may have spread northwards from an Antarctic continent or archipelago, as some of the Australasian plants are supposed to have done ; or it may have come from the north at a time when a more or less close connection existed between New Zealand and North-Eastern Australia. Personally I am inclined to favour the latter hypothesis, which seems to be supported by the distribution of Ooperipatus and certain other animals and plants at the present day. It is generally believed that New Zealand has been disconnected from the Australian continent since at least the close of the Cretaceous epoch, and the distribution of Ooperipatus, therefore, indicates a very remote antiquity for the egg-laying habit. In fact, we may believe that the oviparous species have persisted with little modification since the Cretaceous period. It is, of course, just possible that Ooperipatus spread from New Zealand to Australia, or vice versâ, across the Tasman Sea in comparatively recent times, but this appears to me highly improbable.

Wherever the ancestral form may have originally come from, it appears not only to have maintained itself successfully in Australasia, but to have given rise to several new species which have lost the primitive oviparous habit; in Australia P. Leuckartii and P. occidentalis, and in New Zealand P. novæ-zealandiæ and P. Suteri may be looked upon as descended from a common oviparous ancestor.

Thus the distribution of the Australasian species seems perfectly consistent with the view that the habit of laying large and heavily yolked eggs is more primitive than that of retaining the young in the uterus throughout the period of their development. This view is also strongly supported by the testimony of Sedgwick and Sclater, derived from the study of the development of viviparous species.

Sedgwick, dealing with the development of P. capensis, lays stress upon the large size[1] of the egg combined with the almost complete absence of yolk. He assumes "that the ovum of the Cape species has only recently lost its yolk, and that it may be compared to an ovum of the New Zealand form [P. novæ-zealandiæ] from which the yolk has been almost completely dissolved out by some reagent. As a matter of fact [he adds] it is impossible, with our present methods, to effect this complete solution of yolk and leave its protoplasmic framework; but what we cannot effect has been done by nature in the most complete manner, leaving an ovum which is little more than a loose protoplasmic spongework, excepting at one point where the protoplasm is more dense."

Willey (**1**), in discussing this question, observes that "the view that the egg of Peripatus capensis exhibits a stage in the process of acquiring yolk, instead of being a stage in the loss of yolk, could be maintained with equal force." Surely, however, it is hardly likely that the protoplasm would acquire a vesicular structure in anticipation of the formation of yolk; in order to justify us in accepting this view we should be obliged to show that the vesicular structure has some value altogether apart from yolk formation.

Writing on the development of a South American species (P. Imthurni) Sclater (**1**) also comes to the conclusion that the alecithal condition of the egg is secondary.

In this species the ovum appears to be much smaller than in P. capensis. The segmentation is complete, and there is no appearance of sponginess, such as occurs in P. capensis; "nor would one suspect, from the nature and size of the ovum, that it had been derived from a meroblastic ovum and had only comparatively recently lost its yolk. . . . Now, it seems to me that the loss of yolk has had precisely the same effect in the ovum of Peripatus that it has on the ovum of placental mammals, i. e. (1) diminution of the size of the ovum; (2) total segmentation, and (3) the formation of what I have termed the embryonic vesicle, which appears to me

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[1] Sedgwick gives the length of the youngest ovum found in the oviduct as 0·4 mm.

to be exactly analogous to the blastodermic vesicle of mammals."

I am aware that the loss of yolk by the mammalian ovum has been questioned, but it is possible to doubt anything, and the subject need hardly be discussed in this place.

The small number of legs in all the Australasian species—smaller in O. insignis and O. viridimaculatus than in any other known species except the South African P. brevis—might be used as an argument against their primitive nature. Bouvier, indeed, maintains (1) with some reason that the species with more numerous legs are more primitive than those with a smaller number, and that "in many respects the species belonging to Oceania [from Eastern Australia to New Zealand] mark the present limit of the evolution of the Onychophora." "In any case," he adds, "it appears to be quite certain that Central America and the Caribbean region have been the centre of origin and migration of the species of Peripatus."

Bouvier's knowledge of the Australasian species appears, however, to have been limited. Thus he adheres[1] to the old idea of fifteen pairs of legs being characteristic of the "Oceanian" forms; and, speaking of the jaws, he states that "here the accessory tooth disappears on the outer blade also," as if this were a character of all the Australasian species. He had, when he wrote, apparently never heard of Peripatus Suteri, P. insignis, or P. oviparus, and in another paper (3) he refers to P. novæ-zealandiæ as having fourteen pairs of "pattes." Nevertheless it is not necessary at present to dispute Bouvier's general conclusions as to the course of the evolution of the Onychophora, viz. that as they spread from their original home in America, "their limbs atrophied in succession posteriorly, and, at the same time, their number became more and more constant. The proximal spinulous arches followed, up to a certain point, the same regressive course; the nephridial papillæ of two pairs of limbs advanced by degrees towards the following

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[1] It must be remembered that this was written in 1900.

arch; the wrinkles in the skin became more complicated, then interrupted on the dorsal median line; and lastly, the dentiform armature of the jaws underwent successive reduction."

In accordance with these views, it is obvious that in most respects the genus Ooperipatus is by no means primitive, but it by no means follows that it may not, all the same, have preserved a primitive oviparous habit which has been lost in other forms. It is a singular coincidence that the only egg-laying Mammalia which now exist are confined to the same zoological region.

In concluding this discussion, I may say that, personally, I am strongly inclined to believe that the ancestors of at any rate all the Australasian Onychophora were oviparous, or, in other words, that Ooperipatus represents in this respect the ancestral form of Peripatoides. It also seems highly probable that the egg-laying habit was at one time universal throughout the group Onychophora, while the formation of an elaborate sculptured chorion may possibly be looked upon as another indication of relationship between the Onychophora and the Insects.

III. Description of Species and Synonymy.

1. Ooperipatus oviparus, Dendy. (Figs. 1, 4—26.)

Synonymy.

1887. ? Peripatus Leuckartii ("in all probability"), Fletcher. 'Proc. Linn. Soc. N. S. Wales,' vol. ii, series 2, p. 450.

1888. ? Peripatus Leuckartii, Sedgwick. 'Quarterly Journal of Microscopical Science,' vol. xxviii, p. 463.

1889. (Probably new species,) Dendy. 'Nature,' vol. xxxix, p. 366.

1889. (Probably not new species,) Sedgwick. 'Nature,' vol. xxxix, p. 413.

1889. Peripatus Leuckartii, Dendy. 'Proc. Royal Soc. Victoria,' vol. ii (new series), p. 51.

1890. Peripatus Leuckartii, Dendy. 'Handbook of Melbourne (A.A.A.S.),' p. 95; 'Victorian Naturalist,' vol. vi, p. 173; 'Annals and Magazine of Natural History,' series 6, vol. vi, pp. 121—123; 'Proc. Royal Soc. Victoria,' vol. iii (new series), p. 44.

1890. Peripatus Leuckartii, Fletcher (specimens from Mt. Kosciusko). 'Proc. Linn. Soc. N. S. Wales,' vol. v, series 2, p. 469; 'Annals and Magazine of Natural History,' series 6, vol. vi, p. 352.

1891. Peripatus Leuckartii, Dendy. 'Proc. Royal Soc. Victoria,' vol. iv (new series), p. 31; 'Zoologischer Anzeiger,' xiv, p. 461; 'Nature,' vol. xliv, p. 468; 'Victorian Naturalist,' vol. viii, p. 67.

1892. Peripatus Leuckartii, Spencer. 'Victorian Naturalist,' vol. ix, p. 30.

1892. (Common Victorian species of Peripatus,) Dendy. 'Report of the Australasian Association for the Advancement of Science, Hobart,' 1892, p. 375.

1892. (Larger Victorian Peripatus,) Dendy. 'Proc. Linn. Soc. N. S. Wales,' vol. vii, series 2, p. 267; 'Proc. Royal Soc. Victoria,' vol. v, p. 27.

1893. (Larger Victorian Peripatus,) Dendy. 'Nature,' vol. xlvii, p. 508, and 'Proc. Royal Soc. Victoria,' vol. vi (new series), p. 118.

1895. (Oviparous Victorian form,) Dendy. 'Report of the Australasian Association for the Advancement of Science, Brisbane,' 1895, p. 108.

1895. Peripatus oviparus, Dendy. 'Zoologischer Anzeiger,' xviii, p. 264, and 'Proc. Linn. Soc. N. S. Wales,' vol. x, series 2, p. 195.

1895. (Variety of Peripatus Leuckartii,) Fletcher. 'Proc. Linn. Soc. N. S. Wales,' vol. x, series 2, pp. 183, 194.

1896. Peripatus oviparus, Steel. 'Proc. Linn. Soc. N. S. Wales,' vol. x, series 2, pp. 98, 99, 102.

1897. Peripatus oviparus, Steel. 'Proc. Linn. Soc. N. S. Wales,' vol. xxii, p. 124.

1898. Peripatus oviparus, Willey. 'Anatomy and Development of Peripatus novæ-britanniæ,' pp. 35, 38.

1900. Ooperipatus oviparus, Dendy. 'Zoologischer Anzeiger,' xxiii, p. 510.

Description.—There are fifteen pairs of claw-bearing legs, each (including the last pair) with three pale-coloured spinous pads on its ventral surface. The proximal pad is much narrower but at the same time longer than the others, and the distal one is much the smallest. On the fourth and fifth legs the proximal pad is transversely divided into three parts, the middle part being very small and bearing the aperture of the nephridium. The foot bears three large primary papillæ, anterior, posterior, and dorsal, overhanging the pair of claws.

The inner jaw-blade (fig. 7) has one large tooth and about eight small ones; the number of the latter is probably not constant, and some of them are very minute. The outer blade (figs. 7, 8) has one large tooth, and one small, blunt, and feebly developed accessory tooth.

In the adult female, the ovipositor (fig. 9) is very conspicuous, even in a state of retraction, as an ovoid body of a pale yellow or orange colour, lying between the legs of the last pair. In specimens ordinarily contracted in spirit it is about as large as each of the legs between which it lies, but it is capable of great extension (fig. 10). Its surface is ornamented with minute spine-bearing papillæ, and the genital aperture is a slit at the apex, placed parallel with the long axis of the animal. I have seen no indications of crural glands or accessory genital glands in the female.

In the male, the genital aperture lies between the legs of the last pair, but is not specially prominent. Between it and the anus are a pair of apertures of accessory glands lying close to the middle line. Crural glands probably occur in all the legs except the first pair; their apertures may or may not be visible, according to the state of contraction. Those of the fifteenth pair of legs are rendered conspicuous by a pair of white papillæ lying in the angles between the leg and body at each side of the genital aperture; the others may also be indicated by white papillæ.

The predominant colours of the skin are red and indigo-blue, the former passing into yellow and the latter into black in some specimens. The pattern and relative amounts of the different colours vary greatly, but as far as my own personal experience goes the following appears to be the fundamental arrangement from which other types may be derived (compare fig. 1). On the dorsal surface is a series of segmentally arranged diamond-shaped patches, in which the red colour predominates. Each patch is made up of two triangles, whose bases face one another on each side of the narrow mid-dorsal longitudinal groove, while their apices lie over the legs, and at about one third of the distance from the mid-dorsal line to the insertion of the legs. The separation of the diamonds from one another is by no means complete, so that there are really two continuous bands of red, one on each side of the mid-dorsal line, with their outer margins deeply indented between the legs.

The edges of the mid-dorsal groove are often darkly pigmented, and may give rise to an apparently single median dark line when the lips of the groove are closed together by contraction. There is commonly, also, a dark edging to the red diamonds on their outer margin, forming a zigzag longitudinal stripe. This typical pattern may be almost, if not quite, obliterated by the replacement of the red pigment by dark indigo-blue, but even in very dark specimens it may still be represented by a row of small, pale yellow or red spots, each of which occupies the apex of one of the red triangles in typical specimens. The ventral surface is mottled in the different colours, but is paler than the dorsal, and exhibits no characteristic pattern. There is in the middle line a row of still paler areas, placed one between the legs of each pair but the last. Patches of dark indigo-blue are usually present on the under surfaces of the legs, near to their bases.

A number of variations of pattern have been described by myself (**2**) in specimens from Ballarat, Victoria, and by Fletcher (**3**) in specimens from Mount Kosciusko, which Steel (**2**) has shown to belong to this species.

A good-sized female specimen, when crawling, measured 39 mm. in length, exclusive of the antennæ. Full-grown females preserved in alcohol and contracted in the usual manner (not extended by drowning) measure about 20 mm. in length (exclusive of antennæ) by 4·5 mm. in greatest breadth (exclusive of legs). The presence in the body of the very large eggs may make a female appear much broader than would otherwise be the case (compare fig. 6).

The males seem to be commonly somewhat smaller than the females, but not very much. Further information is wanted on this head, however, and also on the proportions in which the sexes occur. As to the latter question I may say that there does not appear to be any great difference between the numbers of the two. I have not kept any record myself, but Mr. Fletcher (**3**), amongst thirty-five specimens from Mount Kosciusko, found eighteen males and seventeen females.

Discussion of Relationships.—That Ooperipatus oviparus is in many respects very closely related to the common viviparous New South Wales species (Peripatus Leuckartii) there cannot be the slightest doubt. Indeed, apart from the oviparous habit and, in correlation therewith, the presence of an ovipositor in the female and of a chorion outside the vitelline membrane of the egg, I know of no characters by which it could be distinguished, for the pattern of the skin is in both species too variable to be satisfactory, and the two may resemble one another very closely in this respect.

In the case of female specimens, the presence of the conspicuous ovipositor affords an easy means of recognition, and I am glad to be able to quote in this connection the testimony of Mr. T. Steel, who has perhaps examined a larger number of individual specimens of Australian Onychophora than any other observer, having collected in a single summer 579 adult specimens of the viviparous New South Wales species (P. Leuckartii), of which 390 were females.[1] Writing in 1897, Mr. Steel observes (**2**) : " I desire to place on record the occurrence in New South Wales of P. oviparus, Dendy, the Victorian form of Peripatus. While collecting in January of this year, between Exeter and Bundanoon (Moss Vale district), on turning over a log I noticed a Peripatus, which from its attitude and general appearance specially attracted my attention. This proved to be a female specimen of the above species, and, so far as I am aware, this is the first occasion on which its occurrence in this colony has been definitely recorded. The lozenge-shaped pattern which characterises most of the specimens found in Victoria is well displayed ; and the fact of the ovipositor being fully extruded in the specimen, which I now exhibit, is sufficient guarantee of its identity. When visiting the Australian Museum a few days ago, I had an opportunity of examining the specimens of Peripatus preserved there, and I was interested in noticing that those collected by Mr. Helms in 1889 at Mount Kosciusko belong to the same species. All of the females in the museum collection from that locality which I examined have the ovipositor plainly visible, and in many of them it is fully extruded."

The difficulty of distinguishing O. oviparus from P. Leuckartii (except by the ovipositor) was forcibly illustrated in the case of the Queensland specimens collected by Professor Baldwin Spencer at Cooran. " After long searching," says Professor Spencer (**1**), " I came across Peripatus Leuckartii, very dark purple in colour, and evidently similar to the typical form and without the curious diamond-shaped markings characteristic of the Victorian form. Though searching hard, I only found nine specimens altogether, and all these close to Cooran." I myself also believed these specimens (one of which I still have in my possession) to belong to the viviparous species P. Leuckartii, and have

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[1] Steel (**1**).

referred to them as such in earlier publications, being misled partly by the very dark colour, and partly by the fact that the chorion was incompletely developed, the specimens being collected very early in the season (October); but the ovipositor in my specimen is very conspicuous and fully protruded to a length of 4 mm. (fig. 10), the specimen (if I remember rightly) having been killed by drowning, while microscopic investigation of the eggs showed the chorion to be really present although incomplete (figs. 18, 19).

The specific distinction between the males of O. oviparus and P. Leuckartii is a matter of much greater difficulty, and as yet I fail to see how they can be distinguished otherwise than by the company in which they are found. As the females differ, so far as we know at present, only in the structure of the reproductive organs, this is not surprising.

Localities.

Victoria.—Warragul (coll. Baker, probably this species) Warburton (coll. Dendy); Ballarat (coll. Nye and Avery); Macedon (coll. Hogg and Dendy); Mount Baw Baw (coll. Frost); Walhalla (coll. Hogg); Pyalong (coll. Lucas, male only).

New South Wales.—Mount Kosciusko (coll. Helms); Moss Vale District (coll. Steel).

Queensland.—Cooran (coll. Spencer).

2. Ooperipatus viridimaculatus, Dendy. (Figs. 2, 27—33.)

Synonymy.

1900. Peripatus viridimaculatus, Dendy. 'Nature,' vol. lxi, p. 444; 'Trans. and Proc. N. Z. Inst.,' vol. xxxii, p. 436.

1900. ? Peripatus viridimaculatus (probably), Fletcher. 'Proc. Linn. Soc. N.S.W.,' vol. xxv, p. 116.

1900. Ooperipatus viridimaculatus, Dendy. 'Zoologischer Anzeiger,' xxiii, p. 510.

Description.—There are fourteen pairs of claw-bearing legs, each with three spinous pads on its ventral surface. The proximal pad is much narrower than the others, and contains a considerable portion of the orange pigment, while the two others are dark indigo-blue in colour. The proximal pad also sometimes shows a tendency to break up transversely into papillæ, so that it is altogether much less conspicuous than the other two, and in the last pair of legs may be scarcely recognisable. The median pad is the largest. On the fourth and fifth legs the proximal pad is transversely divided into three parts, the middle part being small and bearing the nephridial aperture. The foot bears three large primary papillæ—anterior, posterior, and dorsal overhanging the pair of claws.

The inner jaw-blade (fig. 30) has one large tooth and about seven small ones. The outer blade (fig. 29) has no accessory tooth.

The ovipositor of the female (figs. 27, 31) resembles that of O. oviparus, lying between the legs of the last pair and bearing the genital aperture as a longitudinal slit at its apex. There are no external indications of crural or other accessory glands in the female.

In the male the genital aperture also lies between the legs of the last pair, and just behind it, at the base of the short broad anal cone, lies a pair of small white papillæ, doubtless indicating the apertures of accessory glands. Whitish papillæ, indicating crural glands, occur on all the legs of the last nine pairs, i. e. from the sixth to the fourteenth inclusive. As usual they lie just distal to the nephridial aperture, except in the last pair of legs, where there is apparently no nephridial aperture, and the papillæ lie close to the genital aperture on either side. All these crural papillæ are very conspicuous.

The general coloration of the dorsal surface (fig. 2), when only slightly magnified and examined as an opaque object, appears to be dark grey mottled with orange, with a dark median band, fifteen pairs of green spots arranged segmentally over the appendages from the oral papillæ to the last pair of legs, and a black or nearly black triangular patch between each two successive green spots on each side. The ventral surface under the same conditions appears to be mottled grey or violet, with pale areas between the legs.

Microscopic examination of the skin, after it has been rendered transparent in Canada balsam, shows that three very distinct pigments take part in the production of the pattern, viz. indigo-blue, dull brownish orange, and bright emerald green. In the mid-dorsal line is the usual very narrow unpigmented groove or fissure; this is bordered on either side by a dark narrow band, partly of indigo-blue and partly of orange brown. Outside this comes a broader band, chiefly of orange. Then comes the row of irregularly shaped green spots alternating with triangular dark areas, the latter consisting almost exclusively of dark indigo-blue and the former of bright emerald green, the two colours being separated by outward continuations of the orange bands. Outside the row of green spots comes a zone in which dark indigo-blue and orange-brown papillæ are about equally intermingled, the orange increasing immediately below the intervals between the legs. Ventrally only the orange and indigo-blue occur, and both lighter in tint than on the dorsal surface. The legs are mottled with orange-brown and indigo-blue, the two distal spinous pads and the large primary papillæ of the feet being indigo-blue. The antennæ are for the most part dark indigo-blue, but about every fourth annulus is orange. The ovipositor is pale dull orange.

Of course, as in other species, the colour and pattern may vary, but the above may be taken as typical, and I have never noticed any specimen without the green spots.

The length of an adult female when fully extended and crawling was 31 mm. and the breadth 3 mm., exclusive of antennæ and legs, the fully extended antennæ being about 5 mm. long. The males appear to be a little smaller. The two sexes seem to occur in about equal numbers. Out of thirty specimens which I collected myself at Lake Te Anau nine were female, twelve male, and nine young, while three specimens sent to me subsequently from the same locality by Mr. Donald Ross were all female.

Discussion of Relationship, etc.—Whether or not the specimens recorded by Fletcher (8) as probably belonging to P. viridimaculatus are really referable to this species must remain doubtful until we have further information about them. The only published account of them known to me is the following, which I quote in full:—" Mr. Fletcher exhibited five specimens (male 2, female 3) of a Peripatus with fourteen pairs of walking legs, the males with white papillæ on the legs of the posterior nine pairs, from the North Island of New Zealand. The specimens were obtained by Mr. C. T. Musson near Te Aroha in the early part of last January. They will probably prove to be referable to the species for which Professor Dendy ('Nature,' March 8th, 1900, p. 444) has recently proposed the name P. viridimaculatus, founded on specimens collected at the head of Lake Te Anau in the South Island. The (spirit) specimens exhibited, however, do not in their present condition seem to show the 'fifteen pairs of green spots arranged segmentally,' which Dr. Dendy describes as characteristically present in the specimens from the South Island." Whether these specimens belong to O. viridimaculatus or not, it is indeed a most remarkable coincidence that a fourteen-legged species should have been discovered in the North Island of New Zealand certainly within a few days of the time when I discovered one in the South! The green pigment in my specimens does not appear to be soluble in spirit.

Extremely interesting is the close relationship of O. viridimaculatus to the Tasmanian and Victorian species O. insignis. Indeed it would be difficult, if not impossible, to distinguish the two species except by the characteristic colour markings. I have seen no trace in O. insignis of the bright emerald-green pigment which forms such a characteristic feature in O. viridimaculatus, and the absence of the green spots, if confirmed, may necessitate the identification of the Te Aroha specimens with the Victorian and Tasmanian species.

Localities.

New Zealand.—South Island: Clinton Valley, head of Lake Te Anau (coll. Dendy and Ross). ? North Island: Te Aroha (coll. Musson).

3. Ooperipatus insignis, Dendy. (Figs. 3, 34, 35.)

Synonymy.

1890. Peripatus insignis, Dendy. 'Victorian Naturalist,' vol. vi, p. 173; 'Annals and Magazine of Natural History,' series 6, vol. vi, p. 121; 'Proc. Royal Soc. Victoria,' vol. iii (new series), p. 44.

1894. Peripatus insignis, Spencer. 'Proc. Royal Soc. Victoria,' vol. vii (new series), p. 31.

1895. Peripatus insignis, Dendy. 'Report of the Australasian Association for the Advancement of Science,' Brisbane, 1895, p. 109.

1895. Peripatus Leuckartii, var. typica, Fletcher. 'Proc. Linn. Soc. N.S.W.,' vol. x, series 9, p. 185.

1900. Ooperipatus insignis, Dendy. 'Zoologischer Anzeiger,' xxiii, p. 510.

Description.—There are fourteen pairs of claw-bearing legs, each with three spinous pads on its ventral surface, the proximal pad being, as usual, narrow and interrupted in the fourth and fifth legs by the nephridial papillæ. On some of the legs, and especially on those of the last pair, the proximal pad is ill-defined, and shows a tendency to break up transversely into papillæ. The colour of the pads is pale yellowish, shading into indigo-blue, without any conspicuous difference between the proximal pad and the other two, though the distal one is the darkest of the three. The foot bears three dark-coloured primary papillæ—anterior, posterior, and dorsal, overhanging the pair of claws.

The inner jaw-blade (fig. 35) has one large tooth and about five small ones. The outer blade (fig. 34) has no accessory tooth.

The ovipositor of the female resembles that of the other species of the genus, and is conspicuous between the legs of the last pair as a subcylindrical protuberance of a pale yellow colour, bearing the genital aperture as a longitudinal slit at its apex. There are no crural gland papillæ in the female. In the male the genital aperture occupies the usual position, and there are indications of a pair of white papillæ (perhaps fused together) just behind it on the short anal cone. Crural gland papillæ may occur on the legs of the last nine pairs.

The general coloration of the dorsal surface to the naked eye appears dark, sometimes almost black, speckled with pale orange or yellow. Closer examination of typical specimens shows a very characteristic pattern, which may be described in general terms as "chequered." The general ground colour is dark indigo-blue,[1] often almost black, and this is chequered by more or less regularly arranged patches of pale dull orange or yellow in transverse and longitudinal rows. Though irregular, the patches may generally be described as roughly rectangular in outline, forming a kind of chessboard pattern with the dark ground colour (fig. 3). A longitudinal row of the lighter patches runs down the middle; these are small, and each is divided longitudinally in the middle line by a narrow dark band, which in turn is interrupted by the very narrow, unpigmented, mid-dorsal groove, visible under the microscope. The dark band widens out between the successive light patches of the row, forming alternating dark patches. Then on each side comes a row of larger light patches alternating with those of the middle row. Then another row of light patches alternating with the last, and lying in the same transverse-rows as the median light patches, over the legs. In addition to these patches individual light-coloured

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[1] May be greenish indigo in preserved specimens.

papillæ are scattered in the dark areas, and dark ones in the light areas, the papillæ being arranged as usual on transverse ridges of the skin. Sometimes the light-coloured primary papillæ appear to be arranged to some extent in irregular longitudinal rows, and sometimes the chessboard pattern is almost obliterated, leaving the longitudinal rows of light-coloured papillæ scattered over a nearly uniform background. The dorsal surface of the legs and feet is dark indigo-blue, with two or three orange or yellow papillæ on the legs.

The ground colour of the ventral surface is pale yellowish. Over this are scattered a number of papillæ, mostly of an indigo-blue colour, but some dull orange, arranged in transverse rows on the ridges of the skin. In the mid-ventral line, between the legs of each pair except the last (where the genital aperture is situated), are the usual pale areas of skin devoid of papillæ.

The antennæ are dark indigo-blue, sometimes ringed with orange. The characteristic chessboard pattern of the dorsal surface appears to be very constant, and I have seen it in Tasmanian as well as in Victorian specimens.

I have no measurements of living specimens, and the females in my possession do not appear to be fully grown. After preservation in spirit in the ordinary manner, my largest male specimen (Tasmanian) measures about 11 mm in length by 2·5 mm. in greatest breadth, exclusive of appendages. The specimens collected by Professor Spencer in Tasmania were killed by drowning, and therefore presumably in an extended condition, and he gives the measurements of three of the largest as respectively 23, 17, and 15 mm. in length (exclusive of tentacles), and 4, 3, and 3 mm. in breadth. It is possible, as has been suggested, that the Tasmanian specimens may be normally larger than those of the mainland, but the evidence is not sufficient to enable us to form a definite conclusion on this point. The three Tasmanian specimens in my possession are all male, and I have a male specimen from Victoria of about the same size. Probably the females are a little larger; I have a specimen from Victoria, apparently killed by drowning, which is about 15 mm. long.

Discussion of Relationships.—The close relationship which this species bears to the New Zealand O. viridimaculatus has already been pointed out. It is obviously quite distinct, as shown by the absence of the accessory tooth on the outer jaw-blade, and by the presence of only fourteen pairs of walking legs, both from O. oviparus and from the common New South Wales Peripatus, which I still term P. Leuckartii. Since, however, it has been suggested with some show of reason that my O. insignis may be really Sänger's original P. Leuckartii, and as Mr. Fletcher (7) has definitely adopted this view of the case, it becomes necessary to briefly discuss the question of nomenclature.

(1) As to the number of appendages in the original P. Leuckartii we have no absolutely certain information, for it appears that Leuckart and Sänger gave conflicting accounts. Leuckart (1) first said there were "16 Beinpaaren." Mr. Fletcher observes, "But in regard to the Australian Peripatus, it seems evident that Professor Leuckart intentionally included the oral papillæ among the sixteen pairs, but without indicating the fact."

Sänger, working apparently on the same specimen, states, on the other hand, that there are "fifteen pairs of legs, one pair without claws, fourteen with. This character is also found in P. brevis, described by Blanchard."[1] Mr. Fletcher interprets this to mean that Sänger includes the oral papillæ in the fifteen pairs, and that the original P. Leuckartii had only fourteen pairs of claw-bearing walking legs. I do not think that this interpretation is necessary. Mr. Fletcher himself (7) has recorded the occurrence of a specimen of the common New South Wales Peripatus in which two pairs of legs had the claws missing, and it was quite possible that Leuckart's specimen was also abnormal in this respect (especially if it had been subjected to much handling before coming into

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[1] I quote from a translation of Sänger's paper (1) with which Prof. Spencer kindly furnished me.

Sänger's possession), the fact perhaps not being considered worth noticing in the summary which Sänger gives, and which (quoted by Leuckart) has been generally accepted as bearing the ordinary interpretation. This summary (according to the translation obtained in London by Professor Spencer) runs as follows:—"Fifteen pairs of legs; sexual organs between the last pair; the 'sole' consists of three segments, one long and curved, and two short and straight. New Holland, Australia." In any case Sänger's statement as to the number of legs appears to be completely neutralised by Leuckart's. As to the argument derived from Sänger's comparison of his specimen with P. brevis, it seems probable that Sänger knew very little about P. brevis, for, as Mr. Fletcher shows, he erroneously attributes the description thereof to Blanchard instead of to De Blainville. Moreover against this comparison we may surely set Leuckart's comparison of P. novæ-zealandiæ, Hutton. Leuckart says (as quoted by Fletcher, Hutton's Abhandlung 'On Peripatus novæ-zealandiæ,' 'Ann. Mag. Nat. Hist.' [4], xviii, Nov., 1876, pp. 361—369, pl. xvii) "macht uns mit einer Form bekannt, die 15 Beinpaare besitzt, wie der von Sänger (J. B., 1870, S. 410) beschriebene P. Leuckartii, der unserm Verf. freilich unbekannt geblieben ist, obwohl seine neue Art vielleicht damit zusammenfällt. Jedenfalls ist nicht der P. novæ-zealandiæ, sondern der P. Leuckartii die erste Art des Gen. Peripatus, die aus Australien kommt." Surely if Leuckart, the owner of the specimen, thought it was so similar to P. novæ-zealandiæ with fifteen pairs of legs that it might be identical, it is hardly likely that it after all had only fourteen pairs. There can hardly have been any misunderstanding of Hutton's original description, for Hutton says "fifteen pairs of ambulatory legs, and a pair of oral papillæ."

(2) The locality of Sänger's specimen, "found in New Holland, north-west from Sydney," renders it extremely improbable that it can have been O. insignis, which is rare even in the south, and has never yet been recorded from

New South Wales, where the common viviparous species has been obtained in hundreds.

(3) If Mr. Fletcher's conclusion that Sänger's specimen was a female be correct, then it can hardly have been O. insignis, for no mention is made of the very characteristic ovipositor of that species. If, on the other hand, it was a male, it is hardly likely that Sänger would altogether have overlooked the papillæ of the crural glands.[1] Therefore it was probably a female of the common New South Wales viviparous species, with fifteen pairs of walking legs.

In short, it appears to me only reasonable to adhere to the old view that the common viviparous New South Wales species is P. Leuckartii, and to retain my specific name insignis for the fourteen-legged oviparous Victorian and Tasmanian species, at any rate until such time as a re-examination of Sänger's type may prove this view to be erroneous.

Localities.

Victoria.—Macedon (coll. Hogg); Sassafras Gully; Ferntree Gully; Gembrook.

Tasmania.—Dee Bridge (coll. Spencer); Mount Wellington (coll. Morton).

IV. Summary of Results.

The principal conclusions arrived at in this memoir may be briefly summarised as follows:

1. The genus Ooperipatus includes a number of oviparous Onychophora characteristic of Eastern Australia,

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[1] It may be argued that if my view be correct, Sänger has made a much more serious omission in not mentioning the oral papillæ. He may well have considered, however, that the oral papillæ, exhibiting no specific characters, did not require specific notice. It is hardly likely that he would count the oral papillæ as legs, for he distinctly says that the legs have "soles" (meaning spinous pads), and these, of course, as well as the claws, are wanting in the oral papillæ.

Tasmania, and New Zealand; distinguished by laying large, heavily yolked eggs with a thick sculptured chorion, and by the presence in the female of a conspicuous muscular ovipositor.

2. The egg at the time of laying contains no recognisably developed embryo, and development takes place afterwards with extreme slowness.

3. The oviparous habit is very ancient, dating back at least to the Cretaceous epoch, as indicated by the geographical distribution of the species. The conclusions of Sedgwick and Sclater as to the loss of yolk in the eggs of certain viviparous species are thereby supported.

4. Three species of Ooperipatus are at present known, viz. O. oviparus, O. viridimaculatus, and O. insignis. Some slight doubt attaches to the last, because the eggs have not yet been observed, but the females have the conspicuous ovipositor.

5. The genus Ooperipatus is very closely related to Pocock's Peripatoides, and may be regarded as representing an ancestral form from which the viviparous Australasian species are descended.

6. Except as regards the egg-laying habit and structures associated therewith, the genus Ooperipatus is, according to the views of Bouvier, very far from primitive in its characters, the number of walking legs being reduced to fifteen or fourteen, the spinous pads being only three in number, and the transverse ridges of the integument being interrupted in the mid-dorsal line by a narrow unpigmented groove.

7. There is no sufficient reason for supposing that Ooperipatus insignis, Dendy, is identical with Peripatus Leuckartii, Sänger, which last name must be retained for the common viviparous species of New South Wales.

CHRISTCHURCH, N.Z.; December, 1900.

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VI. EXPLANATION OF PLATES 19—22,

Illustrating Dr. Dendy's memoir "On the Oviparous Species of Onychophora."

Explanation of Lettering.

A. Anus. *B. Tr.* Buccal tracheal pit. *C. G.* Cerebral ganglion. *Ch.* Chorion. *Cr. P.* Crural papilla (bearing aperture of crural gland). *D. F.* Mid-dorsal longitudinal groove or fissure. *E.* Egg in oviduct. *Int.* Intestine. *Intg.* Integument. *L. Od.* Left Oviduct. *N. B.* Nucleoid bodies in clear areas of immature chorion. *N. C.* Nerve-cord. *Ne. A.* Nephridial aperture. *Nl.* Nucleolus. *Nu.* Nucleus. *Od.* Oviduct. *Oes.* Œsophagus. *O. Ov.* Ovarian ova. *Ovp.* Ovipositor. *Ovy.* Ovary. *Ped.* Peduncle of ovarian follicle. *Ph.* Pharynx. *Pr. O.* Protuberances of oviduct opposite to receptaculum seminis. *R.* Rectum. *R. Od.* Right oviduct. *R. S.* Receptaculum seminis. *S. D.* Salivary duct. *S. G.* Salivary gland. *Sl. D.* Slime-duct and reservoir. *Sl. G.* Slime-gland. *Tr. P.* Tracheal pit. *Tr. S.* Triangular sac at base of ovipositor, formed by the union of the two oviducts. *V. M.* Vitelline membrane. *Y.* Yolk.

PLATE 19.

FIG. 1.—Ooperipatus oviparus, Dendy. A Victorian specimen showing the typical pattern. From a drawing by C. C. Brittlebank, Esq. × 6 diameters.

FIG. 2.—Ooperipatus viridimaculatus, Dendy. Specimen from Lake Te Anau, showing the typical pattern. From a drawing by Miss M. M. Ferrar. × 4½ diameters.

FIG. 3.—Ooperipatus insignis, Dendy. A Victorian specimen showin the typical pattern. From a drawing by C. C. Brittlebank, Esq. × 9 diameters.

PLATE 20.

Figs. 4—11. Ooperipatus oviparus.

Fig. 4.—General dissection from the dorsal surface, slightly diagrammatic.

Fig. 5.—Transverse section of male specimen through the region of the pharynx, showing the buccal tracheal pits, union of the salivary ducts, dorsal longitudinal furrow. Drawn under Zeiss A, ocular 2, camera outline.

Fig. 6.—Transverse section of female specimen, showing two eggs in the oviducts. Drawn under Zeiss A (bottom lens removed), ocular 2, camera outline.

Fig. 7.—Outer and inner jaw-blades. Drawn under Zeiss C, ocular 2, camera outline.

Fig. 8.—Another jaw-blade. Drawn under Zeiss C, ocular 2, camera outline.

Fig. 9.—Lower parts of oviducts, with ovipositor.

Fig. 10.—Posterior portion of specimen from Cooran, Queensland, dissected from ventral surface, showing lower parts of oviducts, ovipositor protruded. × 10.

Fig. 11.—Upper portion of oviduct, showing receptaculum seminis and irregular protuberances. Drawn under Zeiss A, ocular 2, camera outline.

PLATE 21.

Figs. 12—26. Ooperipatus oviparus.

Fig. 12.—Ovary, showing separation into right and left halves.

Fig. 13.—Portion of ovary, showing ovarian ova in different stages of development. Drawn under Zeiss A, ocular 1, camera outline.

Fig. 14.—Young ovarian ova, from section stained with borax carmine. Drawn under Zeiss D, ocular 1, camera outline.

Fig. 15.—Older ovarian ovum, from section stained with borax carmine, showing vitelline membrane and formation of yolk granules. Drawn under Zeiss D, ocular 1, camera outline.

Fig. 16.—Yolk corpuscles and granules from still older ovarian ovum from section stained with borax carmine. Drawn under Zeiss D, ocular 1, camera outline.

Fig. 17.—Yolk corpuscles from thick-shelled egg from oviduct; stained with eosin and mounted in oil of cloves. Drawn under Zeiss D, ocular 1, camera outline.

Fig. 18. Part of immature chorion from egg of Queensland specimen. Stained with eosin. Drawn under Zeiss D, ocular 2, camera outline.

Fig. 19.—Optical section of the same specimen. Drawn under the same conditions.

Fig. 20.—Part of chorion of egg from oviduct, from a specimen kept long in spirit. Drawn under Zeiss A, ocular 2, camera outline.

Fig. 21.—Part of surface of same, showing the regularly arranged protuberances containing granules. Drawn under Zeiss D, ocular 2, camera outline.

Fig. 22.—Perspective view of same, drawn under same conditions.

Fig. 23.—Surface of chorion of deposited egg, showing sculptured pattern. Drawn under Zeiss D, ocular 2, camera outline.

Fig. 24.—Surface of chorion of another deposited egg, showing variation n sculptured pattern. Drawn under Zeiss D, ocular 2, camera outline.

Fig. 25.—Optical section of chorion of deposited egg with high protuberances (same egg as Fig. 24). Drawn under Zeiss D, ocular 2, camera outline.

Fig. 26.—Optical section of chorion of deposited egg with low protuberances, showing very distinctly the two layers of which the chorion is composed. Drawn under Zeiss D, ocular 2, camera outline.

PLATE 22.

Figs. 27—33. Ooperipatus viridimaculatus.

Fig. 27.—General dissection from the ventral surface. × 5.

Fig. 28.—Fifth and sixth legs of male specimen, seen from below, showing apertures of nephridia and crural gland, spinous pads, etc.

Fig. 29.—Outer jaw-blade. Drawn under Zeiss C, ocular 2, camera outline.

Fig. 30.—Inner jaw-blade. Drawn under Zeiss C, ocular 2, camera outline.

Fig. 31.—Reproductive organs of female exposed from the ventral surface, but not unravelled.

Fig. 32.—Surface view of portion of chorion of deposited egg, showing sculptured pattern and fissures due to splitting. Drawn under Zeiss C, ocular 3, camera outline.

Fig. 33.—Optical section of same, drawn under same conditions.

Figs. 34, 35. Ooperipatus insignis.

Fig. 34.—Victorian specimen, outer jaw-blade. Drawn under Zeiss C, ocular 2, camera outline.

Fig. 35.—Inner jaw-blade of same. Drawn under same conditions.

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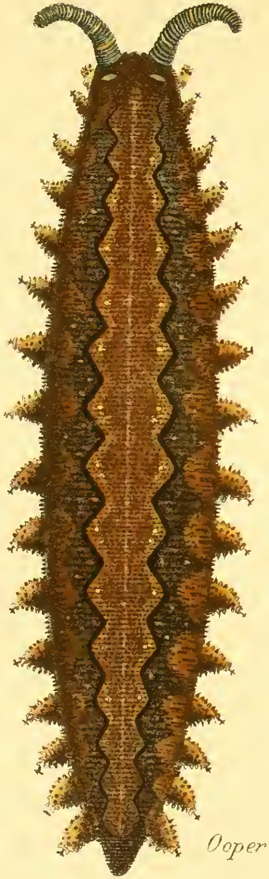
Quart. Journ. Micr. Sci. Vol. 45, N.S. Pl. 1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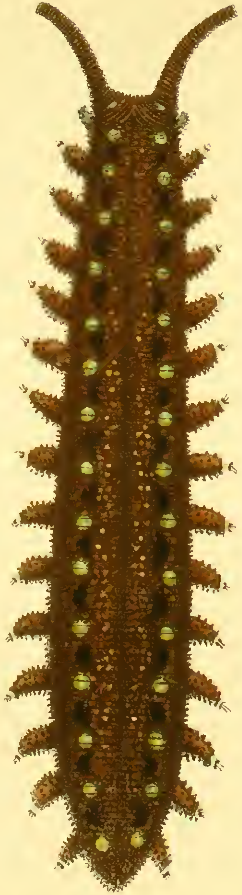
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Ooperipatus viridimaculatus.


3.

Ooperipatus insignis

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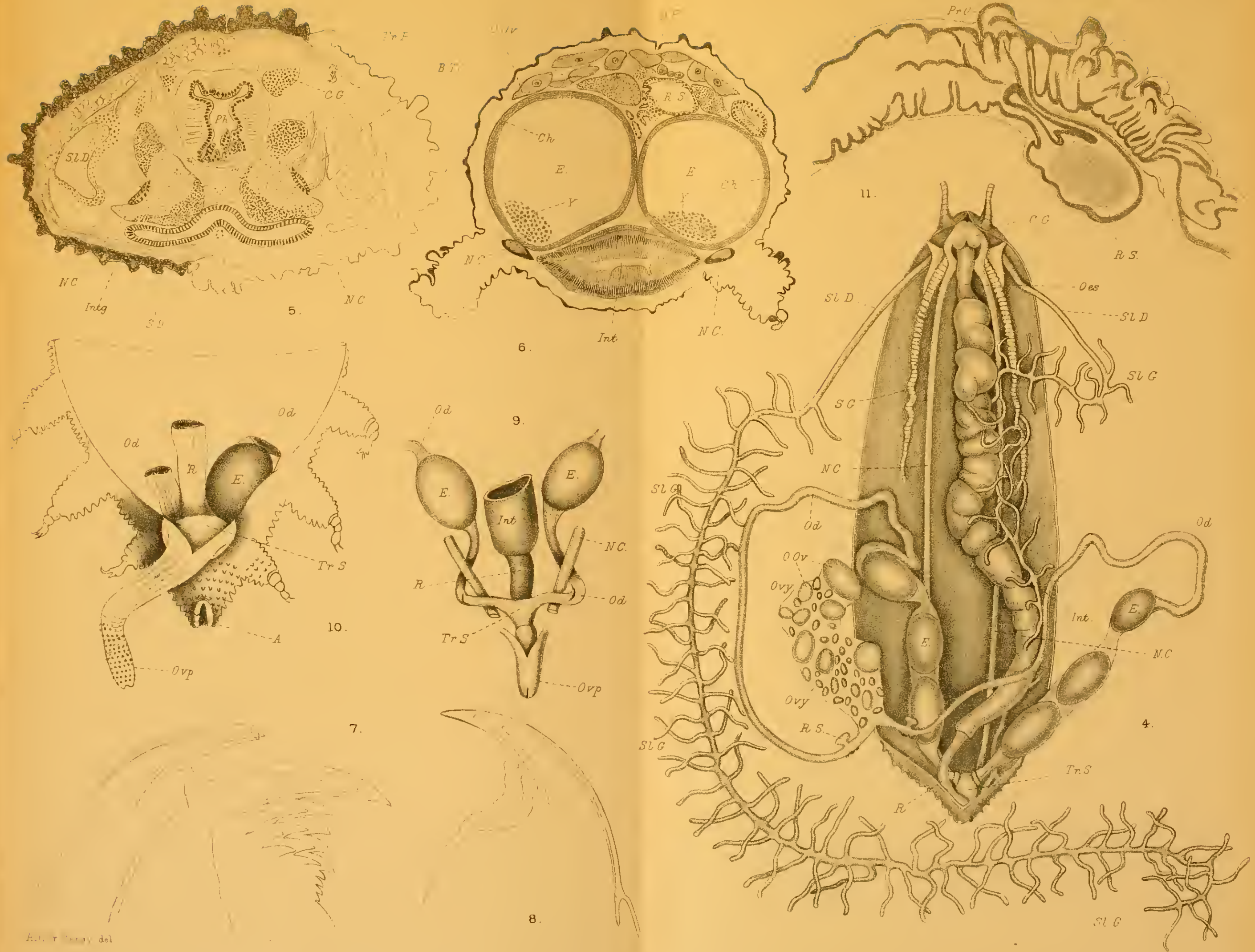
A. S. Huth, Lith^r London



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OOPERIPATUS OVIPARUS. – ANATOMY.

A S Huth Lith.r London


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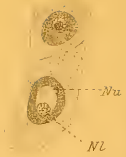
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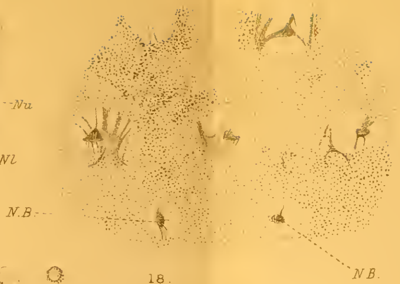
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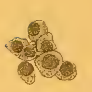
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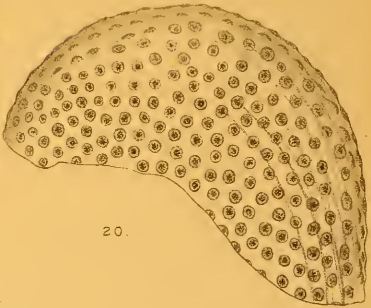
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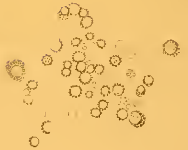
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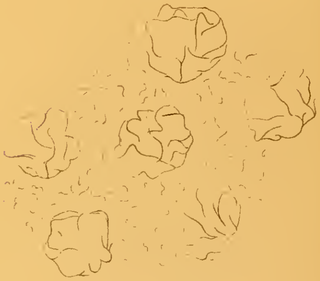
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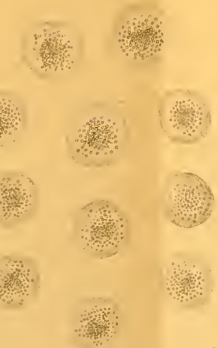
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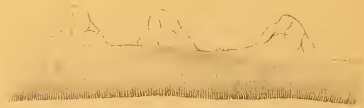
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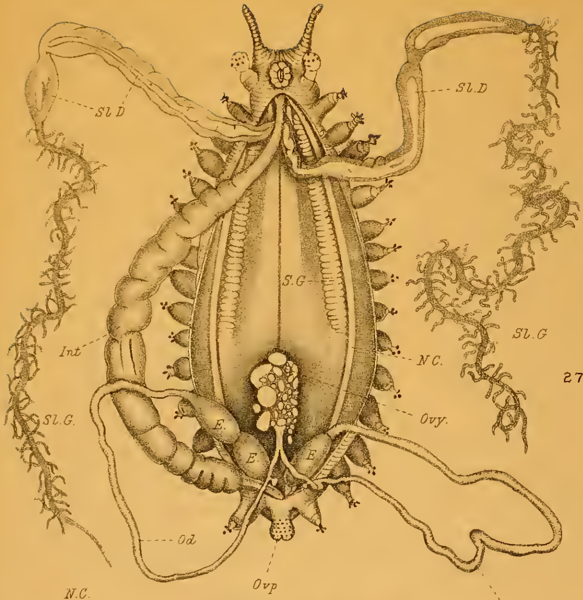
26

OOPERIPATUS OVIPARUS.— OVARY AND EGGS.

A.S.Huth, Lith. London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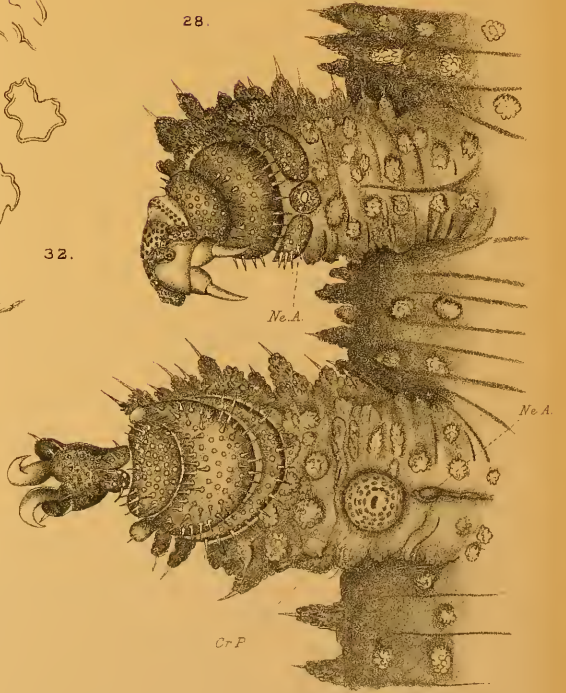
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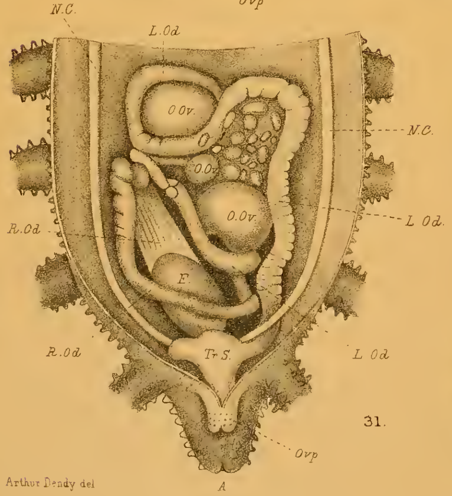
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Arthur Dendy del.

A.S. Huth, Lith^r London.

OOPERIPATUS VIRIDIMACULATUS (Figs 27-33) AND O. INSIGNIS (Figs 34, 35)–ANATOMY.

A New and Annectant Type of Chilopod.

By

R. I. Pocock.

With Plate 23.

Introduction.

The continent of Australia and its adjacent islands have hitherto proved singularly disappointing in the production of interesting types of Chilopoda. Setting aside Cermatobius, which was discovered some fifteen years back in the island of Adenara, none of the genera known up to the present time from the Australian region throw special light upon the phylogeny of the families of this class; none can be regarded as archaic forms that have found refuge in this southern tract of land. Collections made in various districts of the country have yielded specimens of Scutigera, Henicops, Lithobius, Scolopendra, Cryptops, Geophilus—genera which may be met with on a single hillside in almost any part of Southern Europe; of Cormocephalus and Ethmostigmus, which in an almost equal degree are characteristic of tropical Africa or the Oriental region. The entire fauna, in short, bears the stamp of comparatively recent origin by immigration from South Eastern Asia, with perhaps an infusion from the Ethiopian region or Madagascar.

In 1892, however, I received from Mr. G. M. Thomson, of Dunedin, New Zealand, a small consignment of Myriapods from the summit of Mount Rumney, Hobart, Tasmania, which completely falsified the opinion that the Antipodes hold nothing peculiar or primitive in the way of centipede-life and are wholly given over to the occupation of widely distributed and well-known forms. The collection in question contained a couple of centipedes representing a species which proves to be comparable in interest from a morphological standpoint to either of its compatriots, Ceratodus or Ornithorhynchus, inasmuch as it unmistakably represents an archaic type, which has survived in this isolated corner of the world—a type which possesses the two-fold interest of exhibiting certain unique structural peculiarities of its own, coupled with others that serve to link together three of the best-known and most diversified sections of the class; and also of showing the true, but previously unknown and unsuspected, nature of the connection between the metamerism of the Scolopendromorpha and that of the Lithobiomorpha.

This new centipede is the subject-matter of the following essay. The account of it may be conveniently divided into four headings:—(1) A description of the external structural features of the animal; (2) a comparison between it and the other existing orders; (3) its significance in testifying to the transformation of the Scolopendroid into the Lithobioid type; (4) the classification of the Chilopoda.

Part I.—Description of the Genus and Species.

Fam. Craterostigmidæ.

Gen.—Craterostigmus, nov.

The cephalite or head shield (Pl. 23, figs. 1, 3, 8) is longer than wide, leaving the toxicognaths largely uncovered on the dorsal side, as in some genera of Geophilomorpha (i.e. Mecistocephalus); its frontal sulcus is distinct, and its præantennal area sharply recurved to form a long subfrontal area, as in other pleurostigmous Chilopods. The eyes are represented by a single pair of ocelli, as in the Lithobiomorphous genera Henicops and Cermatobius. The antennæ are basally approximated, and project forwards from the fore margin of the cephalite, and consist of about the same number of segments as is found in the primitive Scolopendromorpha. The labral sclerites are distinct, and the labral border is deeply and subquadrately excised in the middle, the sides of the excision being membranous and furnished with bristles, while its anterior border is armed with five teeth (Pl. 23, fig. 9).

Gnathites.—The first pair, or mandibles, are furnished beneath (posteriorly) with a thick fringe of hair, and above (anteriorly) with a large membranous lobe beset with short hairs; between this lobe and the hairy fringe appear nine pectiniform, horny teeth, arranged in slightly overlapping series of three each (Pl. 23, figs. 10—12). The second pair or maxillæ much resemble those of, e.g. Scolopendra, the basal segment (coxa or stipes) having its proximal margin widely rounded, the first segment of the ectocorm (= first malar segment of the external maxilla of Latzel) short, and the second segment (= second malar segment) a little longer than broad and evenly convex along the margin; the entocorm (= internal maxilla) consists of a single short segment. The basal segments of the right and left sides meet in a much longer sutural union than is seen in Scolopendra (Pl. 23, fig. 13).

The palpognaths (= labial palpi, second pair of maxillæ, or first pair of maxillipedes) are also much like those of Scolopendra, but the ectocoxite (= outer segment of the stipes of Latzel) is more strongly produced posteriorly. As in the genus just mentioned, the distal segment is swollen and thickly fringed on its upper (anterior) margin, but the claw is almost concealed in hairs, both from its anterior and posterior aspects (Pl. 23, figs. 14, 14*a*).

The toxicognaths (second pair of maxillipedes, poison-jaws or prehensors) present a combination of characters recalling those of Scolopendra in the presence of dentate præcoxal and præaxial femoral processes; those of Mecistocephalus and some other species of Geophilomorpha in the large-size and subquadrate shape of the coxal plate, the length of the femora, and the extent to which the terminal segment or fang overlaps the cephalite anteriorly; those of the Lithobiomorpha in the completeness of the penultimate and antepenultimate segments (patella and tibia), which postaxially intervene between the distal extremity of the femur and the proximal extremity of the fang (tarsus) (Pl. 23, figs. 1—3).

The pleural sclerites of the toxicognaths extend as far forwards as the anterior border of the tergum of the toxicognathic somite, but fall far short of the proximal end of the femora (Pl. 23, figs. 1, 3, *pl.*).

The tergum of the toxicognaths (= basal plate) resembles that of some Geophilomorpha (e.g. Mecistocephalus) in size; it is as wide as the cephalite, which it underlies in front, but much narrower than the tergum of the first pediferous somite, which it overlaps behind (Pl. 23, figs. 1, 3, *bp.*).

The pediferous somites differ from those of all Chilopoda hitherto known, in that the tergal plates are numerically in excess of the sternal, the latter being fifteen in number, as in the Lithobiomorpha, and the former twenty-one, as in most Scolopendromorpha.

The terga are unequal in size, but not alternately larger and smaller; the first is very large, and considerably overlaps the second, the fourth overlaps the third in front and the fifth behind, the seventh overlaps the sixth in front and the eighth behind, the ninth meets the tenth without distinct overlap, the twelfth overlaps the eleventh in front and the thirteenth behind, the fifteenth overlaps the fourteenth in front and the sixteenth behind, the remainder normally overlapping the anterior border of those that succeed them, the overlapped area being smooth and defined by a transverse groove; the tergum of the last somite is completely coalesced with the chitinised pleural area.

The pleural súrfaces of all the pediferous somites, except the thirteenth, fourteenth, and fifteenth, are furnished with a distinct præcoxal sclerite (= epimeron of Latzel); the stigmatiferous somites are furnished in addition with a usually smaller, stigmatic sclerite in front and a larger metastigmatic sclerite behind, both beneath the edge of the tergum; a sclerite representing the stigmatic in position is also found below the edge of the third, sixth, ninth, eleventh, fourteenth, and seventeenth terga ; and a sclerite corresponding to the metastigmatic is present below the first, second, fifth, eighth, tenth, thirteenth, and sixteenth terga; but below the third, sixth, ninth, eleventh, fourteenth, and seventeenth terga it is less developed, being either small and narrow, or represented by a weakly chitinised integumental ridge. Towards the posterior end of the body the præcoxal sclerite increases in size, and encroaches upon the pleural membrane, until on the last three somites the pleural area is covered with a continuous chitinous plate, which is fused with the sternum, and, in the case of the last somite, with the tergum also, as already stated (Pl. 23, figs. 3—7).

The sterna are subequal and laterally emarginate for the articulation of the legs ; a pair of transversely elongated præsternal sclerites extend in front of their anterior border, as in the Scolopendromorpha ; on the last two somites these sclerites fuse with the sterna (Pl. 23, figs. 3, 4, 6).

The stigmata, subcircular or suboval in shape, are six in number on each side, and lie above the third, fifth, eighth, tenth, twelfth, and fourteenth pairs of legs, as in the genus Lithobius, and beneath the fourth, seventh, twelfth, fifteenth, eighteenth, and twentieth terga. With the exception of those on the penultimate somite, which lie far back, the stigmata are situated more forwards than in other Chilopoda, being slightly in front of the articulation of the legs, and of the middle of the lateral margin of the terga (Pl. 23, figs. 3, 4, 15).

The legs are fifteen in number on each side, as in the Lithobiomorpha ; with the exception of the last pair they consist of what is doubtless the primitive number of segments in the Chilopoda, namely six, the distal segment being undivided, as in the Geophilomorpha and the less specialised genera of Scolopendromorpha and Lithobiomorpha; the basal segments are relatively larger than in the Scolopendromorpha, but smaller than in the Lithobiomorpha, and they show no progressive increase in size towards the posterior end of the body, such as is characteristic of the members of the latter order (Pl. 23, figs. 16, 17). The legs of the fifteenth pair differ in certain particulars from those of all Chilopods. The basal segments or coxæ are of medium size, freely articulated to the posterior end of the last somite, without encroaching in any way upon its pleural area, and like the trochanters of the two preceding pairs are armed below with a long spike. The second segments or trochanters, on the other hand, are reduced in size and completely fused with the proximal end of the femora, as in the Scolopendromorpha. In the members of the latter order, however, as well as in the Geophilomorpha, the coxal segment is indistinguishably united to the enlarged præcoxal pleural sclerite. Again in the Lithobiomorpha and Scutigeromorpha, which resemble Craterostigmus in the freedom of the coxa, this segment occupies the whole of the pleural area of the somite, and the trochanter remains distinct. As in all Chilopoda, with the exception of some Geophilomorpha, the tarsus of the fifteenth leg is bisegmented (Pl. 23, figs. 18, 19).

Projecting between the legs of the last pair is a sclerite, formed by two valves united in the median dorsal line and meeting ventrally, when closed, in a long slit representing the combined genito-anal aperture. This bivalvular sclerite is probably the homologue of the dorsal plate of the anal somite, which in some genera of Chilopoda, e. g. Scolopendra and the male of Lithobius, is of larger size than that of the genital somite, and partially or wholly supersedes it. No trace of skeletal plates of the genital somite or of gonopods is visible externally. The latter in all probability have atrophied from enclosure within the genito-anal cavity, embraced by the above-described sclerite (Pl. 23, figs. 5—7, *ag.*).

Craterostigmus tasmanianus, sp. n.

Measurements in mm.—Total length from anterior border of cephalite to posterior border of twenty-first tergite 37, width across coxal plate of toxicognaths 3·8; length of cephalite 3·4, width 2·2; length of antenna 9·5, of posterior leg 12; length of last tergite 2·4, width 2.

Colour yellowish brown, with the cephalite and toxicognaths darker reddish brown. Integument sparsely hairy and punctured.

Cephalite parallel-sided, its posterior border convexly rounded; frontal area with its sides converging between the eyes and the base of the antennæ.

Eyes some distance behind the antennæ; frontal sulcus projecting posteriorly between the eyes, with strongly convex backward curvature.

Antennæ about one fourth the length of the body and head, rather less than three times as long as the head; the segments hirsute, especially towards the distal end of the appendage, subcylindrical, longer than wide, the first segment strongly constricted in its basal half.

Præcoxal processes of toxicognaths long, armed apically and externally with seven teeth. Inner side of femur and femoral process armed with about five teeth, the proximal of which lies far back just in front of the suture marking the line of union of the trochanter and the femur.

Basal plate with posterior angles rounded.

Terga without longitudinal grooves, with posterior border straight, posterior angles rounded and unthickened margins; the last tergum, and to a lesser degree the last but one, granular; the last with a weak longitudinal lateral crest in its anterior half, its posterior border sinuous, its middle third slightly and convexly produced.

Sterna without grooves, those of the posterior somites granular, the granules, as in the case of those on the terga, formed by the elevations round the setiferous pores; sterna area of last marked anteriorly on each side with an oblique, shallow groove.

Legs shortish, hairy, armed with a single inferior tibial and tarsal spine. Claw with two basal spinules, one inferior and one posterior. Posterior legs long and slender, about one third the length of the body and head, longer than the antennæ, without spines, protarsal and tarsal segments subequal, segments subcylindrical, tarsal and protarsal subequal; femur, patella and tibia progressively decreasing in length. Trochanter of the thirteenth and fourteenth armed below with a horny spike, which is shortest on that of the thirteenth coxa of fifteenth similarly armed.

The genito-anal sclerite is about half the length of the last leg-bearing somite. When viewed from the dorsal or ventral aspect its sides are seen to be convex, and to converge posteriorly to a point. From the lateral aspect its upper edge, which is compressed, is straight and horizontal; its inferior edge convex, the two meeting at an acute angle of about 45°.

PART II.—SUMMARY OF THE CHIEF CHARACTERISTICS OF CRATEROSTIGMUS, AND A COMPARISON BETWEEN THIS GENUS AND OTHER CHILOPODA.

The structural peculiarities of this new Chilopod and the complex nature of its relationship to the other existing types of this class, which are only imperfectly manifested in the above-given description, may be more fully emphasised and revealed in a clearer light by a brief summary: firstly, of the characters in which it particularly resembles each of the three most nearly allied groups; secondly, of those that it shares with two of them to the exclusion of the third; and lastly, of those in which it differs from all. Adopting the terminology I have elsewhere proposed, I shall speak of these groups as the Lithobiomorpha, Scolopendromorpha, and Geophilomorpha, leaving the explanation of the use of these names and the rank assigned to them to be dealt with in a later part of this essay.

With the fourth group, Scutigeromorpha, no comparison of Craterostigmus will be necessary, since the only morphological points the two have in common, apart from those shared by all Chilopods, are those mentioned in the statement of the resemblances between Craterostigmus and the Lithobiomorpha.

One or two of the features of Craterostigmus, namely, the armature of the posterior legs, the structure of the mandibles, etc., have been omitted from the list detailing the peculiarities of this genus, as of doubtful taxonomic value, although the structure of the mandible is likely enough to prove of high importance in this particular.

1. Characters in which Craterostigmus resembles the Lithobiomorpha and differs from the Scolopendromorpha and Geophilomorpha.—The completeness of the penultimate and antepenultimate segments of the toxicognaths, so that the femoral segment and fang are separated from each other on the outer (post-axial) side of the appendage; the presence of fifteen sternal plates and of fifteen pairs of locomotor appendages, with relatively large basal segments; the distinctness of the coxa of the fifteenth pair of legs; the presence of six pairs of stigmata on the somites represented by the third, fifth, eighth, tenth, twelfth, and fourteenth pairs of legs; the presence of a single monomeniscous eye on each side of the head, as in the genera Henicops and Cermatobius.

2. Characters in which Craterostigmus resembles the Scolopendromorpha and differs from the Lithobiomorpha and Geophilomorpha.—The co-existence of large dentate præcoxal and femoral processes on the toxicognaths, as in Scolopendra, Otostigmus, etc. The presence of twenty-one tergal plates. The presence of a large and distinct metastigmatic pleural sclerite, and the increase in size of the præcoxal sclerites towards the posterior end of the body. The fusion of the trochanter (second segment) of the legs of the fifteenth pair with the femur.

3. Characters in which Craterostigmus resembles all or some Geophilomorpha, e. g. Mecistocephalus, and

differs from the Scolopendromorpha and Lithobiomorpha.—The large size of the toxicognaths and the extent to which they overlap the cephalite anteriorly and laterally; the presence of a distinct, subquadrate, basal plate, which is much narrower than the tergum of the first leg-bearing somite and intervenes between it and the cephalite; the entirety of the distal segment of the penultimate pair of legs.

4. Characters in which Craterostigmus resembles the Scolopendromorpha and Geophilomorpha and differs from the Lithobiomorpha.—The enlargement of the tergum of the first leg-bearing somite; the size and completeness of the fusion of the two halves of the coxal plate of the toxicognaths; the relative equality in size between the coxæ of the legs; the presence of the præsternal sclerites upon the ventral area of the somites.

5. Characters in which Craterostigmus resembles some or all of the Lithobiomorpha and Scolopendromorpha and differs from all the Geophilomorpha.—The number of antennal segments exceeding fourteen; the presence of eyes; the inequality in size of the terga; the terga, sterna, and pairs of legs falling short of thirty-one; the reduction in the number of stigmata, which fall short of half the number of somites; the spine armature of the legs.

6. Characters in which Craterostigmus resembles the Lithobiomorpha and Geophilomorpha and differs from the Scolopendromorpha.—The presence of a distinct "basal plate" separating the cephalite from the tergum of the somite bearing the first pair of legs; the inability to withdraw the anal and genital somites within the somite bearing the legs of the last pair.

7. Characters in which Craterostigmus differs from all other known Chilopoda.—The fact that the pleural sclerite of the toxicognath covers only the posterior portion of the upper surface of the coxal plate on each side, and falls far short of the proximal end of the femur; the numerical excess of the terga over the sterna, the pairs of legs and the

stigmata; the fusion of the sternal and pleural sclerites of the penultimate and antepenultimate somites, and the complete coalescence of the tergal, pleural, sternal, and præsternal elements of the last somite to form a compactly chitinised subcylindrical tube; the distinctness of the coxa of the posterior leg, coupled with its articulation to the posterior extremity of the somite and the fusion of the trochanter with the femur; the representation of the external skeletal elements of the genital and anal somites by a pair of valves fused dorsally, but opening ventrally by a long slit-like aperture, whence the genital and anal products escape to the exterior.

The above-given comparisons demonstrate the impossibility of associating Craterostigmus with either of the groups of Chilopoda hitherto recognised, and substantiate its claim to take a rank at least as high as that which is assigned to the others individually, call them families, sub-orders, orders,—what you will.

Part III.—The Testimony supplied by Craterostigmus as to the Descent of the Lithobiomorpha from the Scolopendromorpha.

Apart from the characteristics peculiar to itself, which present us with new facts in Chilopod morphology; apart, too, from those that it shares with either one or more of the previously known divisions of this class of Arthropods, the chief point of interest vested in Craterostigmus lies in the explanation it furnishes of the principal resemblances and differences obtaining between the Lithobiomorphous and Scolopendromorphous types of structure, and also in the new and wholly unexpected light it throws upon the metamerism of these two types, enabling us to picture the process by which the one has been converted into the other.

Except for the numerical difference, the somites of Lithobius and Scolopendra exhibit certain obvious and well-known resemblances with regard to the distribution of the stigmata, and the alternate development of larger and smaller tergal plates.

In both forms the first, third, fifth, seventh, eighth, tenth, twelfth, and fourteenth terga are large, the second, fourth, sixth, ninth, eleventh, thirteenth, and fifteenth small, and stigmata are situated beneath the lateral margins of the third, fifth, eighth, tenth, twelfth, and fourteenth. On the other hand, the difference consists in the circumstance that whereas in Lithobius the genital and anal somites succeed the fifteenth, in Scolopendra no fewer than six somites —repeating the characters of those that precede them, the sixteenth, eighteenth, and twentieth being large and stigmatiferous, the seventeenth, nineteenth, and twenty-first small and astigmous—are intercalated between the fifteenth and the genital.

These facts forcibly suggest the conclusion that the fifteen somites of Lithobius are homologous to the anterior fifteen somites of Scolopendra, and that the reduction in the number of somites in the former is due to the excalation of six somites between the fifteenth and the genital, or to the failure to develop them from the embryonic "caudal lobe," the genital somite being presumably homologous in the two forms, and, in conjunction with the anal somite, representing in the adult the posterior portion of the "caudal lobe" in the embryo.

There is an attractive simplicity about this view of the case which formerly induced me to hold it as a working hypothesis. But the discovery of Craterostigmus puts a quite different complexion on the whole question.

In the first place, the correspondence with respect to numbers of stigmata and legs between Craterostigmus and Lithobius, and the position of the stigmata above the bases of the third, fifth, eighth, tenth, twelfth, and fourteenth legs on each side, fully justifies the supposition that the stigmata and legs are strictly homologous in the two forms. Indeed, it is not easy to see what other opinion on this point is to be held. But the stigmata in Craterostigmus lie beneath the fourth, seventh, twelfth, fifteenth, eighteenth, and twentieth tergal plates; whence it follows that these tergal plates are the dorsal elements of the somites bearing the third, fifth, eighth, tenth, twelfth, and fourteenth pairs of legs. That is to say, Craterostigmus, as compared with Lithobius, has one extra tergal plate without sternal or appendicular representative between the first and third pediferous somites, one between the third and fifth, two between the fifth and eighth, one between the eighth and tenth, and one between the tenth and twelfth, making in all a total of six. Which are these supernumerary terga? the second or the third? the fifth or the sixth? which two of the eighth, ninth, tenth, and eleventh? the thirteenth or fourteenth? the sixteenth or seventeenth?

The answers to these questions are not at first sight easily given, owing to the difficulty of deciding which of two terga overlying a sternum is its representative on the dorsal area. Careful examination, however, of the nature of the folds and the development of sclerites in the pleural integument shows that the terga without sternal complements are the third, sixth, ninth, eleventh, fourteenth, and seventeenth, these being the plates beneath which the representatives of the metastigmatic pleural sclerite is scarcely or not at all developed. Moreover the third, sixth, eleventh, and fourteenth terga are overlapped posteriorly by the terga that lie behind them; the ninth does not overlap the anterior border of the tenth; and the seventeenth, although overlapping the eighteenth in the normal manner, does not overlie the præcoxal sclerite of the eleventh pediferous somite, but is, as it were, wedged in between the tergum of this and of the following somite.

In the second place, the similarity between Craterostigmus and Scolopendra in the structure of the maxillæ, palpognaths, and toxicognaths, in the number of antennal segments, the equality in size of the coxæ, the fusion of the trochanter of the posterior legs with the femur, the presence of præsternal sclerites, etc., renders unavoidable the conclusion that the twenty-one terga in the two forms are homologous plate for plate. Assuming that this is so, and that the opinion given above touching the supernumerary terga is also correct, it follows that the passage from the Scolopendroid type, with twenty-one complete somites, to the Lithobioid type, with fifteen complete somites, was effected by the excalation of the third, sixth, ninth, eleventh, fourteenth, and seventeenth somites of the former type. This new explanation of the connection between the metamerism of the two types is illustrated in the annexed diagrams (p. 433), and may be tabulated as follows :

Scolopendroid Type.	Lithobioid Type.
1 major and astigmous represents	1 major and astigmous or stigmatiferous.
2 minor and astigmous represents	2 minor and astigmous.
3 major and stigmatiferous.	Excalated.
4 minor and astigmous represents	3 major and stigmatiferous.
5 major and stigmatiferous represents	4 minor and astigmous.
6 minor and astigmous.	Excalated.
7 major and astigmous or stigmatiferous represents	5 major and stigmatiferous.
8 major and stigmatiferous represents	6 minor and astigmous.
9 minor and astigmous.	Excalated.
10 major and stigmatiferous	7 major and astigmous.
11 minor and astigmous.	Excalated.
12 major and stigmatiferous represents	8 major and stigmatiferous.
13 minor and astigmous represents	9 minor and astigmous.
14 major and stigmatiferous	Excalated.
15 minor and astigmous represents	10 major and stigmatiferous.
16 major and stigmatiferous represents	11 minor and astigmous.
17 minor and astigmous.	Excalated.
18 major and stigmatiferous represents	12 major and stigmatiferous.
19 minor and astigmous represents	13 minor and astigmous.
20 major and stigmatiferous represents	14 major and stigmatiferous.
21 minor and astigmous represents	15 minor and astigmous.
22 genital represents	16 genital.
23 anal represents	17 anal.

If the theory here set forth be in accord with fact, it is evident that the similarity, exact though it be, between the fifteen leg-bearing somites of Lithobius and the anterior fifteen leg-bearing somites of Scolopendra, with respect to the alternation in size of tergal plates and the number and disposition of stigmata, is the outcome of homoplasy and not of homology.

Startling as this proposition may at first seem, the difficulties in the way of its comprehension are not insuperable.

Accepting the comparison between the somites of the two, as tabulated above, and assuming, as is justifiable, that the stigmata occurring upon the first, third, and tenth somites of the Lithobioid type and unrepresented on the corresponding somites of the Scolopendroid type have not been independently acquired in the former case, we are forced to conclude that the Scolopendroid type itself has been derived from a form possessing stigmata at least upon the first, third, fourth, fifth, seventh, eighth, tenth, twelfth, fourteenth, fifteenth, sixteenth, eighteenth, and twentieth somites, since stigmata are found upon these somites either in the Scolopendroid type or upon their hypothetical equivalents in the Lithobioid.

It is possible, however, to go a step further. Since all the Geophilomorpha, without exception, and one, in this respect, aberrant genus of Scolopendromorpha, namely Plutonium, possess stigmata upon all the leg-bearing metameres except the first and last, it is no strain upon probability to assume that the primitive Scolopendromorph was furnished with stigmata upon all the leg-bearing somites except the last. Furthermore, since stigmata are found only upon major somites, it follows that all the somites were originally of that kind. This contention is fortified by the consideration that similarity in size and structure of the individual segments of a series is one of the first laws of metamerism.

Hence, although it may be impossible to give a physiological explanation of the fact, no difficulty on morphological grounds obstructs the acceptance of the opinion that a typical Scolopendroid, like Rhysida, with stigmata only upon the third, fifth, seventh, eighth, tenth, twelfth, fourteenth, six-

EXPLANATION OF FIGURE OPPOSITE.

Diagram to illustrate the homology of the metameres in Chilopoda of the Scolopendroid, Craterostigmoid, Lithobioid, and Scutigeroid types.

LETTERING AND NUMBERING FOR ALL FIGURES.

at. Antenna. *c.* Cephalite. *b.* Basal plate = tergum of somite-bearing toxicognath. *t.* Toxicognath. *p.* Palpognath. 1—21, 1—15, 1—8. Terga of leg-bearing somites. 1′—21′, 1′—15′. Sterna of leg-bearing somites. *g.* Genital somite. *a.* Anal somite.

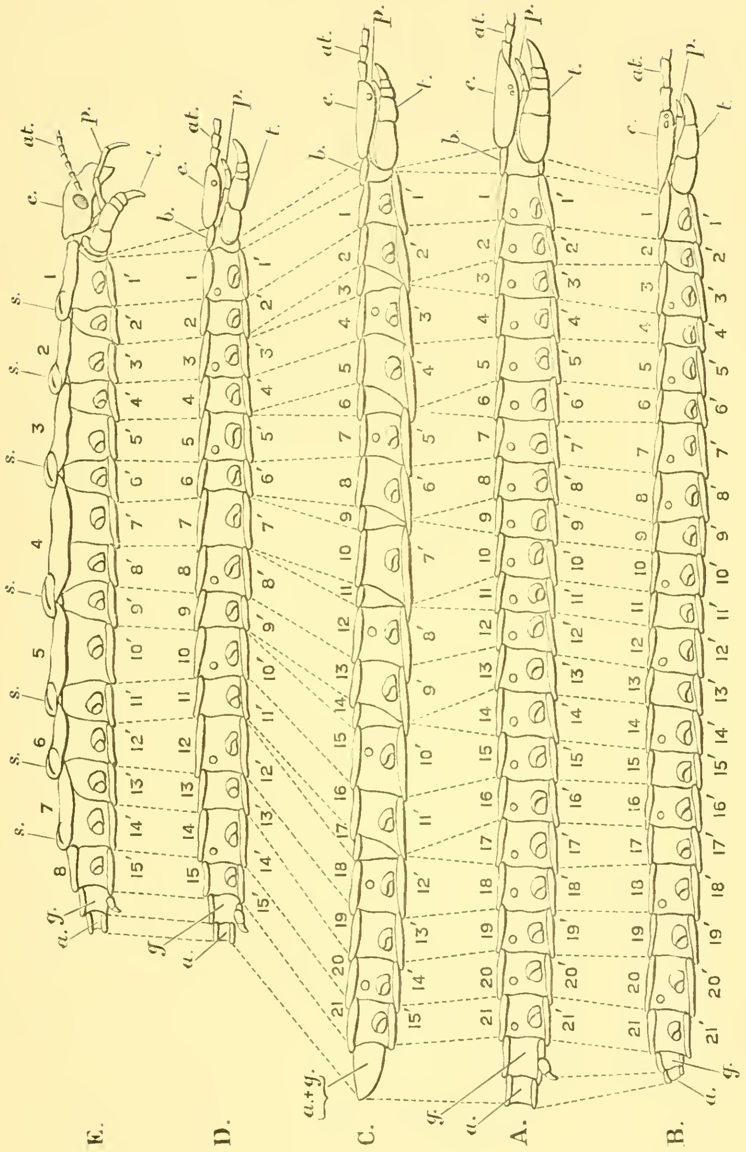
A. Hypothetical primitive Scolopendroid with twenty-one subequal stigmatiferous somites, with gonopods on the genital somite (*g.*), a distinct tergal plate (*b*) on the somite bearing the toxicognaths, and with the penultimate and antepenultimate segments complete on the post-axial side of this appendage.

B. Typical Scolopendroid, resembling Rhysida, derivable from A by the restriction of the stigmata to the somites numbered 3, 5, 7, 8, 10, 12, 14, 16, 18, 20; by the incipient differentiation of the leg-bearing somites into major stigmatiferous and minor astigmous; by the suppression of the gonopods; and by the obliteration of the tergum of the toxicognath and of the penultimate and antepenultimate segments of this appendage on its post-axial side. This figure also shows the juxtaposition of the two major somites numbered 7 and 8.

C. Diagram of Craterostigmus to show its derivation from A by the restriction of the stigmata to the somites numbered on the dorsal side 4, 7, 12, 15, 18, 20, and by the excalation of the sternal area and appendages of the somites numbered 3, 6, 9, 11, 14, 17; also by the coalescence of the elements of the genital and anal somites to form a bivalvular capsule ($a + g$).

D. Typical Lithobioid, resembling Henicops, derivable from C by the completion of the excalation of the half-somites in C numbered on the dorsal side 3, 6, 9, 11, 14, and 17, but retaining the distinctness of the genital and anal somites and the stigmata upon the first leg-bearing somite, as in A. This figure also shows the alternation of major stigmatiferous and minor astigmous somites, the juxtaposition of the two major somites, 7 and 8, and the change of the major somites from the odd to the even numbers in the posterior half of the body.

E. Diagram of Scutigera to show its descent from a Lithobioid of the Henicops type (D) by the dorsal migration and fusion of the stigmata; by the enlargement of the stigma-bearing tergal plates, their backward extension over, and almost complete obliteration of, the terga of the minor somites represented ventrally by the sterna numbered 2′, 4′, 6′, 9′, 11′, 13′, and by the fusion of the terga of the seventh and eighth somites to form a single plate (4)—the two processes resulting in the presence of eight visible tergal plates instead of fifteen. This figure also shows the widely separated antennæ, the polymeniscous eye, the large projecting præantennal area of the cephalite, the long and pediform palpognath and partially rotated toxicognath, characters in which Scutigera differs from all known Chilopods.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a.+g.
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21
1' 2' 3' 4' 5' 6' 7' 8' 9' 10' 11' 12' 13' 14' 15' 16' 17' 18' 19' 20' 21'

teenth, eighteenth, and twentieth somites, and Craterostigmus with these organs restricted to the somites represented by the fourth, seventh, twelfth, fifteenth, eighteenth, and twentieth tergal plates, have descended along divergent lines of evolution from a primitive Scolopendromorph with stigmata upon all the leg-bearing somites except the last.[1] But since the fourth, seventh, twelfth, fifteenth, eighteenth, and twentieth tergal plates in Craterostigmus represent the dorsal elements of the third, fifth, eighth, tenth, twelfth, and fourteenth somites of a Lithobiomorph, the similarity between the latter and a typical Scolopendroid, with respect to the location of stigmata, may be regarded as merely coincidental without any infringement of probability.

So, too, with regard to the resemblance in alternation of larger and smaller somites. This alternation is no doubt beneficial in the way of favouring flexibility and rapidity of torsion. Its acquirement, therefore, may be regarded as advantageous. But this does not explain why there should be an exact correspondence in this particular, if the two forms under consideration have been independently evolved from a type in which all the somites were major. Why, it may be asked, are the second, fourth, sixth, ninth, eleventh, thirteenth, and fifteenth somites minor in their constitution in both cases, and the others major? The explanation is to be found in the situation of the stigmata. The invariable absence of stigmata from minor somites in the Chilopoda justifies the view that the presence of these apertures and of the tracheal trunks that arise from them is incompatible with somites of that nature. This is supported by what occurs in the Geophilomorpha, where a large number of breathing orifices appears necessary for respiration underground, and where all the somites are major and subequal. But functional representatives of the minor somites of the Scolopendroid

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[1] The atrophy of the breathing orifice upon the first leg-bearing somite in the Geophilomorpha, the Scolopendromorpha, and Craterostigmus is no doubt traceable to the modification impressed upon this somite by the great development of the muscularity of the toxicognaths.

and Lithobioid types have been acquired by a secondary segmentation of the metameres which has given rise to the intercalation of a series of small segments between the genuine somites. Unless in the case of these centipedes there were some factor inimical to the presence of stigmata, and the trunks arising therefrom, upon minor somites, it is difficult to explain why the somites do not alternate in size, when the necessity for the alternation is attested by the secondary development of the sub-segments above referred to, and when the capacity for the segmentation of fresh somites from the embryonic caudal lobe seems practically limitless.

Postulating, then, the expediency of alternation in size of somites, and the incompatibility of the presence of stigmata upon those belonging to the minor category; seeing too that the third, fifth, eighth, tenth, twelfth, and fourteenth, both in the Lithobioid and the Scolopendroid types, have retained their stigmata and their major nature; and that the first, although astigmous in the Scolopendroid and often in the Lithobioid, is also major, it is no matter for surprise that the second, fourth, sixth, ninth, eleventh, thirteenth, and fifteenth are minor in both cases.

But again, it may be asked, why does the regular alternation of major and minor somites cease with the somite which in the two types is numerically the seventh from the anterior end—an arrangement which results in the change of the major somites from the odd to the even number, the major being odd and the minor even in front of the seventh, while the converse holds behind it?

As for the change itself, we must remember that it is a law of Chilopod metamerism that the number of leg-bearing metameres is invariably odd. Hence, since the first leg-bearing metamere belongs always to the major and the last always to the minor category, both being odd-numbered, the regular alternate succession of major and minor metameres is an impossibility so long as the law is adhered to. At one point at least in the series an alteration in the order of sequence must be introduced, which will result in two major or two minor somites coming together. And surely we should expect the alteration to be effected, as indeed it is, by the juxtaposition of two major instead of two minor metameres if, as has been suggested, all the somites belonged originally to the major category.

That the change sets in in Lithobius close to the middle of the body, and in Scolopendra in the anterior third, may perhaps be explained by some such consideration as the following. The juxtaposition of two major somites is no doubt unfavourable to free flexibility; and since it is advantageous for the greatest possible freedom of movement to lie in the anterior and posterior ends of the body, which bear the principal external organs set apart for the performance of the vegetative and generative functions, the reason becomes clear for the juxtaposition of two major somites to take place as near as can be to the middle of the body in Lithobius, where the body is relatively short, few-jointed, and less flexible. In Scolopendra, on the other hand, with its longer, more jointed, and therefore more flexible body, it is probably immaterial where the juxtaposition of the major somites exactly occurs, provided it is sufficiently distant from both ends not to interfere with the full flexibility of the head and tail.

There appears, then, to be no insuperable or even serious difficulties in the way of believing that the similarity in segmentation between the Lithobiidæ and typical members of the Scolopendridæ is assignable to homoplasy. If, on the other hand, it is attributable to the direct homology of the somites concerned, the view that Craterostigmus exhibits a stage of segmentation intermediate between those of the other two must be wrong. In that case no genetic significance can be attached to the presence of twenty-one tergal plates in Craterostigmus and in Scolopendra. The numerical likeness must be regarded as purely coincidental. This view of the matter I find it impossible to adopt when the other many and deep-seated structural details in which the two forms approximate to one another are taken into consideration.

Finally, it may be stated with confidence and without fear of contradiction that the true nature of the connection, as above explained, between the metamerism of the Lithobioid and Scolopendroid types would never have been guessed, had it not been for the fortunate survival of this intermediate form with the six additional somites of the last-named type in process of excalation.[1]

PART IV.—CHARACTER AND CLASSIFICATION OF THE CHILOPODA.

It is beyond the scope of this article to give a detailed account of the development of the various classifications of the Chilopoda that have been proposed. The main outlines of the subject need only be sketched. Concerning the division of the class into the four main sections typified by Geophilus, Scolopendra, Lithobius, and Scutigera, there has been a pretty general consentience; but authorities have been divided into two schools of opinion touching the relationship of these sections to one another. The first, maintaining the isolation of the Scutigeridæ, was set on foot by Latreille in 1825 ('Faune du Règne Anim.,' p. 327), was supported by Brandt ('Bull. Acad. St. Petersb.,' vii, p. 311, 1840), and held its own practically unchallenged until the publication of Newport's last monograph in 1856, when Brandt's classification of the class into Schizotarsia for

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[1] It is perhaps necessary to point out that the line of argument here adopted to explain the descent of the Lithobioid from the Scolopendroid type is based upon the conviction that intercalation of somites never occurs. Were this otherwise the process of transformation might be reversed, and the Scolopendroid type derived from the Lithobioid; but this would in no sense invalidate the contention that Craterostigmus occupies an intermediate position between the other two. Haase ('Zeits. ent. Breslau,' pt. viii, 1881, pp. 93—115) held an entirely different view in dealing with the phylogeny of the Chilopoda. He regarded the richer metamerism of the Geophilidæ and Scolopendridæ as a derived, and not as a primitive character. Both Geophilidæ and Scolopendridæ have descended, according to him, from a primitive "epimorphous" stock, which was itself derived from an earlier "anamorphous" type, whence, along independent lines of development, arose the Lithobiidæ and Scutigeridæ.

Scutigera, and Holotarsia for the Lithobiidæ, Scolopendridæ, and Geophilidæ, appeared modified only in minor particulars. The second, uniting Scutigera with Lithobius, to the exclusion of the other two, was founded by Meinert in 1868 ('Nat. Tidskr.,' p. 246), who arranged the groups of Chilopoda as follows:—Geophili, Scolopendræ, and Lithobii, the last including the two tribes Lithobiini and Scutigerini.

Although this system was rejected in 1880 by Latzel ('Die Myr. Österr.-Ungar. Mon. I'), who allowed the four families instituted by Leach and Newport to stand unassociated, it was taken up and amplified by Haase, who, adopting the four families and Meinert's view of the near relationship between Scutigera and Lithobius, went a step further and classified the Chilopoda into the Anamorpha and Epimorpha, the first containing the Scutigeridæ and Lithobiidæ, the second the Scolopendridæ and Geophilidæ ('Schles. Chilopoda,' Breslau, 1880, Inaug.-Dissert.).

This classification of Haase's was adopted unchanged by Meinert ('Trans. Amer. Phil. Soc.,' xxiii, p. 163, 1886), and with certain amplifications by Bollman ('Bull. U.S. Nat. Mus.,' xlvi, p. 163, 1893) and Silvestri ('Ann. Mus.,' Genova (2), xiv, pp. 622—634, 1895).

The variation proposed by Bollman consisted in the subdivision of the "order" Anamorpha into two sub-orders, for the first of which, containing the Scutigeridæ, he used Brandt's term Schizotarsia; while for the second, including the Lithobiidæ and Cermatobiidæ, he introduced the new term "Unguipalpi," in allusion to the presence of a claw upon the palpognaths.

Silvestri followed Bollman in splitting the Anamorpha, and replaced the Schizotarsia and Unguipalpi with the new names Anartiostigmata and Artiostigmata, to which an ordinal value was attached. He further divided the Epimorpha into two orders, namely, Oligostigmata for the Scolopendridæ, and Pantastigmata for the Geophilidæ.

Although Haase's classification has the unquestionable merit of drawing attention to the undeniable relationship subsisting between the Scutigeridæ and the Lithobiidæ on the one hand, and the Scolopendridæ and Geophilidæ on the other, it appears to me to be open to the serious objection of obscuring the value of the great structural differences which separate the Scutigeridæ not only from the Lithobiidæ, but from the Scolopendridæ and Geophilidæ as well, and of ignoring the many and important features in which the Lithobiidæ resemble the Scolopendridæ.[1]

The characters which justify the association of the Lithobiidæ with the Scutigeridæ are the following:—the presence of fifteen pairs of legs in the adult, of seven pairs in the newly hatched young, the rest being added with successive moults; the presence of stigmata upon the same somites; the completeness of the penultimate and antepenultimate segments of the toxicognaths; the absence of all trace of "sub-segments" on the somites; the large size of the coxæ of the legs, and the freedom of those of the posterior pairs, and the presence of powerful gonopods in the female—characters which are not found in the other families.

But although these similarities attest the derivation of the Scutigeridæ from Chilopoda of the Lithobioid type, there can surely be no two opinions as to the extent to which they are outweighed when placed in the balance against the many and deep-seated characteristics in which Scutigera differs from all other existing centipedes.

My views on this point were expressed in the classification

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[1] No doubt Haase found confirmation for his views in the discovery of the genus Cermatobius—a genus differing from all the Lithobiidæ known to him, and approaching the Scutigeridæ in its longer, "funiculate" antennæ, longer and subdivided tarsi, absence of coxal pores, longer female gonopods, and slightly more dorsal stigmata. There is no doubt, however, that Cermatobius is very closely related to Lamyctes and its allies. For example, although typically four or five in number in these forms, the coxal pores are reduced to one on each coxa in Haasiella and in Henicops, as typified by maculatus, the anterior tarsi consist of three segments, and the posterior pairs of six—facts which largely discount the value of the absence of coxal pores and the rich tarsal segmentation in Cermatobius.

proposed in 1896 ('Biol. Centr. Amer.,' Chilopoda)—a classification which, allowing for the alteration in terminology and an elevation in rank of the groups, was that of Latreille, Brandt, and Newport amplified.

Two sub-classes were recognised, the Artiostigma for the order Scutigeromorpha, and the Anartiostigma for the Lithobiomorpha, Scolopendromorpha, and Geophilomorpha.

If, as I venture to think, this system expressed at the time more accurately than Haase's the importance of the characters of Scutigera and the relationship between the Lithobiidæ and the Scolopendridæ, the opinion that it embodies receives the strongest support from the discovery of Craterostigmus. In no sense does this genus tend to lessen the structural interval between the Scutigeroid and Lithobioid types; but it largely depreciates the value of the characters the two have in common—the characters, in short, upon which Meinert and Haase relied when uniting them. Those who in the future maintain the Anamorpha must base this group upon the completeness of the penultimate and antepenultimate segments of the toxicognaths and the numbers of stigmata and pairs of legs, if Craterostigmus be included; for this genus negatives the remaining characters of the group, with exception of the number of legs at hatching, a point about which few would venture to hazard a guess so far as Craterostigmus is concerned.

In connection with the classification here submitted, it is desirable to justify the changes in terminology that have been introduced. Notostigma and Pleurostigma are preferred to Artiostigma and Anartiostigma because the latter were used in a much more restricted sense by Silvestri; and to Schizotarsia and Holotarsia because these two lost their applicability with the discovery of Cermatobius. Ungui-palpi connotes a character which holds only when the Lithobiidæ are associated with the Scutigeridæ; and Pantastigmata and Oligostigmata make no allowance for the pantastigmous character of Plutonium, which nevertheless is closely related to the oligostigmous forms.

Class Chilopoda.

Opisthogoneate tracheate Arthropods descended from a primitive type in which the body consisted of a large number of metameres similar in size and form, each with a broad tergal and sternal plate, connected by a pleural membrane, a pair of stigmata, and a pair of short hexarthrous, mononychous appendages. At an early phylogenetic stage the stigmata disappeared from the last three somites in connection with the special functions these somites were set apart to fulfil, the last or anal losing its appendages and being degraded to the condition of a carrier of the anal orifice; the penultimate or genital being, like the anal, reduced in size as a safeguard against damage, but retaining its appendages in a dwarfed form as manipulators of the ova or spermatophores; and the antepenultimate or last leg-bearing somite having its appendages enlarged and directed backwards to protect the genital somite, and, in later stages, to become modified as tactile, offensive, or secondary sexual organs. Anteriorly two pairs of appendages, retaining a primitive biramous structure, were set apart as gnathites; and a single pair, lying in front of the latter, consisting of not fewer than fourteen homonomous segments, and widely separated at the base, as antennæ. The dorsal area of the three somites represented by the appendages just mentioned was covered by a single plate, the cephalite or head shield, which was furnished laterally with eyes, and was curved downwards in front over the mouth to form a labrum or upper lip. For seizing and holding prey, the six-jointed appendages of the two metameres behind the head were turned forwards towards the mouth, their basal segments becoming enlarged and encroaching upon the sternal area, each appendage at the same time undergoing a partial axial rotation, so as to fold in a horizontal rather than a vertical plane. The first pair of these appendages retained its primitive pediform structure, while in virtue of the development of a poison gland, accompanied by an increase in the thickness of its segments, practically the sole function of prehension was taken over by those of the second pair.

Sub-class Pleurostigma.

Chilopods resembling the primitive type in the possession of a system of tracheal tubes, the orifices of which open upon the pleural area of more or fewer of the somites; and in the presence of a distinct tergum and sternum on each leg-bearing somite, the number of sterna never exceeding that of the terga. Eyes are either preserved or lost; when preserved they are monomeniscous, and variable in number on each side from one to about forty. Correlated with the relative simplicity in the structure of the metameres just mentioned is a marked specialisation of the head and the appendages connected therewith, a specialisation which was initiated apparently by the retroversion of the præantennal area of the cephalite resulting in the projection of the antennæ from the fore-margin of the head thus formed, and in the backward movement of the mouth with the gnathites of the first and second pairs into more intimate connection with the palpognaths and toxicognaths. As concomitants of this process the last-named appendages shortened and thickened, were axially rotated so as to move and fold in a horizontal plane, one segment of the palpognaths was suppressed, and the basal segments of the toxicognaths became firmly fused and incapable of independent movement; and lastly, the gnathites of the second pair being underlain by the two pairs that succeed them, failed to develop or lost the sense-organ which is found in the other sub-class.

Order 1.—Geophilomorpha.

Chilopods retaining a large and indefinite number of metameres in response to the demands of a subterranean existence requiring serpentine powers of movement. To further subserve this end, most of the somites are either partially or completely divided into two anteriorly, a process which, when perfected, gives rise to a series of sub-segments alternating with the true somites, the former being represented by a prætergal and a pair of præsternal plates. Stigmata are retained on all the somites, except the first and last, for purposes of respiration under ground; and the legs, which are short and play but a subsidiary part in locomotion, preserve the primitive number of segments, the basal of which remains small.

The eyes, as useless organs, have disappeared; and the antennæ are relatively short and consist invariably of fourteen segments. The gnathites are specialised and variable in structure; the penultimate and antepenultimate segments of the toxicognaths are reduced on the præaxial side of the appendage to the state of arthrodial integumental folds between the distal segment and the femur, which are firmly articulated together on its post-axial side. The tergal plate of these appendages always remains distinct and usually large, thus separating the cephalite from the tergum of the first leg-bearing somite. The pleural sclerites are well developed, and those of the last leg-bearing somite fuse with the coxa of the appendage, the second segment of which remains free. The anal and genital somites are incapable of retraction within the somite which bears the last pair of legs, and the gonopods typically persist in the male as small-jointed appendages, and in the female also as jointed or unjointed, often lobate sclerites.

Many families—Geophilidæ, Oryidæ, Gonibregmatidæ, etc.

Order 2.—Scolopendromorpha.

Chilopods departing from the primitive type and from the Geophilomorpha in having the number of leg-bearing somites fixed definitely to twenty-three or twenty-one, the reduction in number in the latter case being effected by the excalation of the two somites preceding that which bears the last pair of legs; by the evanescence of the tergal plate of the toxicognaths, which results in contact between the cephalite and the tergum of the first leg-bearing somite; in the ankylosis of the second and third segments of the legs of the last pair; in the incipient differentiation of the metameres into alternating major and minor leg-bearing somites, the regularity of the alternation, however, being interrupted at the seventh and eighth somites, both of which belong to the major category; in the power to withdraw the anal and genital somites out of harm's way into the last leg-bearing somite, in the total disappearance of the female gonopods, and the reduction of the segments of the male gonopods to one. With the shortening of the body and the lessening of the need of serpentine mobility, no prætergal sclerites are definitely cut off from the terga, though pairs of præsternal sclerites are developed. The eyes may be lost; when present they are invariably four in number. The segments of the antennæ never normally fall below seventeen nor above about thirty. On the other hand, the basal segments of the legs are feebly developed as in the Geophilomorpha, and the toxicognaths are modified and the pleural sclerite of the last leg-bearing somite enlarged and fused with the basal segment of the appendage as in the members of that order.

Several families—Scolopendriidæ, Newportiidæ, etc.

Order 3.—Craterostigmomorpha.

Chilopods derivable from a primitive form of Scolopendromorpha (which was furnished with twenty-one pedigerous somites, nineteen pairs of stigmata, complete penultimate and antepenultimate segments on the toxicognaths, distinct tergal plate for these appendages, and undivided tarsal segment on all but the last pair of legs, which had the first segment free), by the excalation of the sternal area and limbs of the third, sixth, ninth, eleventh, fourteenth, and seventeenth somites, thus reducing the number of legs to fifteen pairs; by the retention of six pairs of stigmata upon the somites bearing the third, fifth, eighth, tenth, twelfth, and fourteenth pairs of legs; by the enclosure of the anal and genital orifices in a bivalvular sclerite, representing probably the tergum of the anal somite, and by the complete fusion of the sternum and pleura of the fourteenth, and of the sternum, pleura, and tergum of the fifteenth leg-bearing somites.

One family—Craterostigmidæ (Craterostigmus).

Order 4.—Lithobiomorpha.

Chilopods derivable from the primitive form of Craterostigmomorpha by the excalation of the third, sixth, ninth, eleventh, and seventeenth tergal plates, which brings the terga and sterna into numerical conformity; by the differentiation of the terga into major and minor in the interests of flexibility; by an increase in the size of the basal segment of the legs, especially of the posterior pairs, and the segmentation of the tarsi of all the legs, or at least of the thirteenth and fourteenth pairs, to subserve rapidity of movement. In other respects the members of this order stand nearer the primitive type of the Chilopods than those hitherto considered. The tergum of the first pedigerous somite is relatively small in correlation with the weak muscularity of the toxicognaths, the basal segments of which are less strongly fused; the gonopods, present and jointed in both sexes in more archaic types, are always well developed in the females, and are supported upon a large ventral plate, which results from the fusion of their basal segments with the sternum of the genital somite; and lastly, in two families, the Henicopidæ and Cermatobiidæ, the stigmata are preserved upon the somite that bears the first pair of legs.

Three families—Lithobiidæ (Lithobius, etc.), Henicopidæ (Henicops, etc.), Cermatobiidæ (Cermatobius).

Sub-class Notostigma.

Chilopods descended from the Cermatobioid type of Lithobiomorpha by the replacement of the normal tracheal system by a series of median dorsal pulmonary sacs furnished with tubes dipping into the pericardial space, and opening each by a single stigma which results from the upward migration and coalescence of the normal pair of stigmata upon the first, third, fifth, eighth, tenth, twelfth, and fourteenth somites—a change in the method of respiration which is accompanied by the complete disappearance of the tergum of the seventh somite, either by excalation or by fusion with that of the eighth, and by the evanescence of all the minor terga except that of the fifteenth leg-bearing somite. Further specialisation is attested by the presence of a sense-organ on the gnathites of the second pair, by the polymeniscous eyes,[1] the duplication of the gonopods in the male,[2] and the extreme length and perfected annulation of the antennæ and of the distal segments of the legs, those of the fifteenth pair being clawless and simulating a couple of feelers both in form and function. In virtue probably of these extremely specialised features, mouth parts of a markedly primitive type have been preserved; the long and slender toxicognaths exhibiting only a partial axial rotation, long penultimate segments, and disunited and independently moveable coxæ, the palpognaths being also incompletely rotated, long and pediform, with the same number of segments as the primitive Chilopod limb, and projecting freely at the sides of the head; the præantennal area of the cephalite projects forwards and downwards in front of the bases of the antennæ, which remain widely separated as they are in the early embryonic stages in this

[1] I here provisionally adopt the view already suggested by others, that the faceted eye of Scutigera resulted from the packing together and mutual pressure of a number of monomeniscous eyes like those of Lithobius. But in view of the many primitive features appertaining to the head of Scutigera, the possibility must be borne in mind of the derivation of a set of monomeniscous eyes from one of a polymeniscous type, as has doubtless occurred in the case of the lateral eyes of Scorpio. Or, again, it may be that the large convex eye of Scutigera, with its many facets, corresponds as a whole, either in a derivative or originative sense, to the large single-lensed eye of Cermatobius, the genus which, beyond all possibility of doubt, is most nearly related to Scutigera in all other structural points.

[2] Possibly the additional gonopods represent the missing appendages of the anal somite.

class; and the second pair of gnathites are lengthened especially with regard to the second (femoral) segment to reach the mouth, which lies relatively far forwards.

Order Scutigeromorpha (characters as above).

One family—Scutigeridæ (Scutigera).

EXPLANATION OF PLATE 23,

Illustrating Mr. Pocock's paper, "A New and Annectant Type of Chilopod."

(The figures, depicting the structural features of Craterostigmus tasmanianus, were drawn by Mr. Pocock from the specimens of this centipede which are preserved in the Natural History Museum.)

Fig. 1.—Dorsal view of anterior extremity. *c.* Cephalite or head shield. *o.* Eye. *sf.* Frontal suture. *a.* Antenna. *bp.* "Basal plate" = tergum of toxicognath. *pl.* Pleural sclerite of toxicognath. *cx. p.* Coxal plate. *f.* Femur or third segment. *p.* Patella or fourth segment. *t.* Tibia or fifth segment. *cl.* claw or sixth segment of toxicognath. 1, 2, 3. Terga of first, second, and third somites.

Fig. 2.—Ventral view of toxicognaths, showing the præcoxal processes of the coxal plate (*cx. p.*), the second segment or trochanter (*tr.*), which is fused with the third segment or femur (*f.*), the præaxial teeth of the latter, and the completeness of the fourth and fifth segments (*p.*, *t.*) on the post-axial side of the appendage.

Fig. 3.—Lateral view of head and anterior extremity of body. Lettering of head and toxicognath as in Fig. 1. 1—7. Terga of anterior seven somites, numbers 3 and 6 being without sternal representatives. 1′—5′. Sterna of anterior five leg-bearing somites. *s.* Stigmatic, and *ms.*, metastigmatic sclerite. *pl. m.* Membrane of pleural area. *cx.* Coxa or basal segment of leg. *pcx.* præcoxal sclerite. *ps.* præsternal sclerite.

Fig. 4.—Lateral view of posterior extremity of body. 15—21. Terga of fifteenth to twenty-first somites. 10′—15′. Sterna of tenth to fifteenth leg-bearing somites. The rest of the lettering as in Fig. 3.

Fig. 5.—Dorsal view of last leg-bearing somite with ano-genital capsule (*ag.*) projecting from its posterior extremity. *t.* Tergal area of somite. 1 and 3. First and base of third segment of leg of fifteenth pair.

Fig. 6.—Ventral view of last leg-bearing somite and of ano-genital capsule (*ag.*). 1—3. First, second, and base of third segment of leg of fourteenth pair. 1′, 3′. First and base of third segment of leg of fifteenth pair. *s.* Sternal area of last leg-bearing somite. *ps.* Fused præsternal element.

Fig. 7.—Lateral view of the ano-genital capsule (*ag.*) and of the posterior half of the last leg-bearing somite. *lat.* Lateral area of this somite. 1. Basal segment of the leg.

Fig. 8.—Ventral view of cephalite or head plate. *a.* Basal segment of antenna. *sf.* subfrontal or retroverted præantennal area with labral sclerites.

Fig. 9.—Labrum. *t.* Teeth. *m.* Membranous lateral portion of excision.

Fig. 10.—Lower or posterior aspect of mandible or gnathite of first pair. *f.* Fringe of hairs at its distal extremity.

Fig. 11.—Upper or anterior aspect of the same. *f.* Fringe of hairs. *t.* Pectiniform teeth. *l.* Membranous lobe.

Fig. 12.—Distal extremity of the last still more enlarged, showing the series of nine pectiniform teeth arranged in groups of threes.

Fig. 13.—Inferior or posterior view of gnathites of the second pair (maxillæ). 1. Basal segment bearing the bisegmented ectocorm (1, 2) and the one-jointed ectocorm (*int.*).

Fig. 14.—Lower or posterior view of left palpognath. 1. Ectocoxite. 1′. Entocoxite. 2—5. Second to fifth segments, the second, or trochanter, fused with the third, or femur.

Fig. 14 *a.*—Distal segment of the same from its anterior or upper side, showing fringe of hair.

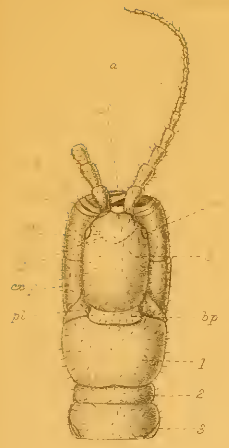
Fig. 15.—Lateral view of part of the third leg-bearing somite (fourth somite from the dorsal side). *t.* Tergum. *s.* Stigmatic sclerite with stigma. *ms.* metastigmatic sclerite. *pl.* Pleural membrane.

Fig. 16.—Leg of fourteenth pair. 1—6. Segments; 2 with inferior spike, 5 and 6 with spines.

Fig. 17.—Basal portion of same. *lat.* Part of lateral portion of the fourteenth leg-bearing somite. 1. Basal segment or coxa of leg with subspherical excrescence or nodule (*n.*). 2. Second segment or trochanter with spike (*sp.*). 3. Base of third segment or femur.

Fig. 18.—Leg of the fifteenth pair. 1—7. First to seventh segments, the sixth and seventh representing the sixth of Fig. 16; 1 with inferior spike, 2 ankylosed to 3.

Fig. 19.—Basal portion of same. *lat.* Lateral area of part of fifteenth leg-bearing somite. 1. Basal segment or coxa with (*n.*) nodular prominence and (*sp.*) spike. 2. Remnant of the second segment or trochanter fused with the base of the third segment or femur (3).



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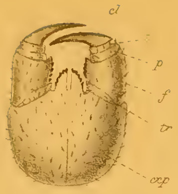

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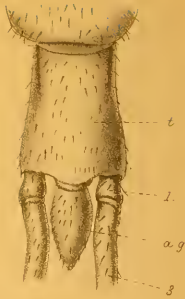

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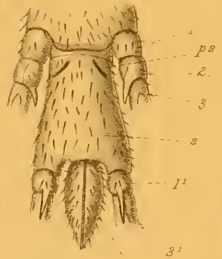

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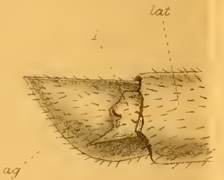

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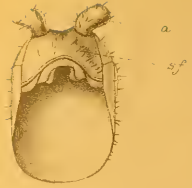

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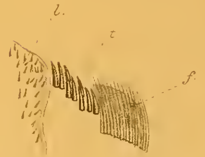

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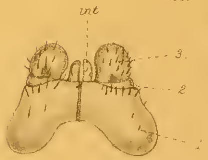

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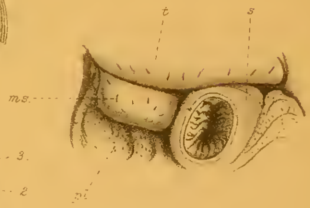

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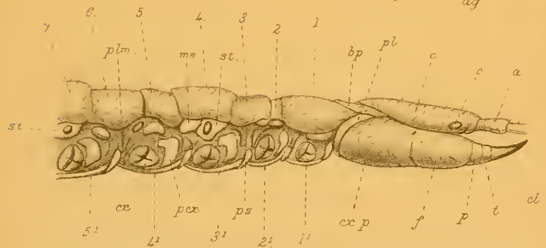

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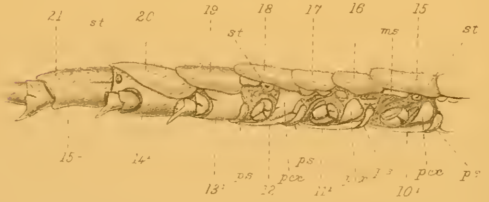

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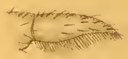

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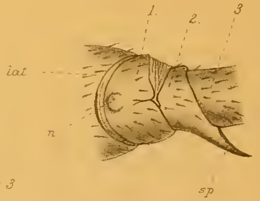

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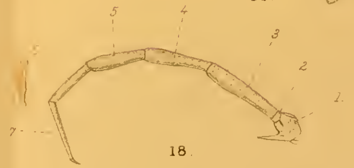

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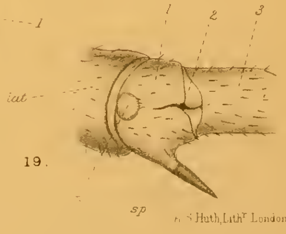

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A. S. Huth, Lith.ʳ London

The Trypanosoma Brucii, the Organism found in Nagana, or Tse-tse Fly Disease.

By

J. R. Bradford, F.R.S.,

and

H. G. Plimmer, F.L.S.

(From the Laboratory of the Brown Institution).

With Plates 24 and 25.

CONTENTS.

I. NOMENCLATURE.

In our preliminary paper[1] on the organism found in the Tse-tse fly disease we suggested Trypanosoma Brucii as a suitable and appropriate name for it. But after this Laveran, in his papers on this organism, gave it the name Herpetomonas Brucii, which apparently he considered to be a more accurate designation biologically. However, in a recent paper by Laveran and Mesnil,[2] discussing these terms from a morphological point of view, they show that Trypanosoma is a more accurate term than Herpetomonas; in fact, that this latter term ought to disappear altogether, and that the generic name Trypanosoma ought to be used to designate all those flagellated organisms at present known, which are parasitic in the blood of vertebrates. Hence we shall retain the name we used in our paper above mentioned, as being probably the more accurate one.

II. THE ADULT FORM OF THE TRYPANOSOMA BRUCII.

A. Examined in the Living State.—The adult form of the Trypanosoma can be easily studied in the fresh blood of an affected animal, by placing a drop on a slide and simply covering it with a cover-glass, and examining it with an objective of suitable power. But, as these organisms are extremely delicate, and are very easily broken up by slight pressure, it is better to make a very thin cell, by running a small drop of melted paraffin on to a slide in the form of a ring or square, by means of a red-hot platinum loop, and to place the drop of blood in the centre, covering it with a cover-glass, which must be sealed with paraffin, in order to prevent evaporation, if the blood is to be examined for any

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[1] "A Preliminary Note on the Morphology and Distribution of the Organism found in the Tse-tse Fly Disease," by H. G. Plimmer and J. Rose Bradford, F.R.S., 'Proc. Roy. Soc.,' vol. lxv, p. 274.

[2] "Sur la structure du Trypanosome des grenouilles et sur l'extension du genre Trypanosoma, Gruby; par Laveran et Mesnil, 'Comptes rendus de la Société de Biologie,' tome liii, No. 23.

length of time. This method obviates pressure, and the organism may be easily studied with even the highest powers. The Trypanosoma will then be seen to consist of a worm-like body, more or less homogeneous in structure, with at one end a blunt, stiff extremity, and at the other a long, wavy flagellum. With good illumination this flagellum can be seen to be continuous with a wavy membrane which extends along one surface of the long axis of the organism. For some time the Trypanosoma will be seen to be in active motion, which is caused by the rapid lashing movements of the flagellum, by the wavy movements of the undulating membrane, and by the contractions and relaxations of the protoplasmic mass forming the body. In order to arrest this movement a drop of 1 per cent. gelatine solution, or of a weak solution of cherry-gum, should be mixed with the blood, which will so reduce the movement that it will be quite easy to study as much of the organism as can be made out in unstained preparations. In order to see the structure of the living organism, dark ground illumination, or monochromatic light must be used. The former is difficult to use with an immersion lens, but can be very satisfactorily used with a 2 mm. immersion objective, after the method of Gebhardt.[1] We have used spectral monochromatic light (blue), but very good results can also be obtained more easily with Gifford's malachite-green screen. With these methods of illumination the organism appears as a highly refractive body, and near the middle is seen a darker mass —the nucleus; and near the blunt, stiff end of the body is seen a tiny dark dot, which we will here call the micronucleus; the question of its proper nomenclature will be discussed later. At the same end of the Trypanosoma, in varying relations to the micronucleus, is seen a vacuole. The protoplasm is now seen not to be uniform, but it appears to have an alveolar structure, as described by Bütschli. With regard to the movements of the organisms, the commoner mode of progression would seem to be with the

[1] 'Zeitschrift für wissenschaftliche Mikroskopie,' Band xv, p. 289.

flagellum forwards, but it is quite easy for them to move as quickly with the blunt end forwards. The size and length of the body vary very much with the period of the disease, and with the kind of animal in which they are growing. Measurements made on the full-sized living Trypanosoma in rat's blood give a length, including the flagellum, of 25—35 μ, and a width at the widest part of about 2 μ.

B. Examined after Fixation and Staining.—1. Methods.—In order to study the real structure of, and changes in, the Trypanosoma, recourse must be had to fixing and staining, and for both of these processes the ordinary methods are of no avail. The films must be made as thin and even as possible, and the method we have found most effective is to place a small drop of the affected blood on one corner of a cover-glass or slide, and to spread it very carefully with a piece of goldbeater's skin, which is held in a pair of forceps. The edge of this must be cut quite straight, and it should be of a little less width than the cover-glass. It is very important that the film should be very carefully made, otherwise both fixing and staining will be imperfect. As regards fixation we have found that osmic and acetic acid vapours (osmic acid 2 per cent. and glacial acetic acid equal parts) give the very best specimens; but for general work a mixture of formalin ten parts and absolute alcohol ninety parts, as suggested by Gulland,[1] gives very good results. Fixation with this latter formula is effected in from five to ten minutes, after which the specimen must be well washed in running water, and then dried before it is stained. The only stain which we have found to be of any value in our work upon the Trypanosoma is that which we indicated in our Preliminary Note; viz. a modification of Romanowsky's practical application of an idea of Ehrlich's, which consists in mixing an acid and a basic stain in such proportions that a third body is formed, which has an extraordinary affinity for chromatin. Our method of applying this idea is as follows. The stains used

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[1] 'Scottish Med. and Surg. Journ.,' 1899, p. 312.

are methylen blue and erythrosin; the methylen blue used must be the methylen blue med. pur. (Höchst). A 1 per cent. solution in distilled water is made, and to it ·5 per cent. potassium carbonate is added and dissolved; the mixture is then incubated at 37° for forty-eight hours; when cold it is filtered, and is then ready for use. Instead of using eosin (under which name many substances of different shades and of different composition are sold) for the second stain, we have found it far more certain and effective to use erythrosin (the tetraiodide of fluorescein), which, as found in commerce, is of more definite and constant composition and colour than eosin; a ·001 per cent. solution is made, to which ·25 per cent. formalin can be added in order to prevent the growth of moulds. Of these two solutions we have found the following to be the best mixture for demonstrating the different structures in the Trypanosoma: 20 c.c. of distilled water are put into each of two beakers, to one of which is added twenty drops of the erythrosin solution, and to the other six to eight drops of the methylen blue solution. These solutions are then quickly mixed, and are immediately poured into a flat dish, in which the slides or cover-glasses to be stained have been placed. About twenty minutes suffices for the differential staining, as shown in the plates, to take place. The specimens are then washed in distilled water till no more colour comes away, and are then allowed to dry in the air. No heat must be used for drying, otherwise the red colour will entirely disappear. They are then mounted, preferably in turpentine colophonium, in which the colours keep, according to our observations, for the longest time.

Various other modifications of this method of staining have been suggested by Nocht, Reuter, Laveran, Leishman, and others, but although they all give the specific reaction, we have not found any which give so brilliant and clear a picture as that described.

2. The Appearances of the Adult Trypanosoma.—When the preparation has been successful the appearances

seen are those shown in figs. 1—6. The body of the organism is stained blue, but not uniformly, there being parts which are stained faintly, and some hardly at all, which is in confirmation of the alveolar structure which has been mentioned above. The macronucleus is stained a pinkish-red, and is, in the resting form, nearly homogeneous, with only traces of a reticular structure; it is also sharply defined and extends right across the short axis of the body. The micronucleus is stained of a darker red colour, and it always stains more intensely than any other part of the organism: it appears as a very small round dot, and we have been unable, with the highest powers, to make out any further structures in it. It is generally surrounded by an unstained halo. The flagellum is stained of a yellowish-pink colour, as well as the edge of the undulating membrane, which can be seen to end in the micronucleus. The edge of this membrane is apparently thickened and merges into the flagellum. In some organisms the part of the body behind the micronucleus stains of a darker blue than the rest of the body, and the darker part may contain a row of faint dots arranged regularly in the long axis of the organism. These are seen especially in those animals from which the spleen has been previously removed.

Besides these forms, the first of which constitutes by far the greater part of those seen in the blood, there are other adult forms which are seen at certain times and in certain places. That shown in fig. 5 is seen in the blood of the rat when the disease is well advanced, about a day or two before death, and they are also found in the blood of spleenless rats from the second day; they are also seen in the blood of the mouse, and in greater numbers especially in the blood from the lungs taken immediately after death. This organism is much larger than the ordinary adult form, and is much wider, often more than double the width, and is more irregular in shape. The protoplasm is quite homogeneous and much more delicate, and it stains very faintly with the methylen blue. The macronucleus is large and roundish in shape, and the chromatin is more condensed at the circumference, so as to give it a ringed shape; and it never extends completely across the short axis of the organism, as is the case in the ordinary form. The chromatin is in the form of coarse threads or rods, and there is almost invariably a clear unstained place in the centre of the nucleus, which may contain a few scattered dots of chromatin. The micronucleus is very distinct, as are also the undulating membrane and flagellum. In this form the thickened edge of the undulating membrane is most distinct.

Another form, which is also found principally in the blood from the lungs in the mouse, is that shown in figs. 6—8. In this, besides the macro- and the micronucleus, there are a number of dots staining very intensely, but of a much darker colour than the micronucleus. In the one figured the macronucleus is still visible, but we have found these forms quite full of these dots, with no visible macronucleus. We thought at the time of our first paper that this form was that following conjugation, as a similar process occurs after conjugation in organisms not far removed biologically from this one, but this question will be discussed later.

III. Reproduction of Adult Forms of Trypanosoma Brucii.

In our former paper we stated that we thought there were two modes of multiplication by division of the adult Trypanosoma, viz. by longitudinal division and by transverse division. We now think that there is only one mode, that of longitudinal division, and we think that the appearances which we interpreted as transverse divisions were those of amœboid forms and not those of division. Besides this means of reproduction by division, there is that of the formation of a plasmodial mass, from which amœboid and adult forms are given off, which will be mentioned later. This form of reproduction is, we think, of the greatest importance and interest.

We will take first the method of reproduction by division.

The process of longitudinal division down the long axis of the organism is shown in figs. 11—17. The first step is a general increase in the size of the organism; the micronucleus first enlarges, and then the macronucleus, which becomes also very distinct (this is well shown in figs. 11—13); the micronucleus lengthens out and divides into two, to the second of which a new undulating membrane, which is by this time developed, is attached (figs. 12 and 17); the macronucleus then divides (figs. 14—17), and a white line is seen extending down the long axis of the body (figs. 14—16); eventually the organisms separate into two fully formed Trypanosomata. The order of the division is in general this:—firstly the micronucleus, then the undulating membrane, then the macronucleus, and lastly the protoplasm.

In fig. 17 is shown the division of one of the large, hyaline variety of the organism, which has been described above. In this kind the process is exactly similar to that in the ordinary variety, only it is much more distinct, on account of the larger size of the organism, and its clearer staining.

IV. CONJUGATION BETWEEN THE ADULT TRYPANOSOMATA BRUCII.

In the blood of the rat, and of all the animals we have examined (mouse, dog, cat, rabbit, guinea-pig, horse, mule, pig, spring-bok, goat), forms have been seen, such as those shown in figs. 18—23, which we think can only be interpreted as conjugations. The organisms can be seen in the living blood joined together by their blunt ends, and moving about in this state by their flagellated extremities, the joined parts remaining motionless. In stained specimens they are found as figured, and the only difference in these is the position of the micronuclei. At first, after the bodies have joined, these micronuclei are in their normal position at the usual distance from the blunt end of each organism (fig. 18), then they are seen to approximate to each other (fig. 19), and then they get still nearer and nearer (figs. 20 and 21), until they become fused into one micronucleus (fig. 22). Several other arrangements of the micronuclei in these conjugating organisms can be seen, such as a dot in one Trypanosoma and a rod in the other, or two dots in one and one in the other. The arrangement of a dividing rod and a dot can be seen in fig. 20; that of a rod and a dot in fig. 21.

Although it is difficult to definitely associate this junction of two individuals with any immediate change in form, yet we think, from the fusion of the micronuclei which takes place, that it must be a true conjugation: and it is known that this takes place in allied organisms, e.g. the Bodoninæ, which separate afterwards and go on as before, but perhaps with renewed energy for division.

After the fusion of the micronuclei we have not been able, notwithstanding the examination of several hundred specimens, to be sure of any constant further stages, but we imagine that the most likely occurrence is that the fused micronucleus lengthens out into the rod form, and then divides into two, one for each organism, and that then the organisms themselves separate. In that case many of the forms which we have seen, in which there is this rod form of micronucleus, or in which the two micronuclei are separated, may be those which have passed the fusion stage and are going on to separation. In many, but not all, of these conjugating forms the macronucleus shows signs of activity, i.e. it enlarges and becomes oval or circular, and the chromatin becomes aggregated at its margin, and we have thought that these forms may be those in which conjugation is ending, and which are about to separate and to go on to renewed longitudinal division.

In our former paper we stated that we thought the dotted forms described above (figs. 6—8) might be those immediately following conjugation. But we have no evidence of this; and moreover, with very careful staining and illumination, these dots are seen to be of a little different tint to the micro- or macro-nucleus. Sometimes they are of a quite dark purple colour, instead of the red nuclear colour, and they are moreover of very varying size. We have never observed conjugation taking place between the large hyaline forms described above.

V. "AMŒBOID" AND "PLASMODIAL" FORMS OF THE TRYPANOSOMA BRUCII.

We do not wish or mean to attach any particular biological meaning to these two terms, which we use here only for convenience of description. Besides the forms described above, there remain two other forms which practically seem to be of the greatest importance of any, as the death of many of the animals we have used seems to depend upon their presence.

The first of these forms is that which for convenience we have called "amœboid." By this we mean a form consisting of a small irregularly shaped mass of protoplasm, with a micro- and macro-nucleus, and with or without a flagellum; they are all very mobile when examined in the living state. This form is depicted in figs. 24—37. The protoplasm is very delicate and uniform, and the micro- and macro-nuclei are small, but very distinct; and this form is only seen well in stained preparations when the differential stain we have described above is used. But they can be seen in fresh unstained preparations with very careful critical illumination; in fact, our first observation of them was in a fresh unstained preparation. The flagella may or may not be seen, but we believe that they are, when free, all flagellated, but that in the preparation of the film the flagella may become detached, as free flagella attached to their micronuclei are seen in most preparations in which these amœboid forms can be found. They are found in the blood from the lungs of most of the animals we have used, especially in that of the rat, mouse, cat, and dog, where they are present in enormous numbers; they are also found in the glands in small numbers, and in the bone marrow of animals from which the spleen has been removed before inoculation. They may also be demonstrated in the blood of spleenless animals, also in that of the more refractory animals, such as the rabbit (as shown in figs. 9 and 10) and guinea-pig, when repeated examination of the blood fails to reveal any of the ordinary adult forms. They are also present in the spleens of all the animals we have examined in greater or less number. Another place where they are specially found—and this is of importance from the clinical side—is in the capillaries of the brain and medulla. Most of our animals have died with symptoms referable to the nervous system; either they become comatose and die in a few hours, showing no symptoms till the coma appears, or they have fits of an irregular character, or they become paralysed in one or more limbs. Many of the cerebral capillaries can in these cases be found to be quite plugged up with these amœboid forms, as is shown in figs. 40 and 41. The similarity of these appearances with those of the cerebral capillaries in pernicious malaria is very striking. In order to demonstrate these forms either in the lung, brain, or elsewhere, films must be made from the organs directly after death, and treated with the same stains as described for blood. We have not found yet any method of fixation of pieces of tissues fine enough to demonstrate them in sections of these organs.

These amœboid forms can be seen in all stages of division, and they appear to multiply much more rapidly than the adult organism. Stages can also be seen intermediate between these and the adult Trypanosoma. The method of division corresponds closely with that of the adult organism. First the micronucleus becomes rod-shaped, and then divides; the macronucleus enlarges at the same time and divides a little after the micronucleus, and lastly, the protoplasm divides. Many irregular forms are seen, especially in the bone marrow, resulting from the irregular division of these amœboid forms.

Besides these there is another form, which we have, also for convenience, called a "plasmodial" form. This is seen in figs. 37—39. It seems to consist of a protoplasmic mass, containing a very large number of micro- and macronuclei irregularly embedded in its substance; in the central part there are no divisions to be seen in the mass of protoplasm surrounding the nuclei, but at the marginal parts amœboid forms can be seen in process of detachment, such as is shown in fig. 37. These masses are best seen in the spleen of the rat or mouse, but can also be observed in the blood of animals from which the spleen has been removed. They can be seen also in less quantity in the blood from the lungs of most animals. In the bone marrow of spleenless animals this form can also be demonstrated. At present, it does not seem possible to say for certain whether this form is a true "plasmodium," i.e. a fusion of several elements, or whether it is merely an aggregation of amœboid forms. Our opinion is in favour of the former view. This form is of the greatest importance, as its presence not only causes the great enlargement of the spleen observed in certain animals, but is also a means of very rapid multiplication of the organism.

VI. THE DISTRIBUTION OF THE TRYPANOSOMA BRUCII; ITS VARIATIONS IN DIFFERENT ANIMALS, AND THEIR RESISTANCE TO IT.

The distribution of the Trypanosoma in the different animals we have used varies considerably. In the rat and mouse—animals that die in the shortest time—the organism is found in the blood from forty-eight hours after inoculation, and they go on steadily increasing till at the time of death, usually from six to nine days, there may be as many as 3,750,000 per cub. mil. These are nearly all of the adult form, and may be seen in all stages of longitudinal division, and in conjugation. The spleen becomes, towards the end of the disease, enormously enlarged, measuring about 5 to 6 cm. by 1 to 2 cm., and it is found to contain an enormous quantity of plasmodial material, as seen in fig. 38, some amœboid forms and a very few adult forms. The blood from the lungs contains a very large number of amœboid forms, a few plasmodia, and a few adult forms. The liver, kidneys, and bone marrow only contain adult forms in quantity corresponding with those in the blood. The glands contain many amœboid forms, and a fair quantity of adult forms. The organism is first found in the gland nearest to the point of inoculation, in eighteen to twenty-four hours after inoculation. The cerebral capillaries at the time of death are in great part blocked with amœboid forms (figs. 40 and 41). In the mouse the appearances are quite similar, but the number in the blood never reaches the number found in the rat. In the dog and cat the spleen is enlarged and contains amœboid and plasmodial forms, but it is not so large relatively as that of the rat. Their blood does not become infectious until the fourth day after inoculation, and never contains such quantities of the organisms as does rats' blood. The glands in both cat and dog are always affected, as in the rat, and contain both amœboid and adult forms; the bone marrow also contains many adult and amœboid forms. In the rabbit the organisms are only found at irregular intervals in the blood, and then only in very small numbers. The glands are not enlarged at the time of death, which may be as long as three months from the date of inoculation. The spleen is not enlarged, and only contains a few amœboid forms; the bone marrow is almost entirely free. In this animal the chief obvious lesions are a swelling of the eyelids with a slowly progressive panophthalmitis, and a soft œdema of the genitals. These also occur, but less markedly, in the dog and cat. It begins always as a plugging up of the lymphatics, which contain numbers of the organisms, principally of the amœboid form, so the disease in these animals seems principally to affect the lymphatic system. The goat shows very little sign, and the organism is not found abundantly in the blood, but the animal gets œdema of the genitals, and the eyes become somewhat opaque. It dies in about two months after inoculation, with paralysis. The spleen is not enlarged; the nasal mucous membrane becomes swollen, and interferes with breathing. In the horse and mule the organisms are constantly found in the blood, and the spleen is enlarged and contains amœboid forms. The sheath becomes swollen, and the abdomen œdematous, and they die in about six or eight weeks with paralysis. The Trypanosoma is longer and thinner in these animals than in any we have used. The guinea-pig shows the organism in the blood in varying numbers and at varying periods; sometimes there are none to be found for long periods, and again they may be numerous for a time. The spleen is not enlarged, and the bone marrow contains no organisms. Amœboid forms can be found in the blood from the lungs. The guinea-pig may live as long as eighteen weeks after inoculation. The pig shows the organism in the blood very rarely and in very small numbers, and dies with pulmonary symptoms. The spleen is not enlarged. The spring-bok dies in about four weeks with nervous symptoms, and with the organisms present in the blood.

It will be seen from the above that there is a good deal of variation in the distribution of the Trypanosoma, and in the form in which it is mostly present in the different animals The rat and mouse show the greatest number and die quickest; the guinea-pig and rabbit show fewer organisms, with a small number of the amœboid forms, and take much longer to die; the goat shows the least sign and is, in our experience, the most resistent animal. In those animals which live longest the amœboid and plasmodial forms are few in number or absent. In certain animals there is a tendency to blocking up of the lymphatics of certain regions (e. g. eye, sheath, abdomen, and legs), and of lymphatic effusion around; and in others, a tendency to blockage of the brain capillaries with amœboid forms, which, in most animals, independent of variations generally, is the proximal cause of death.

In animals (rabbit, cat, dog, rat) from which the spleen has been removed the distribution of the organisms is different. During life there can be seen in the blood tangles, consisting of numbers of the adult organisms writhing about in close apposition to each other. Then the outlines of the individual organisms become indistinct and they apparently fuse together, so as to form a plasmodium, consisting of a mass of protoplasm containing micro- and macro-nuclei, similar to that seen in the spleen and in blood from the lungs of rats and mice. It is principally on account of this appearance in the blood of spleenless animals that we think it possible that the formation of this plasmodial form is due to fusion of adult forms, and a similar process also occurs in related organisms. The detachment of flagellated amœboid forms from these masses can be always seen. The amœboid forms are always present in the bone marrow and glands of spleenless animals.

None of the animals we have used have been found to be immune against the Trypanosoma Brucii. They have all died at varying periods, from five days—which is the shortest time in our experiments—in the case of the rat, to eighteen weeks—which is the longest period—in the case of the guinea-pig. But there is probably in all animals some attempt at resistance, and this, so far as we have seen, is by phagocytosis. We have only observed phagocytosis of the amœboid form of the organism, and never of the adult forms. We have seen this occur in the peritoneal fluid of the guinea-pig, in the spleen of the rat and mouse, and in the blood of the spleenless dog and cat. We have, in figs. 44 and 45, shown phagocytosis occurring in the blood of a spleenless cat, in which animal it can, in our experience, be most easily observed. This cat died in twelve days, whereas the average time the normal cat lives after inoculation is about twenty-five days. All the animals from which we have removed the spleen previous to inoculation have died in a shorter time than the normal animal, so that probably there is, in the earlier stages of the disease, a good deal of phagocytic action taking place in the spleen.

VII. The Differences between the Trypanosoma Brucii and the Trypanosoma found in Sewer Rats.

The distribution of the Trypanosoma Lewisi amongst sewer rats seems to be very variable, the organism being prevalent in some districts and not in others. For instance, we first examined six sewer rats from the south of London with negative results; then twelve from the north of London, of which number five contained the Trypanosoma Lewisi; then twenty-four from the south of London again with negative results.

There are the following points of difference between the sewer rat Trypanosoma and that found in Nagana. The former, the Trypanosoma Lewisi, are a little shorter and somewhat thinner than the Trypanosoma Brucii, and the posterior end is much more pointed, as is shown in fig. 46. The micronucleus is placed transversely as a rule, and is larger. The macronucleus is placed at the end of the body of the organism, instead of in the middle, as in the Trypanosoma Brucii. The protoplasm of the Trypanosoma Lewisi is not so homogeneous as that of the Nagana Trypanosoma. We have not observed any such forms as we have described as conjugations, nor any amœboid nor plasmodial forms in the blood of the sewer rat; apparently in this organism multiplication by longitudinal division only seems to be the rule. If the Trypanosoma Lewisi be examined in the living blood under critical illumination, three dark spots can be seen in nearly all the organisms, apart from the nuclear structures; one is very near the micronucleus, and the other two between this and the macronucleus, on that side of the body opposite the undulating membrane. These are not visible in the stained specimens. The Trypanosoma Lewisi does not protect the animal containing it in the smallest degree from the Trypanosoma Brucii; sewer rats naturally infected with the former were inoculated with the latter, and died in the usual time.

Laveran[1] states that the Trypanosoma of Nagana has the same structure as that of the sewer rat Trypanosoma but that it is a little longer. This latter fact is quite correct, but it will be seen from the above that there are other very noticeable differences of structure between them.

VIII. THE MICRONUCLEUS.

There seems at present to be much uncertainty as to what the exact zoological title of this body should be, to which we gave the above provisional name in our first paper.

In the article by Laveran on the multiplication of the sewer rat Trypanosoma, which we have mentioned above, he uses the term blepharoplast for this body, as being the most accurate one. This term, he says, was employed by Webber to designate analogous bodies in vegetable cells. This term is used to express a body having the reactions of chromatin, to which an undulating membrane, or flagellum, is attached, or from which they take rise. Rabinowitch and Kempner[2] called this body a nucleolus, and Wasielewski and Senn[3] gave it the name of Geisselwurzel (root of flagellum). Henneguy[4] has stated in an earlier paper that the blepharoplast is of the nature of a centrosome, i.e. a centrosomal structure to which a flagellum is attached, or from which it arises.

From our observations on the Nagana Trypanosoma we are obliged at present to adhere to the provisional title of micronucleus. We have seen it apparently coming off from the macronucleus, as shown in fig. 23, and we have seen it fuse with the corresponding body in another organism, as we have described above under the heading

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[1] "Sur le mode de multiplication du Trypanosome du rat," Laveran et Mesnil, 'Comptes rendus de la Société de Biologie,' tome lii, No. 35.

[2] 'Zeitschr. f. Hygiene u. Infectionskr.,' 1899.

[3] Ibid., 1900.

[4] 'Arch. d'Anat. Microsc.,' 1897.

of conjugation. This seems to us a very definite reason for keeping the title we have used, which would correspond to that given to a similar body in organisms not far removed from these, in which conjugation is well known. It has this fact in favour of its being a centrosome, that it nearly always divides before the macronucleus does in the longitudinal division described above. It is also present through all the other stages of the Trypanosoma, in the amœboid and the plasmodial. Guignard[1] has come to the conclusion that the bodies generally called centrosomes have very variable characters, and that the so-called blepharoplasts can be grouped under this name. So that it is, after all, a question of terms, to which various meanings are given by different writers. The main point which induces us at present to adhere to the term micronucleus is the behaviour of this body during the process of conjugation. Laveran apparently has not observed this stage in the Trypanosoma Brucii, hence his insistence on the term blepharoplast, or centrosome.

IX. The Life-history of the Trypanosoma Brucii.

The life-history of this organism appears to be much more complicated than that of the sewer rat Trypanosoma, as described by Laveran and others, on account of the presence of forms which we have described under the headings of Conjugation, and Amœboid and Plasmodial forms, which do not appear to be present in the sewer rat when infected with the Trypanosoma Lewisi.

In our previous paper we placed those forms which are shown in figs. 6—8, and which are described in section II—2, as those following conjugation, supposing that these forms broke up into the amœboid forms, and that these again fused to form the plasmodia. Since that time we have observed these forms with great care, and we have been unable to find any definite intermediate stages

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[1] 'Ann. des sc. nat. botan.,' 1897.

between them; and we are, moreover, very doubtful whether the dots in these organisms are really chromatin, as we have stated when describing them, since they stain a much darker colour. The probability seems to be that they are not. We are now of opinion that the following would be the more probable sequence of the life-history of the Trypanosoma Brucii.

1. Longitudinal division, which is very common, and can be seen more or less in the blood of all the animals we have used.

2. Conjugation, the essential of which is the fusion of the micronuclei of the conjugating pair of organisms. After this process the organisms probably separate and go on as before, probably with renewed energies. This is known to be the case in some nearly allied organisms.

3. We are here inclined to place tentatively the fusion of the adult forms. This process begins by the formation of tangles, and the organisms then lose their individual forms, and fuse into a more or less homogeneous mass, which under the best optical conditions appears to be an irregular aggregation of protoplasm containing many micro- and macro-nuclei.

These latter divide again and again, so that the mass seems to consist of little else but micro- and macro-nuclei; then flagellated amœboid forms are given off from the margin, and these grow and eventually lengthen out into the adult organism. There is a tendency for these masses to be formed in certain structures only: in the rat, mouse, cat, and dog they are found in the spleen, and in the blood just before death. They are also found in the blood from the lungs, in the lymphatics of the eyes and genitals, and in the cerebral capillaries.

A point in favour of the above opinion is the fact that in animals from which the spleen has been previously removed, these masses are found in all stages of formation in the blood during life, and before the animal has begun to get apparently ill; the spleen being removed, in which this fusion process generally occurs, it takes place in the blood itself. In these spleenless animals the bone marrow is always affected, and always contains quantities of the amœboid form, which is not ordinarily the case in normal animals.

As regards the life of the Trypanosoma outside the body there is at present little to say. Laveran succeeded in keeping them alive in blood kept at 0° C. for as long as three months. We have kept them alive in thin films for six days after removal from the body. We have also kept a large quantity of blood containing them in an atmosphere of oxogen, and have found that, although the adult forms soon disappeared, with the formation of tangles, plasmodial masses, and then amœboid forms, the blood was infective for three days at least, at which time our experiment came to an end.

In the ordinary way the blood of animals loses its infectivity in a few hours after death, as decomposition sets in with great rapidity in this disease.

X. EXPLANATION OF PLATES 24 AND 25,

Illustrating Messrs. J. R. Bradford and H. G. Plimmer's paper "On the Trypanosoma Brucii, the Organism found in Nagana or Tse-tse Fly Disease."

All these figures were drawn under a Zeiss 3 mm. apochromatic objective of N.A. 1·40, used with a Zeiss achromatic condenser of N.A. 1·0, and with compensating oculars of various powers, which will be indicated when referring to each figure, or set of figures, separately. The specimens were all stained by the method described in the paper.

Figs. 1—4 (Oc. 8).—Ordinary adult organisms from rat's blood on fourth day, stained lightly to show the general shape and structure. *a.* micronucleus; *b.* vacuole; *c.* macronucleus.

There are three red corpuscles, drawn with Figs 1—9 from rat's blood under Oc. 8, to show the relative size of the organism.

Fig. 5 (Oc. 12).—Large hyaline form, stained deeply to show the undulating membrane and its connection with the micronucleus. From rat's blood, eighth day.

Figs. 6—8 (Fig. 6, Oc. 8; Figs. 7 and 8, Oc. 12).—Forms containing granules, from blood from mouse's lung just after death on seventh day. In Fig. 6 the macronucleus is still distinctly visible, but in Figs. 7 and 8 its position is only just indicated. What happens further to these forms has not been traced.

Figs. 9 and 10 (Oc. 12).—Irregular amœboid forms from blood of rabbit on twenty-ninth day. In Fig. 9 the edge of the undulating membrane is seen attached to the micronucleus, and then nearly surrounding the organism. In Fig. 10 the flagellum and undulating membrane are quite developed and distinct.

Fig. 11 (Oc. 12).—Full-sized organism from rat's blood, sixth day, stained deeply to show the undulating membrane and its attachment to the micronucleus; and also commencing enlargement of the macronucleus.

Fig. 12 (Oc. 12).—From rat's blood, seventh day, showing the early stages of longitudinal division. The micronucleus has divided, and a second undulating membrane has developed. The macronucleus shows commencing enlargement.

Fig. 13 (Oc. 12).—From same specimen, showing the division and separation of the micronucleus, and the great enlargement of the macronucleus.

Fig. 14 (Oc. 12).—From guinea-pig's blood, thirty-ninth day, showing the division of the micro- and macro-nuclei, and the line of division along the long axis of the organism.

Fig. 15 (Oc. 12).—From same specimen as Figs. 12 and 13, showing complete separation of micro- and macro-nuclei, with the line of division very well marked.

Fig. 16 (Oc. 12).—From another rat's blood, seventh day, showing two complete organisms just at point of complete separation.

Fig. 17 (Oc. 12).—From mouse's blood, sixth day, showing division of the large hyaline form, in which the different structures are more clearly seen.

Fig. 18 (Oc. 12).—From rat's blood, fourth day, showing the conjugation of two adult organisms, with the micronuclei at some distance apart.

Fig. 19 (Oc. 12).—From spleenless dog's blood, ninth day, showing conjugation with the micronuclei closely approximated.

Fig. 20 (Oc. 12).—From the same specimen, showing conjugation in which one micronucleus is in the dumb-bell form which it has in the early stages of longitudinal division of the organism, and the other is seen as a round dot.

Fig. 21 (Oc. 12).—From blood of a spleenless cat, showing conjugation in which one micronucleus is in the form of a rod, and the other in the form of a dot.

Fig. 22 (Oc. 12).—From same specimen, showing conjugation completed, in which the two micronuclei are fused into one large dot.

Fig. 23 (Oc. 12).—From blood of rat, eighth day, showing an unusual form of conjugation in which the central micronuclei seem to have disappeared, whilst two others are being detached from the macronuclei.

In all these figures, from 18 to 23, the macronucleus seems to be in a state of activity, as shown by its alteration in shape, the chromatin being principally arranged peripherally.

Figs. 24—27 (Oc. 18).—Amœboid forms from the bone marrow of a spleenless dog, twenty-one days. The flagella are not visible in any of these, but probably were broken off in the process of preparation. In Figs. 25 and 27 division is taking place, and the macronuclei in all appear to be in a state of activity. In Fig. 26 the organism is lengthening out, as if it were becoming an ordinary adult form.

Figs. 28—31 (Oc. 18).—From the bone marrow of a spleenless cat, showing amœboid forms. In these the flagella are visible, and all the organisms are undergoing division. In Fig. 31 there appears to be a complicated process of division, the smaller organism at the upper part appearing to have four micronuclei and two macronuclei, as if preparing for some such form as is shown in Fig. 31 *a*.

Fig. 31 *a* (Oc. 18).—From blood of a spleenless dog, eighth day, showing four adult organisms being given off from an amœboid mass.

Figs. 32, 33 (Oc. 18).—From bone marrow of a spleenless dog, showing in Fig. 32 a simple amœboid form, and in Fig. 33 one in which the micronucleus is divided.

Fig. 34 (Oc. 18).—From blood from lung of mouse, seventh day, showing a flagellated amœboid form full of granules, similar in colour to those seen in certain adult organisms, as shown in Figs. 6—8.

Fig. 35 (Oc. 18).—From same specimen, showing a dividing flagellated amœboid form.

Fig. 36 (Oc. 18).—From the same specimen, showing an amœboid form lengthening out, as if becoming an ordinary adult form.

Fig. 37 (Oc. 18).—From blood from lung of rat, ninth day, showing a plasmodial mass in the centre with micro- and macro-nuclei scattered about in a mass of protoplasm, and at the outside a few amœboid forms being detached.

Fig. 38 (Oc. 12).—Smear from spleen of rat, eight days, showing the plasmodium, with its numbers of micro- and macro-nuclei wedged in between the splenic cells. A few red corpuscles are also drawn.

Fig. 39 (Oc. 12).—From a scraping from the lung of a mouse, seventh day, showing a plasmodial mass with cells from the lungs which are accidentally present as the result of the method of preparation.

FIG. 40 (Oc. 18).—Small branched capillary from a smear from cortical part of brain of rat, showing the lumen completely blocked with amœboid forms.

FIG. 41 (Oc. 18).—Small capillary from smear from medulla of rabbit, showing the lumen more completely blocked with amœboid forms.

The large red bodies in Figs. 40 and 41 are the nuclei of the capillary walls.

FIG. 42 (Oc. 18).—From blood of spleenless cat, twenty-first day, showing the formation of tangles; the central part is already quite like the plasmodium shown in Figs. 38 and 39, containing micro- and macro-nuclei.

FIG. 43 (Oc. 12).—From same specimen, showing a plasmodial mass with flagella around margin; probably the last stage of the formation of a small plasmodium.

FIGS. 44, 45 (Oc. 18).—Leucocytes from blood of a spleenless cat, showing phagocytosis. In Fig. 44 two entire amœboid forms with the micro- and macro-nuclei can be seen, and at lower end a still undestroyed micronucleus, and also two nearly colourless bodies, probably the last stage of destruction of the organism. In Fig. 45 two amœboid forms are seen in fair condition, the one above having still its flagellum attached to it. There is also a larger body with a dot in it, which is probably a destroyed organism, with only the micronucleus left.

FIG. 46 (Oc. 12).—Trypanosoma Lewisi from blood of sewer rat, to show the gross differences between these and the Trypanosoma Brucii.

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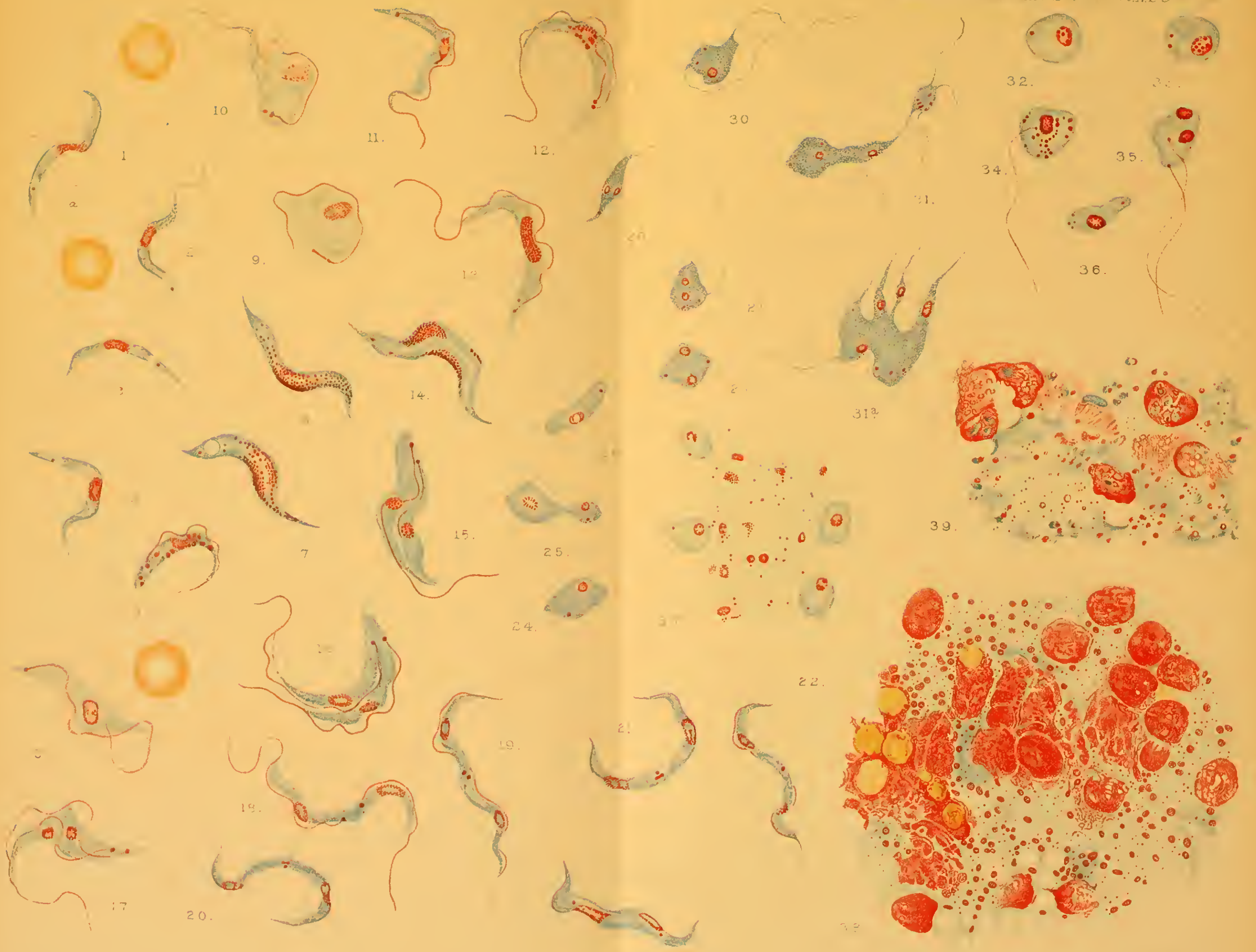

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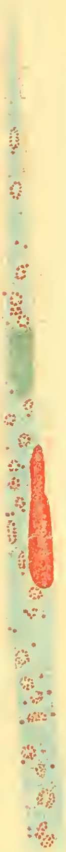
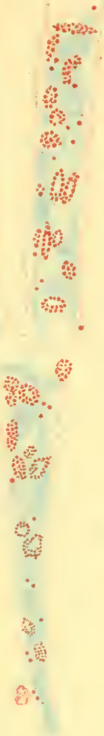
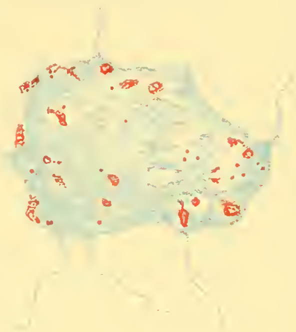
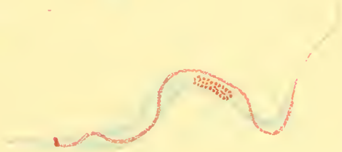
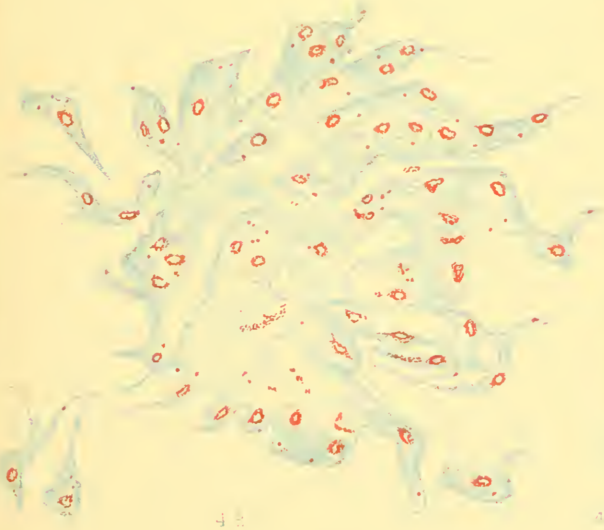
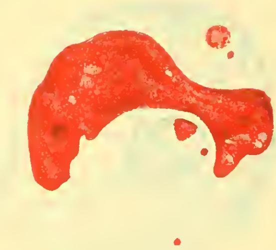




Notes on Actinotrocha.

By

K. Ramunni Menon,
Assistant Professor, Presidency College, Madras.

With Plate 26.

The following notes on Actinotrocha (a careful comparison of which with Brachiopod larvæ seemed desirable) may be of interest in connection with Masterman's recent investigations on this larval form. I wish to express here my deep indebtedness to my kind teacher, Professor Bourne, for affording me every facility and help for working in his laboratory.

The larvæ which were caught during the latter part of October last belong to three different species, none of which I have been able to identify. One of these, which is very rare (owing, perhaps, to its being only an occasional immigrant into the surface water), has a short, thick body, short tentacles, a small hood, and a strong perianal band, and, if the conspicuous broad pigmented zone round the body may be regarded as affording a clue, probably belongs to Phoronis australis. The second species is much longer, has longer tentacles, a well-developed hood, and a transparent body-wall. My observations are based mainly on this species. The third species is much smaller than the second, and but for the fact that it metamorphoses directly into the young Phoronis, would be regarded as a young stage of the second. The larvæ were preserved in corrosive sublimate, osmic acid, and chromo-aceto-osmic mixture, cut in celloidin and stained with hæmalum.

The metamorphosis of the larva is usually completed in a few minutes. Occasionally, however, the ventral diverticulum is evaginated, and it is only after a considerable interval that the alimentary canal is drawn into it—the animal then presenting a curious external resemblance to Rhabdopleura, as far as one can conceive of it from figures. The young Phoronis fixes itself to the bottom of the glass vessel by means of a sticky secretion, and also secretes a transparent cuticular tube round the body. Observation of the living animal shows that the annulation of the body, said to be due to contraction in spirit, is quite natural. These annuli are formed by the ectoderm being raised up into ridges. If the water in which they are kept is not changed daily, the young animals lose their heads—a fact in agreement with Cori's observation that the tentacle crown is often thrown off by Phoronis, especially under unfavourable conditions.

Epistome.—This structure is usually regarded as a remnant of the preoral lobe of the larva. In the young Phoronis, soon after metamorphosis, the epistome is not present. The preoral lobe and the tentacles of the larva are apparently wholly taken into the alimentary canal during the metamorphosis. In the case of slow metamorphosis these persist for a comparatively long time, and their disappearance must be due to disintegration. In the young Phoronis the dorsal part of the region surrounding the mouth and immediately within the ring of tentacles is raised up into a round protuberance (fig. 1). This is the beginning of the epistome. The collar cavity, which was encroached upon by the masses of blood-corpuscles in the old Actinotrocha, does not extend into this swelling, the interior of which is occupied by a nucleated mass containing irregular spaces, and with scattered muscle-fibres and blood-corpuscles. The surface epithelium does not differ from that covering the rest of the oral region. The papilla gradually becomes flattened out into a broad flap (figs. 2—4), having a thick base attached along the dorsal edge of the mouth, and a thin free edge. The internal mass is absorbed; and between the basement tissues of the two surfaces are found small spaces separated from one another by bridges of basement tissue with a few nuclei. The epithelium covering the oral surface consists of columnar ciliated cells with long nuclei, while over the aboral surface it consists of cubical cells; along the free edge the cells are longer and the nuclei more closely arranged. The collar cœlom, which is now a definite space having a well-marked cœlomic epithelium, extends only into the base of the epistome, and is separated from the peripheral spaces by a mesentery. Further extension of the cœlom into the epistome must take place in later stages, as the cavity of the epistome is stated to be cœlomic. In considering the homology of the epistome it must also be remembered that the cavity of the preoral lobe of the larva, of which the epistome is considered to be a remnant, is, whatever its nature may be, quite distinct from the collar cavity, from which it is separated by a well-marked mesentery. The occurrence, though rare, of old Actinotrochæ without any trace of the preoral lobe is also interesting in this connection. Thus there can be no reason to doubt that the epistome is not a remnant of the preoral lobe, but is a new structure, developed as an outgrowth of the collar region.

The most important points adduced by Masterman, in establishing the Chordate affinities of Phoronis, have reference to the following structures in Actinotrocha:—(1) five body-cavities; (2) proboscis pores, collar pores, and trunk nephridia; (3) two notochords; (4) subneural gland (hypophysis), which is homologised with the proboscis vesicle of Balanoglossus; and (5) the tubular nerve-ganglion. These structures will be dealt with in the order given.

(1) Body-cavities.—There are three principal cavities in Actinotrocha. It will be convenient to adopt Masterman's names, and to call them the cavities of the preoral lobe, collar, and trunk. These spaces are separated from one another by mesenteries. The mesentery between the preoral cavity and the collar cavity can be roughly compared to a watch-glass with its edge attached to the body-wall, and with

its convex side directed towards the preoral cavity. The cavity of the preoral lobe is traversed by protoplasmic strands, some of which cross it from the upper wall to the lower, while others run parallel to its free border. A definite cœlomic epithelium cannot be made out in this cavity, the only structures clearly seen beneath the ectoderm being a thin basement membrane (chondroid tissue), with a few isolated patches of nuclei adhering to the inner face of the membrane. Scattered blood-corpuscles and cœlomic corpuscles are occasionally met with in this cavity, the nature of which it is thus difficult to decide without embryological evidence.

Below the nerve-ganglion which lies in the root of the preoral cavity, just in front of the attachment of the mesentery above mentioned, there is a small space, the posterior wall of which is formed by this mesentery, which thus separates it from the collar cavity, and the anterior wall by another mesentery stretched between the upper and lower walls of the preoral lobe, which thus separate it from the rest of the preoral cavity. This is the subneural sinus, and the nerve-ganglion forms part of its roof. It is a completely closed vesicle, and the epithelium forming its wall can be traced along the roof of the sinus immediately below the nerve-ganglion. The nerve-ganglion thus really lies outside the cavity. There are two muscle strands developed in connection with the wall of this cavity, and attached to the dorsal body-wall near the ganglion. The subneural sinus does not communicate with the dorsal blood-vessel; nor does it contain any blood-corpuscles. Masterman compares this sinus to the central blood-sinus of the proboscis of the Enteropneusta. If a comparison is to be made between it and any structure in the Enteropneusta, its complete epithelial wall, and the muscular development in connection with its wall, strangely support Harmer's view that it is the "heart vesicle."

The collar cavity is bounded posteriorly by the mesentery between it and the trunk cavity, which is attached to the body-wall some distance posteriorly to the bases of the tentacles, and runs forwards and inwards to meet the wall of the gut. There is a well-marked epithelium lining the cavity. Dorsal and ventral mesenteries do not appear to be present. The muscle strands above mentioned run through this cavity. Each divides into two bands, one of which runs through the collar cavity and meets the dorsal body-wall, and runs posteriorly along one side of the median line; the other runs ventrally, externally to the œsophagus, meets the ventral body-wall and then runs posteriorly along one side of the median line. The collar cavity, which is well developed in the young larva, becomes, in the later stages, obliterated by the development of a large mass of blood-corpuscles. These are developed around the ventral diverticulum of the stomach, and in the old Actinotrochæ often fill the collar cavity. There is no epithelium between these corpuscles, which form a mass adhering to the wall of the stomach and the collar cavity, and there cannot be any doubt that they lie freely exposed to the collar cavity (fig. 6). This explains Caldwell's statement, often disputed, that free communication exists between the body-cavity in front of the septum (i. e. the collar cavity) and the vascular system. The blood-corpuscles do not, however, float in the fluid in the collar cavity, so that there is no communication between the collar cavity and the vascular system in the sense that blood flows into the collar cavity and mixes with the cœlomic fluid. The mass of corpuscles is connected with the dorsal blood-vessel which runs along the dorsal wall of the stomach posteriorly. The mass of corpuscles breaks up during metamorphosis, and the corpuscles are apparently withdrawn into the blood-vessels. With regard to the origin of the corpuscles, it may be said that they are formed from the splanchnopleure (fig. 5), covering the stomach and its diverticulum, the cells of which proliferate and become blood-corpuscles. Blood-corpuscles are also found between the splanchnopleure and the stomach wall, having been found, apparently, in the same manner. It may be mentioned here that, according to Cori, blood-corpuscles are formed in the adult Phoronis from the endothelium of the blood-vessels.

To return to the body cavities—the trunk cavity is divided into right and left halves by a complete ventral mesentery and by a dorsal mesentery, which is only represented by a small strand at the posterior end. The somatopleure is separated from the ectoderm by a thick layer of chondroid tissue (also developed in the collar, though not to the same extent), from which it is detached in preparations, and often thrown into irregular folds. At the anterior boundary of the perianal band the somatopleure leaves the body-wall and runs inwards and backwards to meet the gut wall, and become continuous with the splanchnopleure. There is thus left a space surrounding the posterior part of the intestine and between the cœlomic epithelium in front, the ectoderm on the outside, and the endoderm on the inside. The ectoderm forming part of the wall of this space is highly vacuolated, the vacuoles being large and regularly arranged, and the cell substance is reduced to an external and an internal limiting layer and strands between the vacuoles. The nuclei of these cells are arranged in the external and internal layers, but mainly in the former. The arrangement of the parts will be made clear by fig. 7. The space under the perianal band thus appears to have a lining of its own. If the cœlomic wall of this space were thrown into a fold projecting into the trunk cœlom we could get a section (without the internal opening, which may be artificial) pretty much like the one shown in Masterman's drawing of the posterior nephridia. I venture to suggest this as a possible explanation of the posterior nephridia, which I have not found as such, especially as Masterman himself seems to be doubtful about them.

(2) Nephridia.—Masterman describes for his Actinotrocha proboscis pores, collar nephridia, and trunk nephridia. I have carefully looked, both in the living larva and in sections, for the cellular tubes and the pores which Masterman homologises with the proboscis pores, but have found no trace of them. There is nothing to be added to what has

been already said about the posterior nephridia. The Actinotrocha studied by Masterman seems worthy of reinvestigation, if for no other reason than to demonstrate the proboscis pores and the posterior nephridia. There are two nephridia in Actinotrocha. They are placed on the mesentery between the collar and trunk cavities, on the face of it turned towards the collar cavity. Each nephridium opens to the exterior ventro-laterally behind the attachment of the mesentery. From its external opening the duct of the nephridium runs forwards, crosses the mesentery, and then bends dorsally and runs forwards along the mesentery. The nephridium opens at its anterior end into the collar cavity by two funnels, one placed below the other (fig. 8). Numerous ovoid cells are attached by long stalks to the edges of the funnels. I have not been able to detect cilia in the lumen of the nephridium. The cœlomic epithelium covers the outer surface of the nephridium. The appearance of the nephridium as seen in the living larva is so well described in the quotation which Masterman gives that it is unnecessary to say anything more about it. It is probable that this type of nephridium, which so strongly recalls the nephridium of Amphioxus, was characteristic of the primitive Chordata. Masterman compares these nephridia to the collar canals of Balanoglossus. There is no doubt a general resemblance between them, and the collar canals may be vestiges of such nephridia; but the detailed structure differs in the two cases. It may also be pointed out that if the small part of the nephridium which lies behind the mesentery were better developed, as it is in the adult Phoronis, the nephridium would be considered as belonging to the trunk, with its funnels opening into the cavity of the segment in front.

These nephridia become the nephridia of the adult Phoronis. In the newly metamorphosed Phoronis the nephridia still project into the irregular collar spaces, but their external apertures have shifted dorso-laterally, owing, no doubt, to the mechanical narrowing of the dorsal surface of the body during metamorphosis.

(3) Notochords.—In the alimentary canal of Actinotrocha, Masterman describes an œsophagus, a collar stomach or pharynx, an œsophagus leading from this into the true stomach, and an intestine. I have been able to make out only three divisions in the alimentary canal—a tube leading from the mouth to the stomach, which obviously corresponds to the œsophagus (Masterman), a stomach placed partly in the collar and partly in the trunk segments, and an intestine. It seems to me that this œsophagus corresponds to the stomodæum, pharynx, and œsophagus of Cephalodiscus, described by the same author. However this may be, the "œsophagus" is often folded transversely (this is also the case in young Phoronis) into pouches, and the subneural gland is a diverticulum of its dorsal wall. The "œsophagus" opens into the large stomach anteriorly and dorsally. The anterior part of the stomach grows forwards in the form of a diverticulum, which is placed ventrally to the œsophagus. This diverticulum is absent in the young forms. The anterior end of the diverticulum may be bilobed, and the two lobes, often unequally developed, lie ventro-laterally or laterally to the œsophagus. There can be no doubt that the diverticulum with the lobes is the structure referred to as "the notochord," "hepatic diverticula," etc., although it must be confessed that I have not seen vacuoles or brown concretions, stated to occur in these structures. Indeed, I have not been able to make out any difference between the lining membrane of the diverticulum and that of the rest of the stomach. The cells are columnar ciliated cells, and are taller than the cells of the "œsophagus," and the nuclei form an irregular layer between the base and the middle of the cells. The protoplasm of the cells presents a granular appearance and stains homogeneously, but not so deeply as the protoplasm of the œsophageal cells, and does not differ in any respect from the protoplasm of the lateral ridges of the stomach. These ridges of protoplasm, containing numerous scattered nuclei and large vacuoles with remnants of food particles in them, are two longitudinal ridges projecting into

the lumen of the stomach and extending along the sides from beyond the opening of the œsophagus to near the posterior end. The cells along the dorsal median line of the stomach, and the cells of the posterior part of the stomach just before it opens into the intestine, have elongated nuclei placed vertically, and resemble the œsophageal cells. There does not appear to be any reason for regarding the diverticulum as anything but a part of the stomach. The stomach could grow forwards only ventrally to the œsophagus, and when the front end of this outgrowth meets the œsophagus, which bends down to the mouth, it is obliged to grow past it along its sides. The form and the position of the diverticulum can thus be explained on mechanical grounds. Whether the diverticulum has any special function; whether, for instance, its association with the large mass of blood-corpuscles is purely an accident, I cannot say.

(4) The Subneural Gland.—This structure has given rise to a good amount of discussion. According to Masterman it arises as an ectodermal invagination in front of the mouth. I have not seen this stage. In the earliest stage of the organ, that I have observed, it is present as a shallow diverticulum of the dorsal wall of the "œsophagus," which projects somewhat backwards into the collar cavity, just behind the mesentery between the preoral and collar cavities. In the latest stage I have seen the gland opens by a wide aperture just within the mouth, and is directed forwards into the preoral lobe, in which it lies between the ectoderm of the lower wall and the cavity of the lobe, and is separated from this cavity by the basement tissue and scattered nuclei which line the preoral cavity. If I interpret these facts correctly, the organ first appears in connection with the collar, and during development shifts forwards into the preoral lobe; and this is in harmony with the development of the "Eicheldarm" of Balanoglossus. In Balanoglossus, the "Eicheldarm" during development is described as lying in a space between this ventral wall and the cavity of the preoral lobe; and it is certainly a remarkable coincidence between this arrangement

and the condition already mentioned as occurring in Actinotrocha. I have not observed any peculiar relation between the organ under consideration and the subneural sinus. There seems to be a general agreement that this structure is homologous with the "notochord" of Rhabdopleura and Cephalodiscus; but whether these structures are homologous with the "Eicheldarm" of Balanoglossus remains undecided. The facts mentioned above certainly support Harmer's views that they are homologous with the "Eicheldarm." The ciliated epithelium of the organ and its position in relation to the mouth, however, indicate in Actinotrocha some function connected with the ingestion of food.

(5) The Tubular Nerve-ganglion.—The ganglion has the structure described by Masterman. The tube formed by ectodermal invagination lies in the actual ganglion, and not merely in front of it. The tube is lined by ciliated cells, and its inner end is sacculated. This ganglion is compared to the dorsal nerve-cord of the collar in Balanoglossus, which, however, lies in the collar, while the ganglion of Actinotrocha lies in the preoral lobe.

Sense-organ.—This organ lies in front of the ganglion, and is absent in the young larva. The ectoderm in this region becomes thickened and raised up into a conical papilla, and there is a development of nervous tissue at its base. The cavity of the preoral lobe is continued into the base of the papilla. Possibly this sense-organ represents the median dorsal tentacle of the larva displaced and retarded in its development. Attention may be drawn here to the compound eyes which Masterman describes as occurring on the tips of the tentacles in Cephalodiscus. Whatever its homology may be, the organ is now a sense-organ of some kind. It is curious that this organ is not developed during the earlier and more active stages of the larva, but makes its appearance during the later stages, and is best developed when the larva becomes slow in its habits and when the need for such an organ appears least. Before metamorphosis, the larva, with its ventral surface directed downwards, glides along the bottom of the vessel in which it is kept, performing a slow pirouette in its course. Probably the sense papilla which is placed on the ventral surface of the hood, and which would thus come in contact with the ground, is the organ by means of which the larva feels its ground before settling down for the rest of its life.

In conclusion it may be added that if Actinotrocha is related to the Chordata at all, as the presence of three divisions of the body with their corresponding cavities, of collar nephridia, of a dorsal diverticulum of the anterior part of the gut, and of a dorsal tubular nerve-ganglion renders probable, the absence of such important structures as the gill-slits, and of the proboscis pores shows that the relationship is to be traced through a form like Rhabdopleura.

EXPLANATION OF PLATE 26,

Illustrating Mr. K. Ramunni Menon's paper entitled "Notes on Actinotrocha."

List of Abbreviations.

an. Anus. *an. bd.* Perianal band. *bl.-c.* Blood-corpuscles. *bl.-v.* blood-vessel. *c. c.* Collar cavity. *c. ep.* Somatopleure. *c. ep*^{1}. Splanchnopleure round œsophagus. *c. ep*^{11}. Splanchnopeure round stomach. *d. bl.-v.* Dorsal blood-vessel. *ep.* Epistome. *hd.* Preoral lobe. *hd. c.* Preoral cavity. *m.* Mouth. *mes.* Mesentery between preoral cavity and collar cavity. *mes*^{1}. Mesentery between collar cavity and trunk cavity. *M. nep.* Posterior nephridium (Masterman). *nep.* Nephridium. *œs.* Œsophagus. *rect.* Rectum. *tent.* Tentacle. *tr. c.* Trunk cavity. *tr. w.* body-wall of the trunk region. *vac. ect.* Vacuolated ectoderm.

Fig. 1.—Horizontal section of the anterior part of a newly metamorphosed Phoronis.

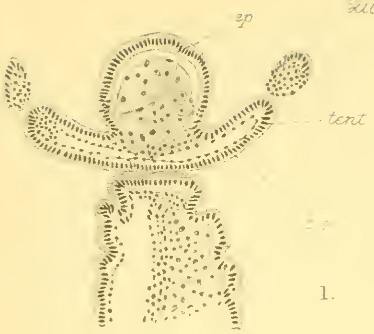
Figs. 2—4.—Sagittal section of the anterior end of young Phoronis, to show the development of the epistome.

Fig. 5.—Transverse section of Actinotrocha in the collar region. The collar wall is only shown in outline.

Fig. 6.—A similar section to show the blood-corpuscles in the collar cavity.

Fig. 7.—Part of a horizontal section of Actinotrocha to show the so-called posterior nephridia.

Fig. 8.—Part of a sagittal section of Actinotrocha to show the nephridium. The ventral wall of the collar and part of the ventral wall of the trunk are drawn.



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A. H. [illegible]

Review of Mr. Iwaji Ikeda's Observations on the Development, Structure, and Metamorphosis of Actinotrocha.[1]

By

A. J. Masterman,
Edinburgh.

Zoologists are indebted to this publication of the Tôkyô University for an account of many valuable zoological researches, and by no means the least important is contained in the volume now lying before us. Mr. Ikeda has been enabled to study the living larva and the embryonic stages at the Misaki marine station. The newly described species, Phoronis ijimai, Oka, furnished the embryonic stages, and for the structure of the larva no less than four species (?) were examined. Of these perhaps the most remarkable is type D, which is a large larva about 5 mm. in length and with about forty-eight tentacles.

In the embryonic development we naturally look at the parts dealing with such a much-disputed point as the origin of the mesoblast. Anyone who has studied the literature of the development of Phoronis will be able to gather a clear account of the general features, and will be led to conclude that the minor differences between the various workers are largely specific. Speaking generally, a total equal segmentation, producing a blastula larva, invagination to form a gastrula, and the persistence of the blastopore as the larval

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[1] 'Journal of the College of Science,' Imperial University, Tôkyô, Japan, vol. xiii, pt. 4, 1901.

mouth may be accepted as general. But when we come to the question of mesoblastic origin we are met with difficulties. Ikeda finds, like Caldwell and myself (my work on the early development, in this JOURNAL, was not in Ikeda's hands till after going to press), that certain bodies, which he calls "plasmic corpuscles," are present in the blastocœle cavity, but are non-nucleated, and hence cannot be regarded as mesoblast cells. At the commencement of invagination he finds that certain hypoblast cells migrate singly into the blastocœle space. These contribute later to the formation of mesoblastic organs. After invagination has been largely completed he finds further mesoblast cells are derived from a pair of anterior diverticula of the hypoblast, lateral to the blastopore. These agree exactly in appearance and position with the similarly named structures of Caldwell. The presence of these "collar somites" has been independently verified by myself, and we are also in agreement that the mesoblast cells produced from them do not at first contain any cavity, as maintained by Caldwell. The presence of these collar somites has been so forcibly denied by both Roule and Schultze that this corroboration is the more gratifying.

A third source of mesoblast cells he finds in the ventral groove, which consists of cells not yet invaginated to form hypoblast, lying along the mid-ventral line of the embryo. These are in the nature of single cells set free into the blastocœlic cavity. Lastly, he corroborates the presence of a posterior invagination (Caldwell's posterior diverticula), but claims that this is merely an ectoblastic nephridial pit which gives rise to the pair of nephridia. For these posterior diverticula I searched in P. Buskii without success, but I have since been enabled to find them in this species and in P. hippocrepia. I am inclined to accept Ikeda's view that they are the "anlage" of the nephridia, the development of which I did not follow in P. Buskii. In passing we may say that Ikeda does not recognise the presence of my "posterior somites," but he figures without comment certain indications of their presence, e. g. his fig. 33. Perhaps I may add that in P. hippocrepia I have found certain mesenchymatous cells at the gastrula stage, and I think it is possible to regard these as having the same relation to the mesoblast arising from the invaginated hypoblast as similar mesenchymatous cells have to the enterocœlic mesoblast of Echinodermata.

From this it will be clear that it is not difficult to gather a fairly consistent account of the origin of the mesoblast from the figures of Caldwell, Ikeda, and myself.

But the second part of Ikeda's memoir, dealing with the larval structure of Actinotrocha, is unquestionably the most important and the most welcome at the present time. Since my paper on this subject in this JOURNAL Professor Roule has, at international congresses, in the 'Zoologische Anzeiger,' and in several French journals ('Comptes rendus,' 'Annales des Sciences naturelles,' etc.), spared no pains in reiterating that the essential facts as described by me, such as the presence of cœlomic cavities, mesenteries, and so on, which led me to regard Actinotrocha as a highly organised cœlomate larva, were mere figments of imagination, or were due to this factor combined with a judicious admixture of defective technique. On the other hand, he has insisted that it is to be regarded as at the morphological level of the trochophore. No one comparing our figures could possibly reconcile the two series of results. Roule was perfectly right in saying that if his descriptions are accurate mine must be untrue, and we are perfectly justified in believing the converse. It is therefore, from the point of view of zoological progress, eminently satisfactory that my work has received so complete a corroboration as the present. Speaking candidly, we do not think that the author has fully appreciated, or at least emphasised, the corroborative nature of his work. With one or two important exceptions, to be noted later, the whole of his anatomical drawings might be used as they stand to illustrate my paper of 1897. We can read through page after page of his description in which the anatomical details are a virtual repetition of the work referred to, yet the agreements are so little emphasised, and the disagreements so dwelt upon, that any reader who had not studied my work could almost suppose that the total result was rather a refutation than a corroboration of the latter. However, Ikeda's figures are so accurately and carefully drawn that it is possible to explain some of the more important differences. The first kind of discrepancy is simply due to a difference of interpretation. For example, he shows clearly in several of his figures (such as the series fig. 59, *a*, *b*, *c*, *d*) the subneural blood-sinus in even greater detail than myself, but he prefers to label it as an artefact. As the blood system of Actinotrocha is hæmocœlic, and hence consists of mere sinuses or spaces between the three primary layers, it is naturally possible to regard it in its entirety as an artefact. The same remark applies equally to the whole vascular system of Cephalodiscus, the greater part of that of Balanoglossus, and that of numerous larvæ. Indeed, there is little to urge against the assertion that the hæmocœlic body-cavity of arthropods is an artefact. On similar grounds he fails to corroborate the presence of the perianal blood-sinus (one of the most conspicuous characters of the larva), and of other parts of the blood system. Similar considerations apply to his refusal to recognise the presence of the epidermic pit ("neuropore") and of the subneural gland. Both of these are clearly figured in his sections with exactly the relations indicated by myself, but he prefers to regard them as artefacts. As in all my fully developed larvæ, alive or dead, I have never failed to find all these organs constant in position and in structure, I can hardly agree that they are mere freaks of reagents.

Ikeda suggests that the epidermic pit in front of the ganglion is produced by contraction of muscles drawing the ganglion backwards (!), and similarly he accounts for the evident presence of the subneural gland by an artificial bulging forwards and outwards of the part of the hood immediately anterior to it (!). Surely the mechanical conditions induced in each case would tend to exactly the opposite result, i. e. that of straightening out these depressions.

A second group of discrepancies is apparently due to specific variation. Amongst these we may instance Ikeda's failure (as in the case of Roule) to find two pleurochords. In the North Sea larvæ the anterior wall of the stomach pushes forward as a diverticulum below the œsophagus, which opens into the antero-dorsal corner of the stomach. If it simplifies matters at all to regard this diverticulum as "ventral" instead of anterior, there seems no objection to doing so. As development proceeds, this diverticulum throws out two lateral pleurochords as I have described. In the Japanese larvæ this stage is never reached, but the diverticulum remains single with only one row of vacuoles; hence we must be prepared for other organs in like manner being abbreviated or even undeveloped. For example, the nephridia in these larvæ, as figured by Ikeda, are very small, very simple, and very embryonic as compared with the large branching tubules in the North Sea type. This consideration may easily account for the failure of Ikeda to find the internal openings of these organs in any of his larvæ. It is possible that the absence of proboscis pores, of a post-oral nerve-band, and of dorsal and ventral nerve-fibres may be due to a similar cause. In future work upon the central plexus of Actinotrocha I shall have a further occasion to refer to these matters.

A third source of seeming discrepancy is due to an unintentional misunderstanding, on the author's part, of my statements.

I had to notice the existence of small processes of the trunk cœlom which lie in the perianal sinus, and in doing so was obliged to hold in view the possibility of their being the first indications of the adult nephridia. Further investigation has convinced me that they have little morphological significance, but both Roule and Ikeda have imputed to me the definite statement that the trunk cœlom has definite nephridia, apparently only for the purpose of contradicting it. Perhaps it would be as well to state once for all that the trunk has no nephridia and possesses no normal openings till after the metamorphosis.

In reference to the oral and "pharyngeal" (? atrial) grooves the author speaks of a "grave error" into which I fell by not examining the living larvæ. With all due deference to him I must state that the existence of these grooves first appeared to me by experimental feeding of the living larva. Indeed, the course of food and water currents indicates their presence far more clearly than does their structural differentiation. In feeding, the larva places the preoral hood well down, and the food particles pass upwards along the ventral surface of the collar (not of the hood, as wrongly quoted by Ikeda, p. 536) in two slight depressions, indications of which are also seen in sections (fig. 29). On the other hand, the atrial water passes in a stream along the line of junction between hood and collar and out at the dorsal edge of the collar. These atrial grooves are also more in physiological than morphological evidence, though my sections show that there is a groove between hood and collar. (Woodcut 5, on p. 301, should sufficiently explain this.) Lastly, the author remarks, "Masterman has made the statement that in its natural attitude the hood had its length disposed parallel to the principal body axis. However, if the larva be examined in the living state, it will at once be discovered that its normal disposition is horizontal" (p. 536). The actual statement was, "The hood is in the position which perhaps may be described as normal" (p. 289), which is not by any means the same thing. Actinotrocha spends most of its time with the hood flexed ventrally, but the extension of the hood forwards is effected at pleasure and usually with great frequency. The term "normal" was used in much the same sense as one would regard the proboscis of the nemertine, when extruded, as being in the normal position, or the extended arm of the human subject. A little careful study of the work which he contradicts would have enabled Ikeda to avoid these seeming discrepancies. In addition to Ikeda's important verifications of the results of his predecessors, and the few differences from my work which I have indicated above, he has also added several interesting and new facts. He describes two retractor muscles of the hood which run from the main nerve-ganglion down to the dorsal body-wall. In one larva he finds a pair of long trunk-retractors. We may also note the description of a pair of globular glands which open on the dorsal wall of the hood in one species of larvæ, but not in the others.

In the third part of his paper the author deals with the metamorphosis. As one who has attempted many times to follow in detail this important process, and each time has been forced to wait for more material, I can speak of his attempt with sympathy. At the same time it will be well to accept with great caution all results, especially referring to the mesodermic organs. The external changes have already been carefully noted by many, and the changes of the alimentary canal are also easy to follow. In describing these latter we may note that Ikeda is able to correct the obvious error of Roule that the intestine ruptures, and that a fresh intestine is created from the cordon dorsal. (As is to be expected, he finds that this organ is the dorsal blood-vessel.) But when we come to the mesoblastic organs the difficulties begin. According to Ikeda, an "adult" collar cavity (or the supra-septal cavity) is formed round the base of the tentacles apparently from part of the larval collar cavity (at least the walls), and the rest of the larval cavity is converted into the blood ring-sinus of the adult. The difficulties relating to the nephridial openings into the trunk, the adult nervous system, and the epistome are discussed, but one would desire the author to pursue his studies on the metamorphosis, and it is pretty certain he will find that arguments from probabilities have no weight whatever with a metamorphosing Phoronis. At least, this is the writer's experience, and it is the main reason which conduces to a belief in the fate of the larval collar cavity as described by the author. But these remarks are not in any way meant to detract from our high appreciation of the merits of the author's work upon so interesting and, at the same time, so difficult a subject as the development of Phoronis.

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CONTENTS OF No. 180.—New Series.

MEMOIRS:

On the Structure of the Excretory Organs of Amphioxus.

Part I.

By

Edwin S. Goodrich, M.A.,
Fellow of Merton College, Oxford.

With Plate 27.

The excretory organs of Amphioxus were independently discovered by Weiss and Boveri in the year 1890 (**1** and **13**). Weiss described a series of small tubules regularly distributed at the top of each secondary tongue-bar throughout the region of the pharynx. The tubules are situated, for the most part, in the wall separating the dorsal cœlom from the atrial cavity; they lie, therefore, between the cœlomic and the atrial epithelium, generally separated from the latter by a network of fine blood-vessels. These kidney tubules open into the atrium by a pore just opposite the dorsal end of the secondary gill-bar. Weiss suspected the presence of an internal opening, but could not find it. The physiological significance of these organs he established by means of feeding experiments with carmine and other colouring matters.

In 1892 Boveri published a detailed and beautifully illustrated account of the excretory organs of Amphioxus (**2**). In this paper such a clear and accurate description of the appearance, general structure, and distribution of the kidneys is given that little remains to be said on these subjects. It will be necessary only to deal in detail here with certain points on which we differ, and concerning which I am able to correct Boveri's account in some important particulars.

The following is a brief statement of Boveri's description of the excretory organs :—Each consists of a tubule ciliated internally, and opening into the atrium by a pore near the top of the secondary gill-bar. In the mid-region of the pharynx, where the canal is best developed, it extends forwards to near the origin of the primary bar in front, and backwards to the primary bar behind, down which it runs for some little distance. Along its course the tubule is said to open into the dorsal cœlom by means of a varying number of small funnels; and spread over the cœlomic wall in the neighbourhood of each funnel are many peculiar pin-shaped cells called "fadenzellen." A long, slender process, starting from each of the "fadenzellen," is attached to the lip of the funnel. To quote from Boveri: "Jede Zelle läuft nämlich in einen feinen, aber deutlich doppelt contourirten Faden aus, der mit den übrigen Ausläufern der gleichen Zellengruppe zu einem Trichter hinzieht und in der Mündung desselben eine Strecke weit verfolgt werden kann;" and further: "Die Fäden ziehen frei durch die Leibeshöhle schräg abwärts in die Trichteröffnung hinein gegen die laterale Wand des Canälchens und heften sich mit ihnen Enden an die Zellen des Nierenepithels an" (2).

Some years ago, being struck with the resemblance these "fadenzellen" bear to the solenocytes I had just discovered in the nephridia of Polychæte worms, I examined the kidneys of Amphioxus, and came to the conclusion that the similarity was only superficial, and that Boveri's description was essentially correct (5, Part III). This winter, however, whilst occupying the British Association table at the Stazione Zoologica in Naples, I determined to re-examine these organs, and I am now able to definitely state that the "fadenzellen" of Amphioxus are indeed solenocytes of typical, though somewhat peculiar structure (7).

The methods pursued are of the most simple kind, and it is within the power of any one with living material at hand to easily verify my results. The Amphioxus is pinned out on its back in a shallow dish of sea water. The atrium is ripped up with a needle along the mid-ventral line, and the two metapleural folds pinned aside. The exposed pharynx is then also ripped up with a needle, and portions of the right or left side of the pharynx can then be torn out with forceps and placed on a slide,[1] care being taken to lay the outer side uppermost. When covered and examined under the microscope the general structure of the kidney can be quite easily seen; but the details which I am about to describe can, unfortunately, only be made out after prolonged study with the highest powers ($\frac{1}{12}$ oil immersion and No. 8 eyepiece, for instance).

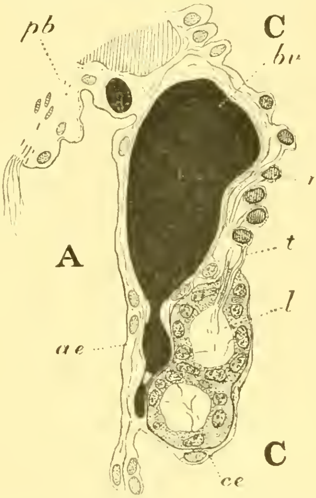

Figure of a portion of a section across the gill-bars showing the excretory canal cut through. *A.* Atrium. *C.* Dorsal cœlom. *pb.* Primary gill-bar. *bv.* Blood-vessel. *ae.* Atrial epithelium. *ce.* Cœlomic epithelium. *l.* Lumen of the excretory canal. *n.* Nucleus of a solenocyte. *t.* Tube of a solenocyte. Cam. and oil immersion.

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[1] Such pieces can be stained and mounted, or cut into sections.

Examined in this way, the "fadenzellen" are seen to consist of a small cell-body containing a nucleus. The cell-body is of somewhat irregular shape, being circular, triangular, or elongated, and occasionally drawn out into a process, reminding one of the outer processes present on some Polychæte solenocytes (5). A neck-like region, sometimes straight, sometimes curved, gradually narrows down and joins the cell-body to the distal extremity of the "thread," which is, in fact, a slender hollow tube of great length (Fig. in text, p. 495, and Pl. 27, figs. 1 and 4).

The longest tubes belong, of course, to those cells which are situated furthest from the renal canal; they reach sometimes a length of 90 μ, or nearly $\frac{1}{10}$ mm. The wall of the tube does not appear to be as stiff as in the case of Polychæte solenocytes; and under the pressure of the cover-glass it is often much curved. In the living animal, however, I believe the tubes are always straight. The proximal end pierces the wall of the excretory duct, and projects a little into the lumen of the canal (figs. 3 and 4). A long flagellum, attached at its base to the cell placed at the end of the tube, works rapidly down the tube and far into the excretory canal (figs. 3 and 4).[1]

Boveri (influenced perhaps by the current dogma, which affirms, in spite of all evidence to the contrary, firstly, that all tubular excretory organs are of homologous nephridial nature; and secondly, that nephridia are derived from the cœlom, and generally, if not always, open into it) described open cœlomic funnels in Amphioxus, as already mentioned above. Neither in the living nor in sections of preserved specimens have I been able to detect any direct communication between the excretory canal and the cœlom. The branches of the tubule may be very numerous, of considerable length, and may themselves divide, but they end blindly (fig. 1). It is to these blind ends that the tubes of the solenocytes converge, and here the wall of the canal is less loaded with

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[1] I was fortunately able to demonstrate the correctness of these observations to Prof. Boveri himself at the zoological station in Naples.

excretory granules, and thinner than elsewhere. The nuclei also, which are so numerous in the other regions of the tubule, are not present just in those parts where the solenocytes traverse its wall (Fig. in text, p. 495).

Briefly to summarise the observations described above, it may be stated that in Amphioxus there is a series of excretory tubules opening into the atrium, but not into the cœlom, and provided at their blind internal ends with a large number of solenocytes. These tubules are situated "morphologically" outside the cœlom, being covered with cœlomic epithelium; the solenocytes alone push through into the cœlomic cavity.

At each end of the pharynx the excretory organs dwindle in size, as already pointed out by Boveri. The tubule in these regions becomes shorter, the branches become reduced in size, or are not developed at all, and the number of solenocytes becomes much less. This is also the case throughout the pharyngeal region of small specimens. Fig. 3 represents a small portion of the kidney of a young Amphioxus 31 mm. long. Not only are the solenocytes not so crowded, but the average length of the tubes is less than in full-grown individuals (fig. 1).

That the segmental kidneys of Amphioxus really fulfil an excretory function has been amply demonstrated by Weiss and Boveri; but the part played by the solenocytes themselves is less clear. Boveri, who remarked that their distribution over the wall of the cœlom coincides with that of a network of blood-vessels, concluded that the "fadenzellen" were concerned in the elimination of waste products from the blood: "diese Zellen dem Chemismus der Excretion dienen." He could not find that they took up colouring matters—a result which agrees with my own observations on the solenocytes of Polychætes (**5**, Part II). It seems to me probable, therefore, that, as I have already suggested for worms (**5**, Part II), the solenocytes are concerned chiefly with the elimination of fluid substances which can pass by osmosis through the thin walls of the tube, well adapted for such a purpose. The flagellum would serve to propel the fluid into the excretory canal and thence to the exterior. That a considerable amount of fluid could pass through the tubes becomes evident when we remember that in a full-grown Amphioxus there are, roughly speaking, 100 kidneys on each side, or some 200 in all. Now each of these has, on an average, about 500 solenocytes—to take a low estimate,—making the number of solenocytes in the whole animal roughly 100,000. The average length of the solenocyte tube may be taken at $\frac{1}{20}$ mm., or 50 μ. There are, therefore, about 5 metres of this thin-walled tube in each full-grown individual, representing no inconsiderable area for osmotic exchange in an animal of such small bulk.

Conclusion.—I do not propose in this paper to enter into a detailed discussion of the homology and taxonomic importance of the segmental kidneys of Amphioxus, but the extraordinary resemblance they bear to the nephridia I have described in the Nephthyidæ, Glyceridæ, and Phyllodocidæ must be insisted upon. For the purpose of comparison, figures are given of the inner end of the nephridium of Phyllodoce Paretti (figs. 2 and 5), which, of all the Polychætes I have studied, most closely resembles Amphioxus in the structure of its renal organ. The nephridium of this beautiful Phyllodocid is large enough to be dissected out. It is then seen to end in the cœlom in a bunch of blind branches, which are provided with a number of solenocytes arranged like the ribs of a fan. The tubes are in double rows, while the cell-bodies of the two rows of solenocytes are closely packed together, and wedged in alternately.[1] In fig. 5 I have given a diagrammatic representation of the extremity of a branch of the nephridium, to compare with the similar diagrammatic figure of a small portion of the kidney of Amphioxus (fig. 4). These figures bring out clearly the wonderful likeness of the two organs.

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[1] I estimate the number of solenocytes in a Phyllodoce Paretti roughly at 600,000, there being about 1500 to each nephridium, and some 200 segments.

It results from these observations, as I have already pointed out in a preliminary paper (**7**), that in their segmental arrangement, in their function, and in their histological structure, the excretory organs of Amphioxus and the nephridia of Phyllodoce are in all essentials identical.

Before committing ourselves to new theories, something must be known of the development of these organs; but, considering how remarkably close is the agreement between the two, it seems more than probable that they are homologous structures. If two such excretory organs as the solenocyte-bearing nephridia of Phyllodoce, and the solenocyte-bearing kidneys of Amphioxus, could be shown to have been independently involved, we should have to give up structural resemblance as a guide to homology.[1] But there seems to be no danger of our being driven to abandon the problem as yet, and all we need assume is, not that the vertebrates have been evolved from the Polychætes, but that the remote common ancestor of these now highly differentiated phyla was of more elaborate structure than most authors have been hitherto inclined to suppose. We must assume that it possessed not only paired cœlomic (genital) sacs and cœlomostomes (**6** and **8**), but also nephridia, whose blind internal end was provided with solenocytes.[2] We may conclude provisionally that now, for the first time, true nephridia have been shown to occur in the vertebrate phylum; and further, we may hope to trace in the vertebrates the same two series of organs—the nephridium and the cœlomostome—which I have elsewhere

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[1] The only case which seems to me at all comparable is that of the nematocysts in Cœlenterates, Planarians, and Molluscs.

[2] This is all the more easy to believe since I have found these cells at the blind inner end of the nephridium of the larva of Phoronis (it will be remembered that Masterman observed cells similar to Boveri's "fadenzellen" in Actinotrocha [**9**], and they have been described by Wagener [**12**]); and "flame-cells" very like solenocytes have been described in Nemertines by Bürger (**4**), in Molluscs by Meisenheimer (**10**), and in Rotifers by Shephard (**11**). Also the "flame-cells" of Platyhelminths and Entoproctous Polyzoa are probably of the same nature (**6**).

endeavoured to prove exist in the majority of cœlomates (**6**, and **5**, Part III).

It follows, from the conclusion provisionally adopted above, that the many theories which have been built on the assumed homology between the separate segmental excretory organs of Amphioxus and the renal organs of cœlomic origin of the higher vertebrates must be allowed to drop for the present. These latter organs (pronephros, mesonephros, and genital ducts) have nothing to do with nephridia, and appear to belong undoubtedly to the category of cœlomostomes (**5**, Part III, and **8**). Their homologues in Amphioxus may be sought in the opening of the larval "head cavities," in the "brown funnels" described by Lankester, and in the segmental genital sacs as already suggested by Boveri (**3**). It is not impossible, however, that true nephridia may yet be found at some stage of development amongst the craniate vertebrates, and more especially in the Cyclostomes.[1]

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EXPLANATION OF PLATE 27,

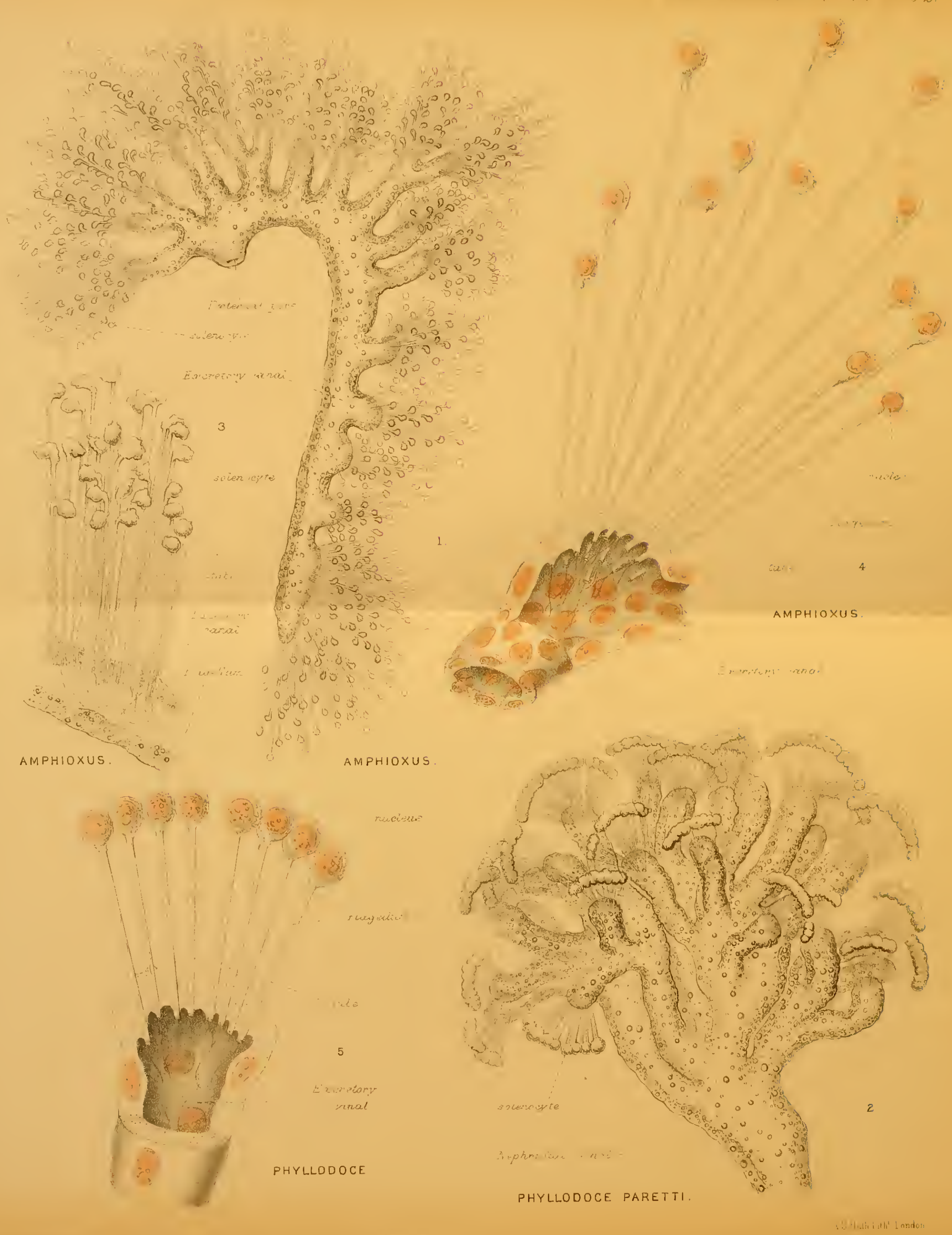
Illustrating Edwin S. Goodrich's paper "On the Structure of the Excretory Organs of Amphioxus."

Fig. 1.—Enlarged view of an excretory organ of Amphioxus, drawn from the living.

Fig. 2.—Enlarged view of the terminal tuft of the nephridium of Phyllodoce Paretti, drawn from the living.

Fig. 3.—A small portion of the excretory canal of a young Amphioxus, with its solenocytes, from the living. Cam. $\frac{1}{12}$ oil immersion, oc. 8.

Figs. 4 and 5.—Semi-diagrammatic views of portions of the excretory organs of Amphioxus and Phyllodoce Paretti, from living and preserved specimens.



AMPHIOXUS.

AMPHIOXUS.

AMPHIOXUS.

PHYLLODOCE

PHYLLODOCE PARETTI.

A.S.Huth Lith^r London

A Contribution to the Morphology of the Teleostean Head Skeleton, based upon a Study of the Developing Skull of the Three-spined Stickleback (Gasterosteus aculeatus).

By

H. H. Swinnerton, B.Sc.,
From the Zoological Laboratory, Royal College of Science, London.

With Plates 28—31 and 5 Text Illustrations.

CONTENTS.

I. INTRODUCTORY.

DURING the years which have elapsed since W. K. Parker (**73**) published his admirable 'Monograph on the Skull of the Salmon,' comparatively little has been done to advance our knowledge of the development of the Teleostean head skeleton; McMurrich (**83**) is the only investigator who has dealt with the development of the whole head skeleton of any other type with any approach to detail; Pouchet (**78**) has dealt with isolated stages of Gobius, Syngnathus, Labrus, Atherina, and Engraulis; Stöhr (**83**) has confined himself to extending or rectifying Parker's observations; whilst Ganin (**80**) has devoted two pages to these processes in the skull of Gasterosteus and Rhodeus. Several others have dealt with the development of parts with more or less detail.

It was with a view towards supplying this deficiency that the investigation, the results of which are here recorded, was undertaken. Acting upon a suggestion originally made by Professor G. B. Howes, the common three-spined stickleback was chosen as the basis of my observations, partly because of the ease with which the material could be obtained, and since, while it offered a more specialised type than the salmon, it seemed to form, according to Cope (**70**) and later systematists, a suitable starting-point for the study of certain specialised and peculiar groups, e.g. Lophobranchs.

Beyond the work of Ganin the only previous observations upon the skull of Gasterosteus which I have been able to find are those of Huxley (**58** and **59**), chiefly in his Croonian Lecture "On the Theory of the Vertebrate Skull." Figuring and describing the hyosuspensorial apparatus of the adult, he gives three figures of the larval skull, which are remarkable for their accuracy. One figure represents a stage coincident with my Stage II, and the other two correspond to my Stage IV. Amongst his original drawings, now preserved in the Huxley laboratory, are several other figures of the same stages, which were evidently studies for parts of those which he published.

I tender my heartiest thanks to Professor G. B. Howes for his ever-ready help in obtaining material, his guidance in working, with the reading, and also to Mr. M. F. Woodward and Mr. G. A. Boulenger for much valuable assistance.

II. Material and Methods.

Part of the material requisite for my investigation was obtained by keeping adult sticklebacks in small aquaria during their breeding season; the rest by hatching, under the tap, spawn found in a stream near London. In this way it seemed possible to obtain a definite idea of the size of the various embryos and larvæ at different ages. During the earlier stages this was possible; but later on, owing to the great variation in length of individuals belonging to the same hatch, the attempt became useless.

The following table contains a list of all the specimens examined, with details which may prove useful to future workers.

Table of Specimens with Descriptions of the Stages.

No.	Age.	Length.	Description of Stages.
1 *a—c*	5th day	*	Stage I.—No hyaline cartilage; no sign of the cranial roof; the symplectic not elongated; the palatine process not yet attached to the ethmoid region.
2 *a—c*	Early 6th day	*	
3	6th day	*	
4 *a—b*	6th day	3·5 mm.	
5 *a—c*	6th day	3·6—3·7 mm.	
6	7th day	*	
7 *a—b*	7th day	3·6 mm.	
8 *a—d*	7th day	4·0—4·2 mm.	
9	8th day	*	Stage II.—Much hyaline cartilage; epiphysial bar present, but no other portion of the cranial roof; symplectic elongated; palatine process attached to the ethmoid.
10	8th day	3·8 mm.	
11	9th day	5·0 mm.	
12	9th day	5·4 mm.	
13 *a—b*	9th day	5·7 mm.	
14	11th day	6·3 mm.	Stage III.—Supra-occipital portion of cranial roof is formed; posterior cranial fontanelle not divided into two lateral ones; hyomandibular merely a rectangular plate. No ossification of cranial cartilage.
15	11th day	6·4 mm.	
16	11th day	6·6 mm.	
17	—	7·2 mm.	
18	—	7·3 mm.	
19	—	9·0 mm.	

* Embryos that were fixed whilst in the egg.

No.	Age.	Length.	Description of Stages.
20	—	11·0 mm.	Stage IV.—Posterior cranial fontanelle divided into two lateral ones; hyomandibular the same shape as in the adult; all cartilage and dermal ossifications present; chondrocranium still largely cartilaginous.
21	—	14·0 mm.	
22	—	16·0 mm.	
23	—	17·0 mm.	
24	—	21·0 mm.	
25	—	25·0 mm.	
26 *a—d*	—	Up to 50·0 mm.	Stage V.

For material used in investigating general questions arising out of the study of the stickleback's skull, I have relied upon the teaching collection of the Royal College of Science, on a series of microscopic preparations which were given to the College by the family of the late Dr. Pollard, and on the fish skeletons now being incorporated in the collections of the British Museum of Natural History. The first two of these were kindly placed at my disposal by Professor Howes, and the last by Mr. Boulenger.

The methods pursued were the same as those used when investigating the skeletogeny of Sphenodon in conjunction with Professor Howes (**01**); and as they are described with some detail in our memoir on that animal, I shall not repeat them here.

For embryonic, larval, and young material I found Perennyi's fluid more useful for fixing purposes than either picro-sulphuric or corrosive sublimate, because it was less liable than these to bring about distortion.

For adults 4 per cent. formalin was used.

III. Descriptive and Comparative.

The Cranium.

Stage I.—Up to the end of the fifth or even early on the sixth day the only definite representative of the skeleton in the head of the stickleback is the notochord, the cells of which have already taken on that highly vacuolated structure so characteristic of advanced chordal tissue (Pl. 30, fig. 25). On the former day, whilst the medullary groove is still open in front, the notochord runs parallel to the egg-shell for the whole of its length; on the latter a slight ventral and also lateral displacement of the anterior or cranial end has taken place. From this time onwards to the time of hatching, this flexure increases no further, but the chorda merely moulds itself to the shape of the brain floor (fig. 58, *ch.*′).

Balfour (**78**, p. 210) has described a similar but much more strongly marked flexure in Elasmobranchs, and has figured it for embryos of the Torpedo, Pristiurus, and Scyllium. In them it may take place through "an angle of 180°," and "is not directly caused by the cranial flexure." Nor is the slight flexure above described in the stickleback due to this cause, for here, under normal conditions, I fail to find any trace of a cranial flexure; the cause should rather be sought for in this case in the rapid development and consequent great increase in size of the brain, and in the presence of a rigid zona radiata (fig. 56 **) which prevents this organ from expanding dorsally.

Under certain circumstances, however, the cranial notochord may exhibit an extremely well-marked ventral flexure. In figs. 56 and 57 are represented, diagrammatically, medium longitudinal sections through embryos of exactly the same age, viz. three days before the time for hatching; but whilst fig. 56 represents one killed within the egg, the other is taken from one which was killed after being artificially released. In the former all the parts of the head were packed closely together, and the head itself flattened out upon the yolk (figs. 54 and 56); in the latter (figs. 55 and 57) it is no longer flattened but distended, and has undergone a well-marked ventral flexure, chiefly through the region of the hind brain (*b. h.*). The roof of the mid-brain (*b. m.*) consequently comes to be the most anterior point of the body, the axis of which is indicated by the arrow. This flexure is still more conspicuously shown by the notochord, which, from being slightly flexed (as shown by the dotted outline, fig. 57, *ch.'*), has now become bent back almost on itself (*ch.*). When three days later the larva hatches out, all sign of flexure has disappeared from the brain (fig. 58), and the intercranial notochord itself has resumed approximately the same shape as that which it exhibited within the egg (fig. 56) on the sixth day.

In a typical Elasmobranch's egg, that of Scyllium, the embryo is at liberty to move about considerably, and therefore exists under conditions practically the same as those in which the prematurely released or hatched stickleback exists. Comparison of the structural peculiarities already referred to in the Elasmobranch embryo must accordingly be, not with the imprisoned, but with the released stickleback.

As to the cause of this flexure exhibited by the free embryo (fig. 57), it is natural to expect that an elastic body like the brain filled with fluid should, when liberated from the pressure of the zona radiata, lose its flattened form and assume a distended one; but it is not so obvious why such an alteration in external conditions should, on the sixth day, produce a strongly marked flexure, and on the ninth a slight straightening out (fig. 58).

It is certain from the facts already put forward that the cause for these unexpected effects is one which can be held in abeyance by mechanical means, such as the resistance of the zona, which disappears with advancing development. The coincidence of the time of appearance of skeletal elements with the time of great flexure suggests that these may be one factor in that cause. Another factor is perhaps to be found in the great difference in the degree of development between the dorsal and ventral portions of the brain; for whilst the latter is very massive, the former is at present little more than an epithelium (figs. 54, 55, *b. h.*). A comparison of figs. 57 and 58 will show that on the sixth day the skeletal elements (*tr.* and *ch.*), as compared with the brain, are relatively much shorter than on the ninth day. The fact that in the released embryo (fig. 57) the optic nerve (11), pituitary body (*pt.*), and infundibulum (*inf.*), notwithstanding the great distension of the head, have undergone no change of position in a longitudinal direction relatively to the trabeculæ and notochord, proves that a close connection exists between these and the floor of the brain. The presence of short, comparatively inelastic elements side by side with a longer and more highly elastic and distensible one, such as the brain, supplies us with structural and mechanical relations analogous to those found in the Brequet's thermometer. In the head of this sixth-day embryo, under a change of external conditions, the long, weak, unrestrained dorsal portion of the brain, from the optic nerve (11) to the line (*), distends more than the short, strong, restrained ventral portion; and the result is the well-marked bend. As development advances, these opposite conditions are done away with. The tissues of the upper surface become stronger, and that portion of the ventral surface supported by the trabeculæ (*tr.*) and notochord (*ch.*) more extensive. Consequently the influence exerted by the latter is no longer one of restraint, but of extension; and therefore, at the time of hatching (fig. 58), the whole head straightens out from the curvature enforced upon it by the zona (**).

It would be digressing too far from the main line of the present memoir to pursue this interesting topic further; suffice it to point out that these facts, by showing the existence of the necessary mechanical conditions, lend support to Sewertzoff's hypothesis concerning the influence of the state of development of one organ upon that of another (**99**, p. 319); that, as shown by the observations of Dendy and Howes (**99**), Howes and Swinnerton (**01**), upon the eggs of Sphenodon, other pressures than the mere passive resistance of the shell exist; and that possibly prematurely released embryos may undergo other distortions, the study of which would throw light upon the mechanics of development.

It has been hinted above that the first traces of the head skeleton, other than the notochord, appear during the latter part of the sixth day. In my youngest embryo which shows any sign of these they have already practically assumed the condition shown in figs. 1 and 6 (Pl. 28),[1] the main difference being that the cartilaginous portions are not yet so extensive.

On either side of the ventrally flexed notochord (fig. 1, *ch.*) the parachordals have become differentiated as long plate-like tracts of skeletal tissue, in each of which there are two distinct regions of chondrification (*p. ch.*, *oc. e.*) separated by an intervening area of pro-cartilage, and corresponding to Sewertzoff's mesotic and occipital sections (**99**, p. 310). In embryos of the seventh day the whole length of each tract is well chondrified, but these two regions may still be easily distinguished.

The mesotic section (*p. ch.*) extends nearly three quarters of the length of the tract, and anteriorly its inner border is separated from the notochord. From its outer border arises a stout process which expands distally to form the auditory capsule. At the same point a ridge starts which divides the section into two parts: an anterior which supports the brain, and a posterior or otic portion which helps to support the auditory organ.

The occipital section (*oc. e.*) is much shorter, and shows none of those signs of segmentation recorded by Sewertzoff for Acanthias. Like the hinder part of the other section and the intervening pro-cartilage, it lies in contact with the side of the notochord.

In the salmon, according to Stöhr, the auditory capsule arises first as a plate of pro-cartilage, under the auditory vesicle, joined to the parachordal by fibrous tissue; in Embryo III this plate becomes chondrified; in Embryo IV, which corresponds to Parker's Stage V, it becomes connected anteriorly with the end of the parachordal by a strip of cartilage, and thus assumes the condition above described for the stickleback. Since the larvæ of Parker's Stage V

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[1] In following the description of this stage it should be borne in mind that the model from which figs. 1 and 6 were taken was made from an embryo of the prematurely released type.

had been hatched a fortnight, and correspond in other respects to my Stage III, it is evident that there has been some influence at work hastening the development of this particular region. The stages during which the otic element should be independent thus seem to have been completely suppressed. On the other hand, such an early connection of the auditory capsule with the basis cranii is a by no means exceptional feature, for in Acanthias (Sewertzoff, **99**, p. 284) it arises as an outgrowth of the latter; and in Sphenodon (Howes and Swinnerton, **01**, pl. iii, figs. 1 and 3), whilst this region is still pro-cartilaginous, it is quite continuous.

From the anterior dorsal border of the auditory capsule there arises the pro-cartilaginous post-orbital process (fig. 6, *sb. p.*) which represents the supra-orbital bar described by Parker in the salmon (**73**, p. 129), and by Sewertzoff in Carassius (**99**, p. 312), and is all that is present of the sphenoid region. Of the separate alisphenoid plate described by Sewertzoff in Acanthias (**97**, p. 413) there is no sign.

Turning now to the prechordal elements (fig. 1, *tr.*) of the cranium, the trabeculæ are already as well differentiated as in Stöhr's salmon, No. III. They are long and rod-like, and chondrified for the greater part of their length. Anteriorly each passes imperceptibly into an expanded plate of procartilage (*e.*) which shows signs of being united to its fellow by tissue rich in nuclei. The anterior halves of the trabeculæ run parallel to one another; the posterior diverge (*pt. f.*) to enclose the infundibulum and pituitary body, and end in a slight enlargement.

The relation of the hinder ends of the trabeculæ (*tr.*) to the parachordals on the sixth day is somewhat variable. The commonest condition is that in which the trabeculæ pass continuously into the anterior end of the parachordals by means of a tract of pro-cartilage. Two seventh-day embryos (Nos. 7, 8) of this stage show a different condition; in the first both the trabeculæ are separated from the parachordals by a comparatively wide space (as indicated by the unshaded portion in fig. 1); in the second the trabecula of the one side shows the usual condition, that of the other the unusual. In the other seventh-day embryos there is no discontinuity between the chordal and prechordal portions of the cranium, though the two regions can be easily recognised by their difference in calibre.

Stage II.—As already described, the intercranial notochord is no longer strongly flexed, but is now almost in a line with that of the trunk, and has, indeed, undergone a straightening out (fig. 58, *ch.*) in the process of hatching.

Comparison of a dorsal view of the cranium (fig. 2) at this stage with that of the previous stage (fig. 1) gives, at first sight, the impression that the notochord (*ch.*) has undergone a reduction. This, however, is only an appearance due to the more rapid growth of the surrounding parts. By comparing median longitudinal sections (figs. 57, 58) of the respective stages, it becomes evident that the notochord (*ch.*) not only does not decrease, but undergoes an actual increase in absolute length.

The parachordal tracts (fig. 2, *p. ch.*), which are no longer divisible histologically into mesotic and occipital sections, have grown considerably in all dimensions, quite independently of the notochord (*ch.*), and their anterior ends (*tr.'*) are now situated far in front of the end of this. The space (*p. ch.'*) situated between them, which received the freely projecting half of the notochord in the first stage, has been carried forward, and now receives only its extremity. This interparachordal space, as in the salmon (Parker, **73**, p. 129), is continuous in front with the pituitary fossa (*pt. f.*). The anterior lateral process of the parachordal has also undergone a similar forward shifting, by means of which it now lies in a level with the extremity of the notochord. The oblique ridge, in the mesotic region, is less strongly marked, and owing to the increased width of this it no longer extends to the notochord, but runs along the middle line of the parachordal plate to the occipital section. The otic portion of the plate, which may be regarded as part of the auditory capsule, occupies a lateral and not a postero-lateral position relative to the rest of the plate, and dips down somewhat below the level of the flat basis cranii which the remainder of the parachordal forms with its fellow.

The occipital section has now sent up on either side a stout occipital arch (figs. 2 and 7, *oc. a.*). On the outer side and near the base of this is a slight projection almost like a transverse process (*oc. a.′*). In front of the arch lies the exit of the vagus nerve (IX and X), whilst all the so-called occipital nerves pass out entirely behind it.

The anterior and external wall of the auditory capsule (*au. c.*) has extended backwards, underneath, and along the outer side of the auditory vesicle to the level of the occiput; but in the cranium figured has no connection with this. In that of a slightly older larva, it is continuous both with the lateral process of the occipital arch (*oc. a.′*) and with the postero-lateral border of the mesotic region, thus forming a complete boundary around the exit for the ninth and tenth nerves (IX, X). In this larva, also, there are two fenestræ in the floor of the auditory capsule (cp. fig. 2, *fe.′*) separated by a bridge of cartilage which is incomplete in the younger one. This bridge is formed in correlation with a slight elevation of the floor of the auditory capsule. This elevation is more strongly marked posteriorly by the presence of a pillar of cartilage (*au. c.′*), around which the external semicircular canal runs. The whole floor of the capsule fits the bottom of the auditory labyrinth, and seems to have been moulded to it, so that where this bulges the cartilage is thinned out, and fenestræ (*fe.′*) are left; where it is constricted a cartilaginous ridge is formed.

The anterior edge of the auditory capsule is greatly thickened. The pro-cartilaginous post-orbital process (fig. 6, *sb. p.*), which has elongated and become more completely chondrified (fig. 7), arises from the dorsal end of this thickening; whilst a similar but more delicate process (*o. pr.′*), lying between the exits of the fifth and seventh nerves, projects from the ventral end. This thickening is undoubtedly to be compared with the alisphenoid region of the salmon, where it arises as a "growth of cartilage downwards from the (supra-orbital) band, and forwards and inwards from the ear-sac" (Parker, **73**, p. 136).

The trabeculæ, now made up wholly of hyaline cartilage, have fused with one another anteriorly to form a broad ethmoid plate, which corresponds to Parker's "subnasal lamina" and McMurrich's "rostral plate" (**83**, p. 625). The brain, which in previous stages extended considerably beyond this region (figs. 56 and 57, *b. f.*), has now relatively retired, so that the prosencephalon lies upon this plate. From its lateral borders arise two large processes (fig. 7, *e. p. c.*), which by reason of their position and ultimate fate may be conveniently termed the parethmoid cornua, and the line joining their posterior margins may be regarded as the posterior boundary of the ethmoid plate. This can then be described as rectangular. For reasons which will appear later it will be useful to apply the name pre-ethmoid cornua (*e. pr.*) to the anterior angles. Behind the ethmoid plate the trabeculæ are united for a short distance, and are then separated by a narrow slit, which widens gradually to form the pituitary fossa (fig. 2, *pt. f.*).

The first trace of a cranial root has appeared in the form of a transverse bar (*ep. c.*), consisting of a pair of chondrifications which in older specimens are connected by pro-cartilage. It lies in the dorsal fissure which separates the fore and mid-brains (fig. 58, *b. f.* and *b. m.*). Immediately in front of it lies the epiphysis; consequently it is to be regarded as the homologue of the epiphysial bar described by Pollard (**95**, p. 414) in the Siluroids, and by Sagemehl in the Characinidæ (**85**, p. 41) and Cyprinidæ (**91**, p. 511).

Stage III.—Apart from the absence of ossifications the chondrocranium has now assumed practically the adult condition. The intra-cranial notochord has undergone no further change beyond a slight increase in absolute length. The interparachordal fossa has been carried some distance in front of the notochord; and the parachordals themselves have united across the intervening space and across the ends of the notochord (*c. p.*, dotted outline fig. 3) in such a way that this projects below, but lies quite close against the basis cranii.

Outside each mesotic ridge lies the floor of the auditory capsule, which, owing to the disappearance of its fenestræ (fig. 2, *fe.'*), is no longer divisible into parachordal and external portions. The outer border of the capsule (fig. 8) has remained unaltered anteriorly, but posteriorly it has grown to the extent of forming a roof over the auditory and cranial cavities—a process in which the occipital arch has taken very little part. At the same time the ridge which separated the two fenestræ has become more marked; whilst its posterior pillar (cp. figs. 2, 8, *au. c.'*) has grown up and fused with a similar downgrowth from the roof. From the point at which these meet, another pillar, over which the posterior semicircular canal runs, has grown back towards and united with the occipital arch (fig. 8, dotted outline near *fe.''*). The whole complex presents internally essentially the appearance seen in the adult (Pl. 29, fig. 20). The capsule as a whole is so moulded to the shape of the auditory organ that the course of the semicircular canals can be traced even externally. Two fenestræ (fig. 8, *fe.''*) have been left in the side walls.

The sphenoidal region is no longer a mere thickening of the anterior auditory wall. The post-orbital process (fig. 3, *sb. p.*) above is at its maximum development, and the pro-otic process (*o. pr.'*) below is broad, plate-like, and fused with the outer border of the parachordal. Thus it completes the anterior boundary of the foramen for the seventh nerve. In front the trabeculæ become increasingly flatter and broader, and are fused along their contiguous margins in such a way as to form a ridge above and a groove below.

The ethmoid region (*e.*) is still rectangular, but as a whole it has elongated, thus separating the pre-ethmoid (*e. pr.*) and parethmoid cornua (*e. p. c.*) from one another more distinctly. The latter are now expanded and wing-like, and pass at their upper extremities into the supra-orbital bands (*sb. b.*).

In association with the withdrawal of the prosencephalon from this region, a median process-like upgrowth (*e. m.*) of the ethmoid plate—the nasal septum of the salmon (Parker, **73**, p. 128)—has appeared. At its upper end this mesethmoid cartilage expands laterally and fuses with the upper ends of the parethmoid cornua.

The ethmoid region of the larval salmon (25 mm.) presents one or two important differences from that of the stickleback. Looked at from beneath it is broad but not rectangular, for whilst both cornua (Pl. 31, fig. 47, *e. pr.*, *e. p. c.*) are recognisable, the anterior border is not straight, but has grown out into a triangular rostrum (*r.*). At the same time on the dorsal surface the nasal septum has extended to the anterior end of this.

In the stickleback the epiphysial cartilage (Pl. 28, fig. 3, *ep. c.*) has grown backwards, but the epiphysis is still closely related to its anterior edge. Laterally it is continuous with the hinder ends of the supra-orbital bands (*sb. b.*), and thus closes in a space which may be called the anterior fontanelle (*a. f.*). In the roof of a salmon 20 mm. long (fig. 61) this cartilage is expanded laterally, and, except for its continuity behind with the post-orbital process (*sb. p.*), and for the fact that the prosencephalon overlies the dorsally excavated mesethmoid cartilage, the whole roof presents the same condition as that above described for the stickleback. In an older salmon (25 mm.) the anterior fontanelle has become covered in by an inward growth of the epiphysial cartilage and supra-orbital bands, except for a smaller space over the epiphysis (*ep. f.*) and a larger one (*a. f.*) at the anterior extremity which corresponds to that marked *m. n. c.* by Parker (**73**, pl. iv, fig. 2, and pl. vii, fig. 4) and to the median fontanelle described by Winslow (**98**, p. 186) in the trout. This fontanelle is now bounded in front by the more fully developed mesethmoid cartilage, now no longer overlapped by the prosencephalon.

Through the kindness of Professor Howes I have been enabled to examine the head of a larval Amia 19 mm. long. The roof of this was in exactly the same condition as that just described for the 25-mm. salmon, even to the presence of the small foramen above the epiphysis. It is safe, therefore, to assume that here also the tegmen cranii is formed, not by back growth of the ethmoid region, but by inward extension of the supra-orbital and epiphysial cartilages over a pre-existing fontanelle.

In Engraulis and Atherina, Pouchet (**78**, pl. x, figs. 44, 49) found both fontanelles. The anterior one is in precisely the same condition as in Gasterosteus ; but the posterior one of Engraulis is divided medianly by a strip of cartilage into two lateral fontanelles. A transverse epiphysial bar is present.

I have found this bar in Siphonostoma also (fig. 48, *ep. c.*).

These facts make it evident, therefore, if we take developmental stages into account, that the epiphysial cartilage, so far from being confined to the Ostariophysi, as Sagemehl (**91**, p. 576) thought, is an element widely distributed among Teleosts, and probably derived by them from an ancestor with no other cranial roof.

In the stickleback it never undergoes any further extension forwards than is shown at this stage. If it is safe to assume that, because primitive Teleosts have a well-developed tegmen cranii, this specialised little fish has lost it phylogenetically, we have, in the epiphysial cartilage, an interesting example of an old character which has survived all the vicissitudes of a shortened ontogenetic record.

In the oldest individuals of this stage all the membrane bones, except the mesethmoid, nasals, and parietals, have appeared; but there is no marked ossification of the chondrocranium itself.

Stage IV.—The notochord has undergone only a slight increase in length, as a comparison of figs. 25 and 26 (Pl. 30) will show ; but it has now begun to assume characters which anticipate the adult condition. In front it has the same proportions as at previous stages, whilst behind it has become expanded and funnel-shaped (fig. 26, *ch. s.*) in preparation for the articulation with the first vertebra. Internally it is no longer filled with a few highly distended vacuolated cells, but, especially at its anterior end, it consists of a great number of collapsed cells of a similar type crowded together. Where the extra cells arise is uncertain, for intercranially the chordal epithelium shows no signs of active growth even in younger individuals of this stage. In the articular region, however, this is rich in nuclei, and appears to be actively giving rise to the substance of the thick fibrous sheath externally and to cells internally; an appearance which suggests that cells from this region may have crowded forwards. Such an interpretation is supported by the fact that those cell walls which are attached to the chordal sheath all have their inner portions inclined forwards, as though there had been a movement in the same direction on the part of the central cells. Externally it is completely enclosed in a casing of a bone—the basioccipital,—whose relation to the notochord was accurately described by Huxley, and compared by him with the urostyle (**58**, p. 440).

Apart from the appearance of numerous ossifications, the changes which at this stage have taken place in the chondrocranium are few (Pl. 28, fig. 9). Owing to the suppression of part of the supra-orbital bands, and of those parts of the trabeculæ which border on the pituitary fossa, the two parts of the chondrocranium which are essentially trabecular and parachordal in origin have become completely separated from one another.

In the hinder or parachordal portion the interparachordal fossa (fig. 12, *p. ch.'*) has been carried so far away in front of the notochord that the plate formed by the median union of the parachordal now furnishes a considerable portion of the basis cranii. Those parts lying immediately on either side of the fossa have now begun to undergo a movement of depression, by which they have already come to lie slightly below the level of the basis cranii.

This is perhaps associated with a similar movement on the part of the recti muscles. In the previous stage the inner ends of these were inserted into one another and into the tissue which fills the hinder part of the fossa. Owing to the point of their insertion on the eyeball (fig. 58, *m. e.*) being in a plane situated a little in front of this, but considerably above that of the basis cranii, their course outwards over the anterior ends of the parachordals was obliquely upwards. In this stage, however, their posterior insertion has come to lie under the hinder border of the fossa (fig. 38, *me.*, *o.pr.*), whilst that on the eyeball is now tending to pass down with the latter to the level of the basis cranii. In consequence of this tendency, which finds its consummation in the adult (fig. 59, *me.*), the course of the muscles is still more obliquely forwards and less obliquely upwards.

Passing to the anterior or trabecular portion of the chondrocranium, the ethmoid plate (fig. 9, *e.*) has greatly elongated. The connections between the mesethmoid and the parethmoid cornua have become more extended, and give the appearance, when viewed dorsally (fig. 4), of a rudimentary tegmen cranii. In front of the mesethmoid the ethmoid still retains its original plate-like character, but the pre-ethmoid cornua (*e. pr.*) have now become slightly drawn out dorso-ventrally. Fig. 30, which represents a section through the pre-ethmoid region (*e.*), passes through the extreme upper end of this process (*e. pr.*); a few sections further back the two parts become continuous.

Apart from its great length the ethmoid of Siphonostoma (fig. 48, *e.*) is just the same as in the stickleback.

Concerning the regions in which, in the stickleback, suppression has taken place, remnants of the supra-orbital bands are still seen in the backward processes of the rudimentary tegmen cranii; whilst those parts of the trabeculæ which in the previous stage were fused together, now remain as a posterior prolongation of the ethmoid plate. Of the parts which have disappeared no trace remains; nor is any cause forthcoming, unless it be that they are functionally replaced by the frontals and parasphenoid respectively.

The epiphysial cartilage, now quite free of the ethmoid region, has grown considerably posteriorly, and become connected with the hinder cranial roof by a thin strip of cartilage running through bone (*e. p. s.*). This strip is the homologue of the massive cartilage which lies between the small lateral cranial fontanelles in the adult salmon, and of the small process (fig. 62, *e. p. s.*) of the epiphysial cartilage which projects back into the posterior cranial fontanelle (*p. f.*) of the larva. The condition in the stickleback is now identical with that described and figured by Walther (**82**, p. 10) for the young pike, and Pouchet (**78**) for Engraulis.

All the ossifications present in the adult are now represented, but as yet are widely separated by cartilaginous areas.

The basioccipital (fig. 12, *oc. b.*), owing to the hinder funnel-shaped enlargement of the notochord, has begun to take on the usual centrum-like condition. At its extreme anterior edge the ventral lamina of bone leaves the cartilage and projects freely forwards, as indicated by the yellow pointed portion in fig. 12, and is better understood from the longitudinal section of this region of the adult (Pl. 30, fig. 37, *ey. c.*). This free portion lies between the posterior prolongations of the parasphenoid (fig. 36, *p. s.*), and is formed by ossification in connective tissue.

The vagus and pneumogastric nerves pass out through the exoccipital (figs. 9, 12, *oc. e.*) by a common foramen, as in the previous stages; but in the individual figured the pneumogastric nerve of one side passed out by a small foramen, separated from that of the vagus by a narrow bridge of bone. This is the beginning of a process which continues on both sides, and ultimately carries the two foramina far from one another.

Posteriorly the exoccipital, by extending into the surrounding tissue, has enclosed the first spino-occipital nerve (fig. 9, *oc. n.′*) completely, and the second (*oc. n.″*) partially.

The supra-occipital (fig. 4, *oc. s.*) extends along the strip of cartilage which joins the posterior cranial roof to the epiphysial cartilage, almost to the level of the post-orbital processes. The ossification does not yet affect any part of the epiphysial cartilage itself, but it extends laterally into regions where no cartilage exists or has existed during ontogeny; that is to say, into the connective tissue which roofs over the fontanelles. It cannot therefore be regarded as a simple cartilage bone; but it may be that this lateral extension is indicative of a former greater extension of the cartilage.

Of the otic bones (figs 9, 12, *o. e.*, *o. p.*, *o. sp.*, *o. pr.*) the opisthotic is absent, and the remainder are represented by rounded areas of ossification, but are still widely separated by cartilage. The circular form and wide separation of the ossifications calls to mind the condition of the same set of bones in the adult Amia (Sagemehl, **84**, p. 202). The main part of the pro-otic (*o. pr.*) completely surrounds the exit for the seventh nerve, whilst its anterior border is deeply indented for the passage of the second and third branches of the fifth. The portion which lies between these two nerves is the portion hitherto called the pro-otic process. The front part of the sphenotic is formed by ossification of the plate-like extension of the auditory capsule—the sphenoidal region.

In the younger individuals of this stage, except for the pro-otic, each of these ossifications is confined mainly to the external surface of the cartilage. Under the central portions of the epiotic, pterotic, and sphenotic the cartilage has disappeared, and consequently this outer lamina of bone comes to form part of the internal wall of the capsular and cranial cavities. Apart from this, the condition exhibited at this stage bears a close resemblance to that found in Amia (Bridge, **77**, p. 612), in which the pro-otic is the only bone of this series visible internally.

In the anterior portions of the skull the expanded plate-like portions of the parethmoid cornua have given rise to the parethmoid bones (figs. 4, 9, *e. p. b.*), whilst a centre of ossification, the mesethmoid (*e. m.*), has appeared on the dorsal surface of the corresponding cartilage. The edges of the latter ossification extend freely into the surrounding tissue, and give the impression of a membrane bone whose central portion has united with the cartilage, leaving the edges quite free. Though no further evidence that this has actually taken place is forthcoming in any of the examples which I have examined, there can be little doubt that the impression thus formed is a true one. In the salmon (Parker, **73**, pp. 98, 138) this bone exists even in the adult as a membrane bone, perfectly free of the underlying cartilage. In the Characinidæ (Sagemehl, **85**, p. 14) and Cyprinidæ (ibid., **91**, pp. 497, 499) every gradation exists from the condition here shown in the young stickleback to that found in the Scomber (fig. 44, *e. m.*), in which, as in the majority of Teleosts, this bone has lost all sign of a membranous origin, and consists entirely of ossified mesethmoid cartilage.

All the cranial membrane bones are now present.

Adult.—In assuming the adult condition the chondrocranium undergoes but little change, beyond a continuation of those ossificatory processes which had already set in at the last stage. Consequently, the cartilaginous portion is now confined mainly to regions where primary ossifications have met and formed sutures, and to the ethmoid region, where it is still moderately massive.

Its upper and under surfaces are sharply marked off from one another by a plane in which lie the pre-ethmoid region, the parethmoid, and a conspicuous ridge running along the middle of the sphenotic and pterotic bones. The upper surface does not present that strongly crested and grooved appearance so characteristic of Teleosts, but is perfectly even from end to end and from side to side. It thus presents a condition comparable to that of Amia. The temporal fossa is a shallow uncovered depression, and, as in Amia, is the only portion of the dorsal surface upon which trunk muscles encroach. The rest of the roof is covered by a thin skin. A further similarity to the Amioid or Ganoid condition is seen in the fact that the surfaces of all the roofing bones are beautifully sculptured and polished (Pl. 29, fig. 18), the rugæ on any one bone generally radiating from a central point. This sculpturing is a feature by no means universal among Teleosts, and those forms in which it does occur to any appreciable extent are frequently among the lowliest of the group to which they belong; e. g. Erythrinus and Sarcodaces (Sagemehl, **85**, p. 34) among Characinidæ, Araparima among Malacopterygii, and to a lesser degree Sphyræna among higher Teleosts. Nevertheless the condition in such a form as Uranoscopus warns us not to place too much reliance on mere sculpturing.

The intercranial notochord (Pl. 30, fig. 27) has continued to increase somewhat in total length, and by reason of the multiplication of cells its internal structure, especially at its extremity, has become denser even than in the previous stage. In the same region it has become slightly attenuated, but posteriorly its diameter has more than quadrupled (fig. 27). Possibly in association with this increased bulk the internal tissue is much looser and the vacuoles are normal. The funnel-shaped expansion thus made gives to this region of the basioccipital, when viewed from behind, that conically concave appearance so characteristic of it in many Teleosts.

It is thus seen that at no stage in development is there any sign of a reduction or suppression of the intercranial notochord; the real fact of the case being that during the whole period of skeletogenesis the length of the notochord increases only thrice, whilst that of the cranium itself increases approximately twenty times (cp. figs. 59 and 21, *ch.*). The natural outcome of this disproportionate growth is the retirement of the notochord or, more accurately, the advancement of the skeletal elements, so that the pituitary and interparachordal fossæ are carried far away in front of the notochord. A similar apparent retirement has been noted by Parker in Lepidosteus (**81** *b*, p. 458) and in Salmo (**73**, pp. 125, 102). Since he gives no details, however, concerning the condition in the adult, it is impossible to make any comparisons as to the relative rate of growth in these forms.

The suture between the basioccipital and exoccipital (fig. 21, *oc. e.*) differs from that between the other bones of the chondrocranium, in being formed by the interdigitation of bony lamellæ. Between it and the pro-otic there still remains (fig. 21) a small area of exposed cartilage. Medianly it is overlapped by the forked end of the parasphenoid, for the reception of which it has a deep channel formed by a downgrowth of the cartilage and bone on either side (Pl. 30, fig. 36). From the middle of the roof of this channel the basioccipital sends down a crest of bone (figs. 36 and 37) which lies between and under the back processes of the parasphenoid (fig. 36, *ps.*). Within the substance of the fore-part of this crest is a cavity (figs. 36 and 37, *ey. c.*) which opens in front and receives the hinder end of the external rectus muscle; this is the homologue of the anterior conical excavation of the basioccipital of the pike (Huxley, **71**, p. 133) and of many other Teleosts.

The exoccipital is separated from its fellow in the middle line, above by the supra-occipital, and below by the basioccipital (Pl. 29, fig. 24). The facet for articulation with the first neural arch present in so many bony fishes is quite unrepresented. The internal plate, which in the majority of Teleosts (Klein, **84**, p. 131) shuts out part or all of the basioccipital from forming the floor of the cavum cranii, is here not altogether absent, as Klein states (**85**, p. 133), but is represented by a slight ingrowth extending anteriorly over the basioccipital (Pl. 30, fig. 36, *oc. e.*).

The ninth and tenth nerves no longer have a common exit, but the process which commenced in Stage IV (fig. 12) has given rise to two foramina widely separated from one another (fig. 21, IX, X). In Amia, in which these are both present, that for the ninth lies just behind the pro-otic and bears no relation to the exoccipital, that for the tenth between this and the opisthotic (Bridge, **77**, p. 4). By coming to include the vagus foramen it evidently trespasses somewhat on the region of the opisthotic. In the part which immediately surrounds the foramen magnum ossification has continued to extend into surrounding tissue, so that the second occipital nerve (fig. 19, *oc. n.''*) now has a foramen also. In this region in Amia both Bridge (**77**, p. 611) and Sagemehl (**84**, p. 194) recognised the homologues of two, or possibly three, vertebral arches; Gegenbaur (**87**) shows that the elements they refer to are present in some, but not in all Teleosts. If the two occipital nerve foramina in the stickleback are indicative of two originally distinct arches, it seems strange that whilst the first true vertebral arch is preformed in cartilage, these are not. Nor does the development and structure of the basioccipital or its enclosed notochord show any signs that centra have been absorbed. It may be, of course, that this is another case in which during ontogeny features have been suppressed which were present in the ancestors of this fish.

The supra-occipital is an unusually large bone (fig. 24, *oc. s.*). Anteriorly it seems to partially separate the frontals; in reality it extends under them (fig. 20) almost to the level of the outstanding post-orbital processes, and now embraces the larger part of the epiphysial cartilage itself also. It is quite absent in Amia. In the salmon, pike, Alepocephalus, Characinidæ, and Cyprinidæ it falls far short of that of the stickleback in forward and lateral extension. But whilst in Characinidæ and Cyprinidæ, the majority of which have more completely osseous chondrocrania than the stickleback, the parietals are never separated by the supra-occipital; in other physostomes—excluding the siluroids, in which the parietals are either absent or are fused with the supra-occipital—there is every gradation from the primitive Amioid condition, with its parietals side by side, to the condition in which they are widely separated. The former is seen, for example, in Osteoglossum, Araparima, and many Clupeoids; the transitional forms are seen in some Salmonoids, and the latter condition is seen in the rest. In the case of Stenodus, a Salmonoid, the separation or non-separation seems to be merely a matter of age, for in young individuals the parietals are apart, in old ones they are in contact (Boulenger, **95**, p. 299).

Allowing for the existence of the peculiar fenestræ between the frontals and parietals in the Ostariophysi, the constancy of the approximation of the parietals in them, on the one hand; and the inconstancy of the same feature, or the general separation of these bones in the non-ostariophysous fishes, on the other; are but superficial expressions of a fundamental difference between the chondrocranial roofs of these two great groups. In the former, the supra-occipital can never extend far forwards, because in the adult the post-cranial fontanelle is very large (Sagemehl, **85**, p. 41; **91**, p. 512; Pollard, **95**, figures), and the posterior portion of the cranial roof is not extensive. Hence the whole bears a close resemblance to the cranial roof of the young salmon (fig. 61) or stickleback (fig. 3). The approximation of the parietals is therefore a necessity for actual roofing purposes. In the non-ostariophysous Teleosteans, however, the posterior cranial fontanelle, judged by the development of the salmon, stickleback, pike, Engraulis, and by the adult Alepocephalus, always becomes divided by a more or less massive median bridge of cartilage, and either greatly reduced or completely suppressed by the growth of this and of the posterior cranial roof (cp. fig. 4). Thus the supra-occipital ossification has free scope to advance forward or laterally to any extent, and consequently the necessity for the parietals as roofing elements of the cranial cavity diminishes. For the same reason these bones, as compared with the frontals, are generally large in one group and small in the other. These features in themselves are almost important enough to separate the two groups, and while they lend great support to the validity of the group Ostariophysi, they also support Sagemehl's suggestion that these fish might have been derived from a type even lower than Amia (**85**, **91**).

Concerning the origin of the supra-occipital, Sagemehl (**91**, p. 523) sought to show that it was the dorsal ossification belonging to the morphological first vertebral arch. Its position does not, however, support this view, for both in salmon and stickleback it arises, not between the upper ends of the exoccipital, but further forward, between the epiotics. In some cases (e. g. Pleuronectidæ) it may be separated from the foramen magnum not merely by the exoccipital but also by the epiotics (Klein, **84**, p. 131). Whatever its origin, as Sagemehl pointed out (**91**, p. 521), it is the youngest bone in the Teleostean skull, and has arisen wholly within this class.

In the presence of a vertical ridge, and in the relation of this to the exits of the fifth and seventh nerves, the sphenotic region closely resembles that of Alepocephalus.

The pro-otic (*o. pr.*) has now extended to the borders of the interparachordal fossa, and has met its fellow in the middle line for some distance behind that. In the pike, salmon, and Alepocephalus it completely surrounds the exit of the fifth nerve, but here that part which lies in front of this foramen is suppressed, and is functionally replaced by overlapping processes of the sphenotic, frontal, and parasphenoid.

The process of depression of those parts bounding the interparachordal fossa laterally has continued, so that this region now appears to be a mere downward process of the pro-otic (fig. 20, *o. pr.″*), with its cartilaginous extremity mortised into the sides of the parasphenoid (fig. 35, *ps.*, *o. pr.″*). This appearance is enhanced by the fact that posteriorly each process is continued into a ridge running along the under surface of the hinder portion of the pro-otic (fig. 20). These two ridges are continuous with those already described under the basioccipital, and there is a channel thus formed which runs a considerable length of the basis cranii, is closed ventrally by the parasphenoid, and opens anteriorly into the cavum cranii by means of the interparachordal fossa. In the salmon this canal is much more strongly developed, and opens posteriorly. Klein (**84**, p. 135) gives a list of those families with and those without an eye-muscle canal, but he errs in including Gasterosteus among the latter. A study of his lists and of many of the original skulls themselves strongly suggests that the degree of development of this feature is not of fundamental importance, but is largely dependent on the shape of the head—on its depth or its depression.

A similar canal is described by Bridge and Sagemehl, and with greater detail by Allis in Amia. Sagemehl regarded it as a portion of the cavum cranii, which has become roofed over by two horizontal lamellæ from the pro-otic (**84**, p. 207). The same idea is conveyed by him in regard to this feature in Cyprinidæ and Characinidæ, and also by Gegenbaur in Alepocephalus. Each of these authors describes the roof as a bridge formed by lamellæ projecting from the pro-otic. According to Allis, “the eye-muscle canal in Amia and

Lepidosteus, and hence probably in all fishes, is thus an intercranial space opened secondarily to the orbits" (**97**, p. 10). This can apply, however, only to the anterior part of this canal in Teleosts. In Amia this canal is apparently completely closed behind and beneath by cartilage. In Alepocephalus only the anterior region is thus closed, whilst the hinder is, as in the stickleback, closed by the parasphenoid. In larval Amia this canal is not present, but there is a well-marked interparachordal fossa to which the eye muscles bear the same relation as in the stickleback. It is probable, therefore, that in this fish also a process of depression and secondary growth goes on on either side of the fossa and below the pro-otic; but that, whereas in the other types the fossa persists and transmits the eye muscles back again out of the cranial cavity beneath the basis cranii, in Amia it disappears, owing to continued cartilaginous growth. As far back as the so-called pro-otic bridge, these muscles may be said to run in an actual derivative of the cranial cavity; behind that they run in an extra-cranial space secondarily enclosed.

This interparachordal fossa is a common feature among Teleosts. Sagemehl (**85**, p. 66) speaks of it as the space between the pro-otics, and expresses doubt as to the homology of this with the pituitary fenestra of other vertebrates. Development justifies his doubt, by showing that the fossa is related to the parachordals and the fenestra to the hinder ends of the trabeculæ.

Though the Teleostean pro-otic bears the same relations to the seventh nerve and the auditory organs as in the higher vertebrates, those of its other parts which meet in the middle line behind the interparachordal fossa have trespassed upon the area occupied by the reptilian basisphenoid (Howes and Swinnerton, **01**, pl. iv, fig. 6). The interest of this is increased by the fact that among reptiles there are traces of a paired origin for the basisphenoid (ibid., p. 42). When allowance is made for the fact that, owing to the union of the trabeculæ with the anterior end of the parachordals in Teleosts, and with the ventral surface in reptiles, the pituitary fenestra has a relatively different position in the two types, the resemblance becomes more striking. It is, therefore, possible to regard this bone either as a pro-otic which has taken on the functions of a reptilian basisphenoid; or a basisphenoid which, like the exoccipital, has taken on relationships to the auditory organ and a cranial nerve (cp. exoccipital).

In the ethmoid region the general shape of the whole is of considerable importance. Looked at from beneath (fig. 21), after the removal of the nasals (*na.'*), it has the appearance of a rectangle, somewhat expanded anteriorly and posteriorly, with its long axis parallel to that of the skull, and, except for a slight median groove continuous with that formed by the fusion of the trabeculæ behind, it is quite flat. The expanded portions correspond to the pre-ethmoid and parethmoid cornua respectively. The former still serves as the point of attachment for the palatine (fig. 51, *pa.'*; fig. 31, *e. pr.*, *pa.*). From the middle of its dorsal surface arises the mesethmoid in the form of a high longitudinal ridge of cartilage (figs. 32, 42, 51, *em. c.*). Laterally and in front of this the ethmoid retains its original plate-like character (cp. figs. 31, 32, 42, 51, *e.*).

In describing the same region in Alepocephalus, Gegenbaur calls attention to the fact that there it is normally broad, but its anterior portion is drawn out into a terminally expanded rostrum (**78**, p. 4), against which the projecting anterior portion of the palatine bone abuts (p. 11), the whole differing from that of the pike only in length (p. 4). Except for the proportionately greater height of the mesethmoid ridge and its more complete ossification, exactly the same might be said of the ethmoid region of the stickleback (cp. Huxley, **71**, p. 132).

The significance of this becomes more obvious when the corresponding region is examined in the salmon. During the developmental stages it shows a general resemblance to that above described, but does not possess a terminal expansion for the attachment of the palatine (Parker, **73**, pl. v, figs. 3, 4). In the adult, when looked at from beneath, this region (ibid., pl. vii, fig. 2) is triangular; and the nasal septum is very massive, extending not merely to the anterior end, but also to the lateral edges of the ethmoid plate or subnasal lamina (ibid., pl. vii, figs. 5—8).

In the absence of well-marked laminal or lateral remnants of the ethmoid plate; in the forward extension of the massive mesethmoid cartilage to the anterior end; in the removal of the pre-ethmoid cornu (figs. 44, 45, *pa.'*) from the end of the rostrum, the typical Acanthopterygian ethmoid departs from that of Alepocephalus, pike, and stickleback, and approaches that of the salmon. There are, however, some Acanthopterygians (e. g. Mesoprion) whose ethmoid is but a modification of the other type.

Only three primary ossifications are present in this region, viz. the two parethmoids and the mesethmoid.

The mesethmoid is no longer a mere superficial ossification, but it has penetrated in the case of old individuals far into the substance of the cartilage (figs. 20, 42, *e. m.*). Superficially its central area is coated with a thin layer of peculiar cartilaginous tissue (fig. 42), to which I shall return when dealing with the premaxillæ.

In Amia, Bridge (**77**, p. 615) describes two ossifications in the antero-lateral angles of the subnasal lamina, and regards them as the homologues of the "paired endosteal ossifications which are to be found at the distal end of the great pre-nasal rostrum in the pike." He also suggests that they are homologous with the "septo-maxillary bone, described by Mr. Parker as existing in the floor of the nasal capsules in the frog." Sagemehl (**84**, p. 204) agrees with him in homologising this bone with that found in the pike; but though he regards its homology with the septo-maxillary of the frog as doubtful, he does not venture to give it a new name. In his posthumous work on the Cyprinidæ two similarly situated ossifications are described, but here, though they are quite enclosed in cartilage, they are referred to as septo-maxillary bones (**91**, p. 511). Allis (**98**, p. 446, et seq.) has recently summarised all that is known concerning its presence or absence in fishes, and describes it in considerable detail for Amia. Throughout he refers to it as the septo-maxillary. Thus it has come about that to a bone in fishes undoubtedly endosteal, there has been applied a name given by Parker to one whose precise nature in the frog he does not state, but which he classes among the "true dermal bones" in Lacerta (**78**, p. 601). The same bone is present in Sphenodon (Howes and Swinnerton, **01**, p. 56), and is there undoubtedly a true dermal bone.

A somewhat similar state of affairs exists for other bones. In higher vertebrates the squamosal, post-frontal, and prefrontal are purely dermal bones; but the bones in the Teleostean skull to which these names are frequently applied, viz. pterotic, sphenotic, and parethmoid, are cartilage bones with a possible dermal origin. That the original dermal elements in the latter case are the homologues of the dermal elements in the former is still an unsettled question; but even supposing them to be homologous, it has still to be decided whether the ossification in cartilage which has lost all sign of its dermal origin should be regarded as the homologue of the purely dermal ossification.[1] For these reasons the latter terminology has been adopted throughout this memoir.

The particular bone we are now considering should, therefore, have given to it some name which involves no doubtful homologues, but accurately expresses its topographical relations. Following the terminology which is applied to other ossifications of the ethmoid cartilage, I would suggest the name *Pre-ethmoid* for it, as expressive of its relation to the pre-ethmoid cornu.

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[1] In cases where actual genetic relationship has been established between dermal and cartilage bones, e.g. squamosal of Amia and pterotic of Teleosts, such relationship could easily be expressed, and at the same time distinction be maintained, by a more extended use of the prefixes dermo- and chondro—thus, dermo-pterotic, chondro-pterotic,—the former being used for bones which are quite free of the cartilage, and the latter for those which involve cartilage, irrespective of the degree of ossification of this, or of the retention of dermal characters (cp. Bridge, 77).

The pre-ethmoid bone is absent in Gasterosteus.

The fact that it is present in Belone (fig. 50, *e. pr. b.*), on either side of the mesethmoid, suggests that it may be more generally present than is supposed.

The parietals (fig. 18, *par.*) overlap the supra-occipital, the epiotic, the pterotic, and the sphenotic, and are widely separated from one another. Owing to the presence of cartilage beneath it and between these bones (fig. 20) it is completely shut out from taking any part in the roofing of the cranium.

The frontals (fig. 18, *fr.*) roof over the anterior and lateral cranial fontanelles (cp. figs. 4, 5, 18). Immediately in front of the sphenotic each sends down a process which meets an ascending process from the parasphenoid. These two overlap in such a way that the latter predominates externally. A similar relation has been noticed by Klein (**84**, p. 145) in Uranoscopus and Lophius.

The anterior end of each nasal (figs. 10, 19, *na.′*) sends down a process which forms the anterior boundary of the nasal aperture, lies directly on the ethmoid cartilage (fig. 31, *na.′*), and wraps round on to the ventral surface of this behind the pre-ethmoid cornu (fig. 22, *na.′*), and thus gives the appearance, when viewed ventrally, of being an anterior ossification of the ethmoid.

The two lateral wing-like processes of the parasphenoid (fig. 21), by reason of their position in front of the exit of the fifth nerve, cannot be regarded as the homologues of the similar processes in Amia. Between them this bone is pierced by two foramina for the carotid arteries.

The only representative of the sphenoidal region seen during development is the anterior plate-like extension of the auditory capsule, which passes above into the post-orbital process, and below into the bridge between the exits of the trigeminal and facial nerves. The upper part of this ossifies to form the sphenotic (*o. sp.*); the lower, the pro-otic (*o. pr.*); whilst the post-orbital process, which in other Teleosts forms part of the alisphenoid, remains unossified.

Orbitosphenoid, alisphenoid, basisphenoid are absent. Consequently the cranial cavity opens anteriorly into the orbital region by an extremely wide aperture.

The Visceral Skeleton.

Stage I.—The branchial apparatus (Pl. 28, fig. 6) at this stage consists of four pairs of simple rods of cartilage (*br.* 1—4), each widely separated from its fellow. Lying in the ventral space between the members of the first and second pairs is another rod (*br. b.*), the homologue of the similarly situated one in the embryo salmon—the copulare commune of Stöhr (**83**, p. 7). Unlike that, however, it does not extend in between the hyoid arches.

The first pair of branchial arches is the most advanced, the fourth least advanced, and the fifth is as yet quite unrecognisable. Above the roof of the buccal cavity, i. e. where the future pharyngo-branchials will appear, there is no sign of skeletal rudiments.

Thus this portion of the visceral skeleton presents, at this stage, exactly the same condition as it does in the youngest salmon described by Stöhr (**82**, p. 2); and if, for convenience' sake, we may take the development of the latter as a standard of comparison, it has not attained to the same stage as the parachordal tracts.

In the hyoid arch all the parts are represented except the hypohyals and basihyal. The lower part consists of a stout bar of cartilage (*hy.*) representing the future ceratohyal and epihyal, which above is attached by the slender pro-cartilaginous stylohyal to the upper part, and below is separated from its fellow by a mass of undifferentiated tissue.

In the upper part the hyomandibular (*hym.*) and symplectic (*sym.*) regions are not differentiated by an intervening area of pro-cartilage, as in the salmon, but together form a continuous chondrified plate. To the middle of the hinder border of this the stylohyal is attached. This point of connection serves to denote the boundary between the hyomandibular and symplectic, which is not indicated in any other way—not even by any sign of the sharp bend present in the adult (fig. 23, *hym.*, *sym.*). The axis of the plate projects obliquely forwards and downwards from the auditory capsule, but not at so great an angle as in the later stages. Perhaps it is in association with this that the line of attachment to the auditory capsule, instead of being horizontal, is almost vertical, and it is not marked by any change of structure indicative of a future articulation, but hyomandibular and capsule together form a continuous whole (fig. 41, *au. c. hym.*).

In the mandibular arch the quadrate (*qu.*) and Meckel's cartilage (*mk.*) are already marked off by definite signs of chondrification from the dense tissue which lies between them. Anteriorly and posteriorly the quadrate passes imperceptibly into pro-cartilaginous processes. The former, the palatine process (*qu. pa.*), is long and slender, and extends halfway towards the free end of the adjoining trabecula; from its fellow of the other side it is proportionately more widely separated than at any later stage. The latter, the metapterygoid process (*qu. m.*), is stouter, and lies with its lower border close to, and parallel with, the upper border of the symplectic.

Meckel's cartilage, as regards its general shape, is comparable to that of Stöhr's Embryo No. II (**83**, p. 10), but as regards completeness of chondrification it more closely resembles his larva No. IV. In shape it is slender, and meets its fellow in the middle line (figs. 1, 6, *mk.*) without the intervention of pro-cartilage.

Thus the general developmental processes of the first two visceral arches agree closely with those of the salmon, but in the time at which these take place there is a considerable difference. Here, as with the fore-part of the auditory capsule, there has been some influence at work hastening events. Thus, whilst the branchial arches at this stage are comparable with those of Stöhr's youngest embryo, these two arches, by the absence of pro-cartilage between symplectic and hyomandibular, and the elements of the mandible; and by the presence of a well-developed pro-cartilaginous palatine process of the quadrate, exhibit the condition found in a young salmon intermediate between Stöhr's Stages III and IV, of which the latter had been hatched some days. It seems, therefore, that the simple quadrate without palatine process, described by Stöhr (**83**, p. 9) in salmon, and Pollard (**94**, p. 69) in Gobius and Blennius, is either very transitory or entirely omitted in the development of the stickleback. These parts, which have been accelerated in development, serve as a means of support to the mouth and operculum, or as a means of attachment to the associated muscles. This suggests that the acceleration may be due to these features being of greater importance to this fish at an earlier stage than to the salmon. In the stickleback there is practically no alevin stage; it hatches out on the ninth day, and by the end of the eleventh its supply of yolk has been used up, and it has begun to swim about freely and to use its mouth for foraging. It seems as though in this fish those elements develop most rapidly during the embryonic period which are most necessary to meet the immediate exigences of larval life.

Stage II.—The changes which have taken place in the assumption of this stage are greater than any which take place subsequently. All the elements in the adult preformed in cartilage are already represented, and any further development consists mainly in processes of remoulding and ossifying.

In the branchial apparatus all the arches are present, but are still unsegmented (figs. 7 and 14). The first three (*br.* $^{1-3}$) are equally developed, the fourth (*br.* ^{4}) complete but reduced, and the fifth incomplete and still further reduced (*br.* ^{5}). Each complete arch has a flattened, expanded ventral end, whilst its upper end is hook-shaped, and extends into the tissue above the roof of the buccal cavity. Both these features are lacking in the last arch.

The copulare commune (fig. 14, *br. b.* $^{1-3}$), still unsegmented, has extended forwards between the elements of the hyoid arch and back to the level of the third branchial arch. From these relationships it is evidently to be regarded as the representative of the basibranchial elements of the first three arches. Behind it and between the lower ends of the fourth arch, a small cartilaginous fourth basibranchial (*br. b.*^{4}) has appeared.

The first representative of the pharyngo-branchial elements is an oblong plate (*br. p.* $^{3—4}$), but, owing to the absence of any connections, it is impossible to decide definitely to which arch it belongs.

Huxley (**58**, p. 408) described the general appearance and some of the main features of the first two arches of this stage and of the adult, but both his figures and descriptions make it evident that, owing to the methods at his disposal, several interesting and important details escaped his notice. It will therefore be better to give here a detailed description of all the parts, even at the risk of some slight repetition.

The hyoid arch is now quite complete. Medianly there is present a basihyal (*hy. b.*), broader in front than behind, and much stronger than the copulare commune with which, between the hypohyalia, it is connected only by pro-cartilage. This element, therefore, chondrifies quite independently of the copulare, and it thus differs from that of the salmon in its mode of origin, as described by Stöhr (p. 7), who speaks of it as segmenting off from this. My observations, however, agree with those of Pouchet (**78**, p. 57) on Gobius.

The cartilage representing the combined ceratohyal and epihyal (*hy.*) is still simple and bar-like; but, proportionally to the branchial arches, is much more massive than in the previous stage. Below, it fits into the concave outer surface of the corresponding hypohyal (*hy. h.*), which, as in the salmon (Stöhr, **83**, p. 10), arises by differentiation of the pro-cartilage surrounding its ventral ends. At its upper extremity it is connected by a delicate pedicle of cartilage, the stylohyal, with the remainder of the arch. This little element arises as a separate chondrification in the pro-cartilaginous tract described in this region for Stage I.

The hyomandibular and symplectic (*hym.*, *sym.*) are quite continuous, the only indication of boundary between them being, as before, the point of attachment of the stylohyal. Owing to the great elongation of the symplectic, a feature which is still more strikingly seen in Syngnathus (McMurrich, **83**, and Pouchet, **78**) and Siphonostoma (fig. 58, *sym.*), this point is no longer in the middle of the tract of cartilage formed by these two elements. The axis of this tract is now gently curved downwards and forwards from the auditory capsule, and in association with this the line of connection between the hyomandibular and the capsule has become almost horizontal. The hyomandibular as a whole is triangular, with the foramen for the hyomandibular nerve close to its front side.

The mandibular arch as a whole has essentially the same shape as in Stage I, but all its parts are now well defined, and consist of hyaline cartilage.

The quadrate is triangular, with the mandibular articulation at its apex. Resting as it does on the symplectic, it seems to have been carried forward by the elongation of this, so that the articulation now lies under the anterior border of the orbit, and thus shows a striking contrast to the salmon (Parker, **73**, pl. iv, fig. 1) or trout (Winslow, **98**, pl. iv, fig. 28); in the former it lies beneath and in the latter behind the orbit. Consequently in these forms the mouth is half the length of the whole skull, and the symplectic and hyomandibular have preserved the same proportions as in the stickleback at Stage I.

The metapterygoid process, when compared with the same region of the salmon or trout (Text fig. 4, p. 571), is reduced almost to vanishing point. A similar condition occurs in Gobius and Atherina (Pouchet, **78**) and Belone (Text fig. 2). The vanishing point is reached in Syngnathus (McMurrich and Pouchet) and Siphonostoma (Pl. 31, fig. 48), in which this process is represented by the posterior upper corner (*qu. m.*). This position is of course quite secondary, for in the earliest stages the quadrate cartilage lies parallel to the symplectic (McMurrich, **83**, p. 631). A transitional stage between that exhibited by the stickleback and that found in the salmon, trout, and even also in Amia (fig. 61), occurs in such a type as Zoarces (Text fig. 3). These facts seem to point to a process of reduction, going on within the teleostean series as we pass from lowly to more specialised types. In the stickleback the metapterygoid process lies for its whole length on the symplectic, with its extremity inclined somewhat to the inside and situated on a level with the attachment of the stylohyal.

The palatine process (*qu. pa.*) is also attenuated, but in this respect it resembles the condition found in the salmon. In stickleback and pipefish, owing to the forward position of the mouth, this process is very short. Its extremity is now connected with the ethmoid by means of an insignificant tract of pro-cartilage. Though this connection is established, there is no sign of any part of the process having arisen independently, but chondrification has taken place from the quadrate outwards. Stöhr has said of the salmon that "der pterygopalatintheil is demnach ein Auswuchs des Quadratknorpels" (**83**, p. 11). The same is equally true of the stickleback. In Syngnathus, McMurrich (**83**) has described an independent cartilage, which he calls the ethmopalatine, attached to the ethmoid in front and separated by a tract of connective tissue from the "pterygoid process" of the quadrate behind. The same element is present in Siphonostoma at all the later stages I have examined, viz. in individuals varying from 14 mm. to 26 mm. in length, but it is joined to the upper end of the rod-like quadrate by a tract of procartilage which apparently never becomes chondrified.

Particular interest attaches to the relationship of the extremity of the palatine process to the ethmoid. To fully appreciate this it is necessary here to briefly describe this as it is found in the larval Amia and pike of a slightly later stage.

In Amia (Pl. 31, fig. 60), as in the salmon and trout, the extremity of the palatine process is expanded, but it differs in that it gives a long continuous surface of attachment to the ethmoid cartilage (*e.*) from the parethmoid cornu (*e. p. c.*) to the pre-ethmoid cornu (*e. pr.*).

Walther (**83**, pl. 1, figs. 1, 7) gives two figures of the Pike's chondrocranium at two very early stages. In the one the ethmoid is very short, and the expanded extremity of the palatine process bears to it apparently the same relationship as that just described for Amia. In the other, which was older, the ethmoid is of considerable length, and exhibits well-marked pre-ethmoid and parethmoid cornua; with each of these the palatine process is connected, but not with the intervening portion of the ethmoid. The anterior connection is by far the stronger, whilst the hinder is so weak as to suggest that it is secondary. Whether this is so, or whether the two are formed by a breaking into two of the single connection by fenestration, it is impossible to decide; the fact remains that at this early stage two such connections exist.

In the stickleback the attachment is solely to the pre-ethmoid cornu (fig. 7, *e. pr.*). The same is true for Syngnathus and Siphonostoma (fig. 48, *qu. pa.*), for the ethmopalatine (*pa.*) must undoubtedly be regarded as the homologue of the palatine process.

Thus in the development of these four distinct types of fishes there are three different modes of attachment between the palatine process and ethmoid, which by reason of their early appearance in ontogeny seem to exhibit something of a fundamental nature (*v. pp.*).

Meckel's cartilage has now a recognisable coronoid and angular processes, with an articular facet between, and as a whole it is little more than one third the length of the hyomandibulo-symplectic tract. That of the trout (Winslow, **98**) is nearly twice the length of this. The shortness of the palatine process, combined with the equally short mandible, gives to the stickleback its characteristically small gape.

Thus all the peculiarities in the development of the ethmoid, and of the hyoid and mandibular arches, which distinguish Gasterosteus, Syngnathus, and Siphonostoma, from the salmon, trout, and pike, seem to be associated with the production of a small mouth; and the differences between the two types may be summed up by saying that in the latter the symplectic and metapterygoid processes remain short whilst the gape enlarges, and in the former these parts elongate whilst the gape remains small.

Unlike the cranium, the visceral skeleton is not wholly devoid of bones at this stage, for the dentary, maxilla, and operculum, are already present. Of these the last two remain throughout life as purely dermal elements; but the first, though now merely a delicate sheet of bone lying outside of Meckel's cartilage, becomes later on closely related to this.

Stage III.—In the branchial apparatus (Pl. 28, fig. 15) each of the original rod-like arches has now begun to break up into segments. In the first three arches the flattened ventral extremities form the hypobranchials; in the fourth it never becomes separate. The epibranchial of the first ends freely; that of the second articulates partly with the corresponding pharyngo-branchial, and partly with the side of the large element behind. This latter also gives attachment to the third and fourth epibranchials, and may be regarded as the representative of the corresponding pharyngo-branchial. The connection of the second epibranchial to this is probably secondary, and indicative of a tendency to complete reduction of the second pharyngo-branchial with transference of its function to the one behind.

Both representatives of the pharyngo-branchial series are now armed with teeth, and the hinder one has already become partially ossified.

The copulare commune (fig. 15, *br. b.* $^{1-3}$) has extended further backwards, and is now in contact with the basibranchial of the fourth arch (*br. b.* ^{4}), which has undergone no change.

In the hyoid arch, the basihyal, and hypohyal, are practically the same as before; but the combined ceratohyal and epihyal (fig. 8, *hy.*) has lost its bar-like character in the upper half and become converted into a square plate, and thus resembles the same element in Syngnathus (McMurrich, **83**, p. 631).

The symplectic is unchanged, but the hyomandibular (fig. 8, *hym.*) has grown rapidly in such a way as to transform the triangle of the previous stage into a rectangle, whose long axis is parallel to that of the skull, and whose attachment to the ear capsule is now horizontal. At each end of this attachment the cartilage has swollen somewhat to form an articular head, whilst the intervening portion remains unchanged. Thus at this stage the hyomandibular articulation is beginning to depart from that simple elongated type which it exhibited in the earlier stages, and which is retained in the adult state in many Teleosts, e. g. salmon; and to take on that two-headed type of articulation seen in the pike, and so commonly possessed by Acanthopterous fishes. The condition at this stage might with fairness be compared to that described by Gegenbaur for Alepocephalus (**78**, p. 14). There the double-headed type is indicated, but the simple type is not yet quite lost.

Owing to these growth processes, the hyomandibular nerve foramen lies in the centre instead of near the anterior border of the hyomandibular.

The quadrate (fig. 8, *qu.*) has also grown, but is still triangular with the articular head for the mandible, and the palatine, and the metapterygoid processes in the same relative positions as before. The latter process is proportionately smaller, but this is due to growth of quadrate rather than to actual reduction of the process, for its extremity is still opposite the insertion of the stylohyal. In young Gasterosteus spinachia the extremity of the metapterygoid is removed far in front of this point, owing to the continued elongation of symplectic and ethmoid. The mouth and its associated parts are thus carried much further forwards from the eye than in G. aculeatus.

The palatine process retains its uniformity of thickness, and is in direct contact with the pre-ethmoid cornu, whilst still lacking relationship to the parethmoid (*e. p. c.*). These features are much better seen now that the ethmoid region has begun to elongate. Beyond the articulation with the pre-ethmoid cornu the palatine sends a small projection, the future maxillary process, forwards on to the upper end of the maxilla.

A fusion of the quadrate cartilage with the hyoid arch, such as that seen by Pollard (**94**, p. 19) in Blennius and Gobius, is nowhere indicated.

Of the osseous elements belonging to these two arches, all, except the palatine and pterygoid, have appeared in the older larvæ of the stage.

Stage IV.—As with the cranium, so with the visceral skeleton, this stage is distinguished chiefly by the presence of nearly all the osseous elements possessed by the adult, and of most of the cartilaginous ones. Except when otherwise stated, the ossification of a cartilaginous portion must be taken to mean that only the surface is ossified, whilst the cartilage inside remains intact.

In the branchial apparatus (fig. 16) the copulare commune has become ossified in three places, and thus the same number of basibranchials (*br. b.* $^{1-3}$) are recognisable. Apart from this it has undergone no further change except, perhaps, for a slight tendency on the part of the unossified cartilage to be less hyaline than the rest. The first basibranchial (*br. b.* ^{1}) sends obliquely backwards and downwards from its ventral surface a strong osseous process tipped with cartilage for the articulation of the urohyal. The second and third basibranchials (*br. b.* $^{2-3}$) remain simple, and the fourth (*br. b.* ^{4}) is still separate, small, and cartilaginous. Each lies in front of the arch to which it belongs.

The hypobranchials (*br. h.*) of the first three arches and the flattened ventral extremity of the fourth are still wholly cartilaginous. All the cerato-branchials are ossified, and in case of the fifth, except for a small portion at the lower end, all the cartilage has disappeared. Thus, though it was the last to chondrify, it is the first to become completely ossified.

Similarly all the epibranchials (*br. e.*) are ossified; the first is connected by its inner pointed extremity with the anterior end of the second pharyngo-branchial; the second, whilst still remaining fully connected with this, has also taken on a still more intimate relation to the compound pharyngo-branchial behind; the third is slightly changed in shape by the formation of a small cartilaginous process dorsally, but otherwise, with the fourth, it retains all the relationships of the earlier stage. Both pharyngo-branchials (*br. p.*) bear teeth and are completely ossified, though a little cartilage remains at the anterior end.

The basihyal (*hy. b.*) has become osseous for the greater part of its length, its anterior portion alone being wholly cartilaginous. The posterior portion sends down a keel of bone, and abuts behind directly on the first basibranchial.

Each hypohyal (fig. 13, *hy. h.*) has commenced to ossify from two centres, a dorsal and a ventral. The outer surface of the ventral forms a concave facet into which the convex inner end of the ceratohyal (*hy. c.*) fits; that of the other part, on the contrary, is strongly convex, and fits into a corresponding facet in the upper surface of the same bone.

The ceratohyal occupies the whole of the rod-like, and the lower third of the expanded portions of the original hyoid cartilage. Externally the ossification extends into the surrounding tissue, and thus partly encloses the upper hypohyal; internally a similar but more laminar extension (*hy. c.'*) overlaps a considerable part of the epihyal, which is formed from the remainder of the cartilage.

As in the previous stage, the hyomandibular (fig. 13, *hym.*) exhibits the most striking change in shape. This time, however, the change is brought about by the rapid growth of the anterior half of the lower border, whereby the stylohyal (*hy. i.*) and the metapterygoid (*pg. m.*) are carried a considerable distance from the auditory capsule. Pollard (**94**,

p. 19) describes a similar sequence of events in the development of this region in Blennius and Gobius, but is probably inaccurate in speaking of a shifting of the stylohyal attachment; it is not the stylohyal which shifts, but the hyomandibular which elongates. The articular border of the latter has differentiated still more distinctly into two articular heads, which fit into corresponding facets (fig. 12, *hym.″*), the hinder one on the pterotic, the front one between the pro-otic and sphenotic. The intervening portion of the border has thus become practically functionless for suspensory purposes. Both these heads, as well as the opercular process (fig. 13, *hym.′*), remain cartilaginous. Looking at the bone internally (fig. 13) the hyomandibular nerve foramen (*hym. f.*) occupies the same position as it did in the last stage, but externally (fig. 9) at first sight it seems to have disappeared; in reality it has been carried to the ventral edge (*hym. f.*) by overgrowth of bone.

Though the cartilaginous core of the symplectic (figs. 13, 39, *sym.*) has undergone no change either in shape or thickness, its osseous portion has sent out extensive laminæ of bone dorsally and ventrally; consequently if no attention is paid to the condition of the original cartilage an entirely false idea of the true relationships of this bone will be gained. Its distal end is still unossified, and lies almost completely enclosed by the quadrate above, and by a long bony process of the quadrate below.

Under the symplectic, and at the level of the hinder end of the process just mentioned, there is a small oblong cartilage (figs. 39 and 40, *x.*) which is present only in individuals Nos. 22 and 23, and is quite unrepresented as far as I can ascertain in any individual larger or smaller than these. I have been unable to determine its homologies. That it is not a separate portion of the symplectic is proved by its appearing long after this is completely enclosed in bone. Nor can it be regarded as an articular cartilage of any kind, for none of the surrounding bones, all of them more or less rigidly fixed, present anything which can be regarded as an articular surface. Its total disappearance in older individuals also tells strongly against this view.

The ossification of the quadrate, which commenced around the articular head, has now extended over a considerable portion of the main body. From its lower edge, and just behind the articulation, the bone sends out a long process-like extension, triradiate in cross-section, and half the length of the quadrate.

The metapterygoid process (*qu. m.*) still maintains its relationship to the symplectic, and its extremity has become the metapterygoid bone. Owing to the extension of bone far beyond the end of the cartilage the process now seems to end some distance above the level of the stylohyal, as in the salmon; therefore this feature, being secondary, is not important.

The palatine bone (*pa.*), unlike the metapterygoid, is not at the end of the process, but around it, and mainly behind its attachment to the ethmoid. The process (fig. 9) is, relatively, much slenderer than at any previous stage, and its extremity, owing to the continued growth of the maxillary process (figs. 9, 13, *pa. m.*), is expanded. Behind this the cartilage is not merely in contact, but in actual continuity with that of the pre-ethmoid cornu (fig. 30, *e. pr.*). The palatine bone surrounds this point, and extends back almost to the level of the parethmoid. For a short distance, about the middle of its length, this bone has completely replaced the enclosed cartilage (as indicated by the yellow in fig. 9, *pa.*). Thus at this stage the cartilage of the palatine process becomes broken into an anterior portion, having the same relationships as the "ethmo-palatine" of Syngnathus or Siphonostoma (fig. 48, *pa.*); and a hinder portion, widely separated from this and continuous posteriorly with the quadrate cartilage, and therefore homologous with the "pterygoid process" of these forms. It is quite conceivable, therefore, that in these highly specialised forms, the ontogenetic stage, having the "ethmo-palatine" continuous with the "pterygoid process" (as, for example, that shown in Stage III, fig. 8, *qu. pa.*, of the stickleback), has been quite suppresssed, or is merely represented in pro-cartilage. McMurrich compares this "ethmo-palatine" with that cartilage spoken of by Parker as the "pterygo-palatine." Shortly before he wrote his paper, however, Stöhr showed that Parker's description was erroneous, and that the so-called pterygo-palatine, i. e. the whole of the palatine process, was never separate from the quadrate, though its slender connection with that rendered it liable to be torn away. This is just what Parker did. Entering into the development of this region in greater detail, he described a ledge of pro-cartilage near the inner end of the maxilla, not far from the end of the trabecula. This, he says, may chondrify separately, and may fuse with the extremity of the "pterygo-palatine" or palatine process. Thus Parker's separate element does not exist, and even if it did, it would be something entirely different from the inconstant element described by Stöhr. Pollard, working upon the cartilages in the head of Siluroids, describes a separate element which lies upon the upper end of the maxilla in front, and may fuse with the ethmoid behind; this has, therefore, all the essential relations of the maxillary process. He calls it the pre-palatine and says, "This piece is well known (Stöhr and Parker) to arise in Teleostei independently of the cartilaginous upper jaw" (**94**, p. 356). From this it is evident that he misunderstood the description of these two authors. His ability to speak of the pre-palatine as arising independently is wholly due to the course he pursued in making his models, for he represented only those portions which were still cartilaginous, and neglected those which were osseous, even though they might possibly have replaced cartilage developmentally. If the same had been done for the ethmoid and palatine in fig. 9, the palatine bone would, of course, have been omitted, and the real extremity of the palatine process would have appeared as a cartilage, wholly independent of the cartilaginous upper jaw, but continuous with the ethmoid. This, however, would give an absolutely false idea of the parts. Examination of sections through the head of Auchenaspis and Silurus show that his figures give such an idea. The individuals he dealt with were as far advanced in respect to ossification as the stage we are now considering, and accordingly were unreliable for proving the presence or absence of a primarily independent cartilage in this region. If such an element existed, we should naturally expect to find it in such lowly forms as Amia and Lepidosteus; but my observations on the larva of the former, and Parker's on the development of the latter, show that it is not forthcoming. Whatever may be the significance of the small, separate chondrification described by Stöhr, it is certain that, as far as present knowledge goes, no part of the cartilaginous upper jaw of Teleosts is primarily of independent origin, but that at least as far as the connection with the ethmoid it is a direct extension of the quadrate.

Standing out from each side, but quite separate from the anterior end of the dentary, is a small rod of cartilage (figs. 9, 10, 28, 29, *l.*), which lies wholly within the lower labial fold (*l. f.*). Brooks (**83**, p. 179) describes a similar "rod-like body" in the haddock, and homologises it with "the lower labial cartilage in Elasmobranchs." There can be no doubt that it is the same element that is present in Gasterosteus. The cartilage forming it in the latter is not so hyaline as that in the rest of the skull, but histologically it agrees closely with that found in the tentacular skeleton of the Siluroids. Though it lacks a basal plate, its basal portion is more strongly developed (cp. figs. 28, 29, *l.*), and the whole bears a close resemblance in position to the mental tentacle of Silurus, and is probably homologous with that. This rod of cartilage is probably of more frequent occurrence among Teleosts than is usually supposed, for it is present in Perca.

Among the membrane bones, the pterygoids and suborbitals have now appeared, and thus the full total of ossifications present in the adult is made up.

The pterygoid bone (fig. 13, *pg. en.*) as looked at from inside is triradiate; its antero-dorsal ray is proximally tubular, completely enclosing the delicate palatine cartilage, and distally spicular, lying along the inner surface of the palatine; its antero-ventral ray is the smallest, and lies on the anterior edge of the quadrate, thus occupying the position of an ectopterygoid (Parker's pterygoid); its posterior ray, which is the largest, lies along the inner side and upper border of the quadrate, and thus functions as an entopterygoid (Parker's mesopterygoid). Possessing, as it does, all these complicated relationships, there is some difficulty in ascertaining its homologies. The position of its largest portion, in relation to the inside and upper border of the quadrate, strengthens the probability that it represents the entopterygoid.

From these details it will be seen that Huxley (**58**, p. 409) was correct in his delineation and description of the position and origin of the hyomandibular, symplectic, operculum, metapterygoid, and mandibular bones, but that he overlooked the true palatine and mistook the pterygoid for this.

Adult.—There is little to record concerning the branchial apparatus (fig. 22) beyond the appearance of a centre of ossification in each hypobranchial; the more complete ossification of all the parts; the formation on the fourth epibranchial of a small ascending process which at its apex meets the corresponding one on the third (*br. e.*^{3}); and the shifting of the insertion of the hypobranchials belonging to the third and fourth arches from the sutures between the basibranchials on to these themselves.

Cope (**70**) observed that the pharyngo-branchials were small in accordance with the general tendency of the whole apparatus to become weak; he also pointed out (p. 457) that they bear a close resemblance to those of Belone. The first, present in so many Acanthopterygii as a styloid bone, frequently called the suspensory pharyngeal, is quite absent in both these fish.

At Stage IV. the ceratohyal was equal in size to the epihyal (*hy. e.*), but now, owing to a considerable increase in length, it seems to bear the latter like an epiphysis at its upper end.

The hyomandibular and symplectic are widely separated from one another by a broad area of cartilage. As a whole, the former presents a striking contrast to the simple hyomandibular of the salmon, and seems to be made up of four radii connected by more or less extensive laminæ of bone. The two uppermost end in cartilaginous articular heads (*hym.″*) which fit into facets described above. The edge of the lamina between them takes no part in the articulation, so that during the development of this region there is a complete transition from the long simple articulation present in the adult salmon to the double articulation with two rounded heads. The pike has the double-headed articulation; the heads, however, are not rounded. In Belone this articulation is intermediate between that of the salmon and the pike. The anterior lower radius now passes obliquely forward, as in pike and Belone.

The hyomandibular nerve has the same course as in the previous stage. In the cod it passes in front of the main radius, and thus seems to suggest that even within the Teleostei this nerve does not bear a constant relationship to the hyomandibular—a conclusion to which Pollard (**94**, p. 24) was led by a comparison of its position in Ganoids.

The symplectic (*sym.*) is still nearly twice the length of the hyomandibular—itself a long bone,—and thus presents a striking contrast to this in other forms, for both in pike and Alepocephalus it is shorter than the hyomandibular, and in the salmon it is but an insignificant appendage of this. Belone offers an intermediate condition, for in it the bones are of equal length. In the stickleback its extremity remains cartilaginous, and is almost completely enclosed by the quadrate and its laminar outgrowth.

The metapterygoid is unaltered except for the fact that in surface view the original shape and extent of the cartilage, now largely ossified, is disguised by the great laminar extensions of bone dorsally and ventrally. Nevertheless, the reduced condition of that cartilage is more than indicated by its width at the point where it enters the ossification. In the majority of Teleosts the metapterygoid abuts directly on the quadrate, but here it is separated by a wide space, partly occupied by the pterygoid bone, and this is, no doubt, largely due to the forward shifting of the quadrate. In Belone the two bones (fig. 49, *qu.* and *p.g.m.*) lie one against another; and, as the suture between them is cartilaginous, it gives an indication of the original weakness of the metapterygoid cartilage—an indication all the more trustworthy because the laminar outgrowth of this bone is suturally connected with the pterygoid and not with the quadrate, which has no such extension dorsally. These relations seem to be the prevalent ones, so that the length of the suture between the metapterygoid and quadrate may generally be taken as indicative of the extent of the original cartilage. If so, then in pike (fig. 43), Zanclus (fig. 52), Balistes (fig. 53), and other Plectognathi, the Acronuridæ, Cyprinodontidæ, and the great majority of Acanthopterygii, the cartilage was strongly developed; as opposed to its marked reduction in Belone and Gasterosteus, and its complete suppression in Syngnathus and Siphonostoma. In the adult of the last two forms, as well as of Fistularia, all the bones of this region, including the quadrate, have sent out extensive laminæ to form the side walls of the tubular snout, so that only the study of ontogeny can show the true distribution of the original cartilages.

The palatine bone (*pa.*), as already described, appears as an ossification of the palatine cartilage around and behind its connection with the ethmoid. As in Siluroids (Pollard, **94**, p. 355), the continuity between these two cartilages becomes lost with advancing ossification; but the bone still articulates with the pre-ethmoid cornu. The outer surface of its anterior half appears in a lateral view of the head skeleton (fig. 17, *pa.*) as a sculptured bone lying between the nasal and the first bone of the suborbital series (*so.*^{1}), and bears such a close resemblance to the pre-orbital bone (antorbital, Sagemehl) of Amia that one would be almost forced to acknowledge its homology with that if one did not already know that Amia possessed a palatine bone. The resemblance is all the more striking, because of the presence of several sensory papillæ (fig. 31) on the skin which overlies it.

The cartilage which the pterygoid enclosed has disappeared, not because of the encroachments of ossification, as in the parethmoid (fig. 32, *e. p. b.*), but because of actual reduction, as in the case of the supra-orbital band and the hinder portion of the trabeculæ.

The relation of the palatine and pterygoid bones and adjoining cartilages to the ethmoid region in Teleosts is of great importance, and a closer study of it will be found extremely useful in the attempt to ascertain the inter-relationships of these fishes.

For this purpose no fish presents so instructive a condition and so convenient a starting-point as the pike (fig. 43). In it the palatine is a long and massive bone, formed, as in the stickleback, by ossification of the distal portion of the palatine process. At its extremity it bifurcates slightly, and partially encloses the pre-ethmoid cornu with its ossification. Behind this bifurcation, and on the outer side, it presents a rough facet, with projecting upper border (*pa. m.*) for the insertion of the inner end of the maxilla. The whole of its ventro-internal surface is armed with numerous powerful teeth. For a short distance behind this the original cartilage persists, enclosed by the ectopterygoid externally and the entopterygoid internally. Opposite the parethmoid cornu this cartilage enlarges considerably, and offers a well-developed concave surface for articulation with, or more accurately, for sliding on, the rounded ventral surface (*pa.″*) of the cornu. Thus in the adult, as in the larva, there are two points for attachment of the palatine process to the ethmoid, a pre-palatine and a post-palatine.

In SCOMBER (fig. 44) the same condition exists, but the parts are more specialised. As in the pike, the palatine bone (*pa.*) is massive and dentigerous, but here the anterior extremity of the bone is prolonged into a well-developed, curved maxillary process (*pa. m.*). Internally to the base of this is a facet, which fits on to and forms a typical articulation with the pre-ethmoid cornu (*pa.'*). The latter, owing to the formation of a rostrum, such as was described for the young salmon, is situated some distance behind the extremity of the ethmoid, and, because of the almost complete ossification of this, is bounded by the vomer below and nearly surrounded by the mesethmoid above. Behind the palatine bone the cartilage (*qu. pa.*) persists, and, as in the pike, it offers a well-formed concave surface, which slides with a lateral motion on the rounded, cartilaginous ventral surface of the parethmoid.

In Pagellus centrodontus (fig. 45) another modification of the same type exists. Here, as before, the palatine (*pa.*) is massive and dentigerous, but its maxillary process (*pa. m.*) is much longer, more curved, more powerful. Bearing the same relation to this as in Scomber is a facet for the pre-palatine articulation. Here again, owing to the formation of a rostrum even stronger than that of the Scomber, the pre-ethmoid cornua are situated far back behind the end of the ethmoid (*e.*), and lie mainly on the anterior portion of the parethmoid bone, close to the suture between it and the vomer. In this example, however, probably owing to the shortness of the ethmoid, the post-palatine sliding surface is formed not by cartilage, but by the hinder end of the palatine bone.

As already pointed out, the larval salmon has both pre- and post-palatine articulations. They are also present in the adult Salmo trutta, but owing to the ethmoid being wholly cartilaginous, the facets are not so conspicuous as in Scomber and Pagellus. The pre-ethmoid cornu is much smaller, and not so distinct as the other, but it nevertheless exists, and was evidently seen, though not noticed by Parker, for he represents it in his figure of the ventral surface (pl. 7, fig. 2) of Salmo salar at the posterior end of the "curved ridge." Thus the palato-ethmoid region in the salmon, on the whole, conforms to that of the pike, and differs mainly in the fact that elongation of the ethmoid takes place in the latter between the cornua, and in the former in front of the pre-ethmoid. If this region in the salmon were more completely ossified there would be little to distinguish it from that of Pagellus.

The condition in the Cyprinodonts is a little difficult to make out, but is well seen in Characodon luitpoldi. By careful examination of this, and by serial sections of this region in a specimen of Haplochilus fasciatus, which Mr. G. A. Boulenger kindly placed at my disposal, I am satisfied that the condition in them differs from that in the pike only in the shortness of the ethmoid, the more complete ossification of parts, and in the absence of teeth on the palatine.

The Acanthopterygii, with one or two notable exceptions, conform to one or other of the conditions just described, or are modifications of these. For example, in Pagellus erythrinus the ethmoid is perfectly ossified, the parethmoid cornu has practically disappeared, and the pre-ethmoid is greatly reduced; nevertheless the shape of the palatine and its maxillary process, and the form of the ethmoid with its well-marked rostrum, leave no doubt that it belongs to the same type as that shown by its kindred species (fig. 45). Again, in Odax Richardsoni the post-palatine articulation appears to be formed by the pterygoid bones.

It is no uncommon thing for the palatine to be strongly attached to the vomer by ligament, and even to present a flattened surface to that bone, e. g. Sciæna, but this is not a feature of primary importance, nor does it affect the presence of the other articulations.

These facts prove that in Salmonidæ, Esocidæ, Cyprinodontidæ, and Acanthopterygii (with exceptions to be dealt with), one type of palato-ethmoidal relation exists, viz. one in which the palatine process or its derivatives are attached to the ethmoid at two points, the pre-ethmoid cornu and parethmoid cornu, by two facets, the pre-palatine and post-palatine.

In the stickleback, during development, a post-palatine attachment is always absent, a pre-palatine always present (figs. 8, 9, *e. pr.*). The palatine bone itself is small, edentulous, and possesses an insignificant maxillary process. The ethmoid region is of the same type as that of the pike in the absence of a well-marked rostrum; hence the pre-palatine articulation (fig. 51, *pa.'*) is situated at its anterior extremity, and, as in the pike, the facet is not specialised.

Both in the young (Text fig. 2) and adult Belone (fig. 49) precisely the same conditions prevail; indeed, in one small individual the palatine and pre-ethmoid cartilages were even fused together. The region of this is indicated by the dotted line in fig. 49 (*pa.'*). The palatine (*pa.*) bone is simple in shape, lacks a maxillary process, and is edentulous; posteriorly it sends a lamina of bone along the outer side of the palatine cartilage (*qu. pa.*) to meet a similar process from the quadrate (*qu.*). Thus the ectopterygoid is functionally replaced and is absent. The cartilage itself, which never breaks down though exposed dorsally, does not enlarge at any point to form a post-palatine articulation. The ethmoid is predominantly cartilaginous, and in the absence of a well-developed rostrum is of the same type as that of the pike, but is much shorter.

The condition in Exocoetus is identical.

While the almost wholly cartilaginous condition in the Belone is the retention of a primitive condition, the greatly ossified palato-ethmoid region of Syngnathus is at the opposite extreme of specialisation (fig. 50). The palatine bone (*pa.*) has the same characters as in the stickleback, and like that is partially enclosed posteriorly by the single pterygoid (*c.*) (McMurrich, **83**). The ethmoid region when compared with that of young Siphonostoma (fig. 48, *e.*) is seen to owe its great length to elongation, not of the hinder half, containing the mesethmoid cartilage, but to that of the front half, consisting purely of ethmoid plate. Nevertheless the mesethmoid bone (fig. 50, *e. m.*) has apparently extended quite to the anterior end (McMurrich, **83**), including the pre-ethmoid cornu. The palatine bone (*pa.*) which is attached to the pre-ethmoid cornu (*pa.'*) between the mesethmoid bone and vomer is carried too far forward for it to bear any relationship to the parethmoid bone (*e. p. b.*).

Fistularia differs from Syngnathus only in the fact that though the palatine is small it possesses a moderately developed process and is beset with teeth, thereby showing that the absence of these features in all the other forms possessing this type of palato-ethmoidal relationship is by no means an essential accompaniment of it.

Among Acanthopterygii the Zanclidæ and Acronuridæ, whose position is by no means a settled question, are characterised by the possession of this type of palato-ethmoid relation.

In Zanclus cornutus (fig. 52) the small palatine (*pa.*) has an insignificant maxillary process behind, which is the facet for the pre-palatine articulation. The ethmoid region is of the type usually associated with the possession of this single articulation, and its shape as a whole calls to mind that of young Siphonostoma (fig. 48) and is still largely cartilaginous anteriorly.

The Acanthurus ceruleus (one of the Acronuridæ) presents a condition so closely similar to that of Balistes maculatus (fig. 53) that a description of the latter—a Plectognath—will do service for both. Its palatine has the same relations as that of Zanclus. The ethmoid region is not so long, but is much more massive. In my specimen the pre-ethmoid cornu, with its well-defined articular surface (*pa.'*), is still cartilaginous, and is bounded beneath by the vomer and above by the mesethmoid bone. There is no trace either of rostrum or of post-palatine articulation. Klein, when describing the ethmoid region of Acanthurus (Teuthis; **84**, pp. 187, 219) and Balistina (ibid., pp. 190, 237), called attention to the close resemblance between them.

Thus all the Scomberesocidæ, Hemibranchii, Lophobranchii, Plectognathi, and among Acanthopterygii, the Zanclidæ and Acronuridæ, are characterised by the possession of only one palato-ethmoidal connection, viz. the pre-palatine, and of an ethmoid region with its pre-ethmoid cornua carried at the extremity.

The majority of these forms are characterised by the great elongation of the ethmoid region and by the shortness of the mandible, thus suggesting a possibility that the post-palatine connection may have been lost through the coincidence of these two features; but a comparison of figs. 43—53 (each of which has been drawn so that the whole skull would be the same length as that indicated in fig. 43, from the tip of the ethmoid to the arrow marked *) shows that this is not the case, for both Belone (fig. 49) and Gasterosteus (fig. 51) have a short ethmoid as compared with that of the pike and Scomber; and the former at the same time possesses a long mandible. If a long ethmoid were a condition necessary to the absence of post-palatine articulation, then it should be absent in the pike. Again, if a long gape and short ethmoid were the essential accompaniments of a double attachment, the Belone should have this. But as the pike possesses a well-formed post-palatine attachment, and the Belone does not, it becomes clear that the two types are wholly independent of either length of ethmoid or size of gape.

When, in connection with these facts, we consider that both the single and double types are quite distinct throughout development, that notwithstanding all the changes of form which the head undergoes among Acanthopterygii, from the short-snouted Bovicthys to the long-snouted Scomber, from the deepened Drepane to the flattened Platycephalus, the double articulation is retained, we cannot refrain from concluding that the distinction we make between the two types is not a superficial one, and that the single articulation is due, not to the existence of a long-snouted Lophobranch or Plectognath, but that these owe their origin to the existence of this type. Whether this conclusion is right or wrong, future work alone will decide; meanwhile, the fact remains that two such types exist, and consequently the necessity arises in descriptive work for distinguishing between them concisely. Accordingly, all forms possessing both pre- and post-palatine articulations, irrespective of the possession or non-possession of a rostrum, may be described as Disartete; and all possessed only of the pre-palatine articulation, and of an ethmoid whose pre-ethmoid cornua are situated on each side of its anterior extremity, may be described as Acartete.

In the light of these facts, considerable interest attaches to the condition found in Amia, which has been carefully described by Allis. Speaking of the septo-maxillary (my pre-ethmoid), he says, "The ventral surface of the lateral edge of the bone forms the anterior end of a low, longitudinal, condylar eminence, which extends backwards along the ventral surface of the lateral edge of the ant-orbital process of the chondrocranium, and gives articulation to the palato-quadrate arch" (98, p. 447). Here, then, is a type of articulation which seems to combine the characters of the disartete and the acrartete conditions, and yet differs from these in the fact that the attachment of the palatal to the ethmoidal region is neither broken into two, nor confined to the pre-ethmoid. For the description of this type, the term Panartete seems most suitable. From these considerations, and from the developmental facts given above, it is evident that this is a type of articulation which very probably gave rise to the disartete condition, and may possibly have done the same for the acrartete. The settlement of this question rests with a closer study of the Malacopterygii and Lepidosteus: in the former, according to Gegenbaur's descriptions and figures of Alepocephalus, we may expect to find the panartete condition passing into the disartete; and in the latter, according to Parker, a condition exists which bears the same relations to the acrartete as does that of the salmon to the disartete, for it possesses a rostrum. It is quite conceivable that all these types of articulation were exhibited also by the immediate Ganoid ancestors of the Teleosts.

In the lower jaw of the adult stickleback the labial cartilage (*l.*) is still present.

The premaxilla alone bounds the gape above. At the previous stage the upper ends of the ascending portions ended in a mass of densely nucleated tissue, which lay chiefly on their under side. This mass has now become chondrified (Pl. 30, fig. 42, *pmx.'*), and passes into the bony tissue almost without boundary line. This chondrified tissue closely resembles that of the labial cartilage. In the earlier stages of development of Siphonostoma the reduced premaxillary processes end in similar tissue, which, however, in the latter stages, forms a separate cartilage homologous with Sagemehl's rostrale (**85**, p. 100). It seems highly probable, therefore, that the cartilage we are considering in the stickleback also has the same homologies. Whether the same is true of the similar layer on the mesethmoid bone is an open question. Whatever their morphological significance may be, functionally these cartilages serve as a means for allowing the premaxillæ to slide on the ethmoid.

IV. General Considerations.

Looking back over the past thirty years of investigation into Teleostean phylogeny, one of the many features which calls for attention is the gradual shifting of the centre of interest from the Elasmobranchs to the Marsipobranchs. At the beginning of this period Haeckel was so impressed by the many peculiarities of the latter group that he created for its reception a division, the Monorrhina, equal in value to another, the Amphirrhina, containing all the other craniata (**70**, p. 507). Representing his views of the inter-relationships of the latter in a diagram, he placed the Selachii at the point of origin of the rest (p. 513). In these views he was followed by Gegenbaur (**72**), who, whilst he acknowledged the existence of several special features in the Selachii, considered that on the whole the organisation of the ancestral form of other fishes must have been similar to that presented by them (p. 22). Referring especially to the cranium, he gave expression to the opinion that the primordial cranium of higher vertebrates was but a transitory reproduction of the cartilaginous shark's skull, and that it was impossible for the latter to be derived from an originally bony condition.

The natural outcome of all this could only be an attempt to harmonise the conditions exhibited by the Teleosts and the closely allied Ganoids with those found in Selachii. Thus Sagemehl (**84**), in dealing with the cranium of Amia, explains the absence of a cartilaginous wall between the auditory capsule and cavum cranii by assuming a tendency for fenestration to proceed from the peripheries of nerve foramina (p. 207), and considers that many of the parts point to a type most nearly approached by the Notidanidæ (p. 227).

Meanwhile, Huxley (**76**), by a comparative study of the heads of Petromyzon and tadpole, was led to conclude that there was "no sufficient foundation in the present state of knowledge for regarding the Marsipobranch skull as one which departs in any important respect from the general vertebrate type" (p. 427).

Since then various workers, especially during the last decade, have brought forward much further evidence to show that the same may be said of the other organs, and that living Selachii are more specialised than Gegenbaur supposed. Foremost among these was Beard (**90**), who, basing his remarks chiefly on the structure of the brain, pronephros, lung, and swim-bladder, proposed to place the Marsipobranchs, Ganoids, and Teleosts in a group separate from and equal to one containing the Selachii, Dipnoi, and Amphibia. Allowing for a transference of the Dipnoi from the latter, Howes (**91**) was led to a similar conclusion by a study of the urinogenital organs. Klautsch's work on the development of the vertebral column resulted in an entire agreement with Beard. The most recent contributions to this subject are those of Hatta (**00**) and Goette (**01**). The former, dealing with the development of the pronephros of Petromyzon, says, "The whole system of the pronephros of Cyclostomata, Teleostei, and Amphibia is not perfectly homologous with the Selachian pronephric system" (p. 407). The latter, working at the development of the gills and branchial vessels in fishes, finds that the gills in Cyclostomes (Enterobranchies) are not the homologues of those in Teleostomes and Selachii (Dermatobranchies), but represent a very old type ; and that as regards the origin of their afferent and efferent branchial vessels the Teleostomes and Selachii exhibit two divergent lines of modification.

Thus it appears that whatever may be thought concerning Amphibia and the Dipnoi, there is a general consensus of opinion that the Teleosts and Ganoids are not so closely allied to Selachii as was once thought to be the case. In order to ascertain how far this is supported by the head skeleton, I propose now to briefly review what is known of this part in the development and the adult of Teleostomes under the following headings:—The relation of the trabeculæ to the parachordals; the primordial cranium; the relation of the visceral skeleton to the cranium.

The Relation of the Trabeculæ to the Parachordals.

In writing two interesting and instructive memoirs on the development of the skull, Sewertzoff (**97** and **99**) has brought together many scattered facts relating to this in the various great classes of vertebrates, and has sought to reduce them to some kind of order. Thus, for example, in dealing with the position of the trabeculæ, he has introduced the term "horizontal" to describe their position when their hinder ends fuse or arise in continuity with the extremity of the parachordals; and "vertical," when fusion takes place with their ventral surface and some distance behind their anterior ends (**99**, p. 316). He also distinguishes two types of skull: (1) that in which the trabeculæ arise separately from the parachordals; (2) that in which the trabeculæ arise in continuity with a plate which is or becomes the anterior part of the parachordals. The fact that in the stickleback these two types appear to be mere matters of individual variation suggests that this distinction is not an important one. Again, he tried to show that these two positions—"horizontal" and "vertical"—were intimately associated with the time of appearance of the mesocephalic flexure, of the medullary flexure, and of the trabeculæ.

In the stickleback, as in Selachii, the time of appearance for the trabeculæ coincides with that of the greatest flexure. Though the development of these parts takes place under conditions which correspond to absence of cranial flexure, yet in other Teleosts, e. g. Gobius, which have a capacious egg, and consequently flexed head during development, the horizontal position is assumed.

The study of the stickleback's head (cp. fig. 57) shows that flexure here is not so much at one point as at all points; that the anterior ends of the parachordals as well as the closely associated trabeculæ are involved in this curvature; and that the flexure here is much less than in the Selachian, where the fore-brain lies practically under the hind brain, and apparently does not involve the parachordals. These facts lead to the inference that the position of the trabeculæ in Ichthyopsida is related mainly to the degree of mesocephalic flexure and to the part which the parachordals take in it. That is, so long as it is small—through not more than 90°,—there is nothing to prevent the trabeculæ from uniting with the ends of the parachordals; but immediately it oversteps that, and the fore-brain begins to pass backwards under the hind brain and parachordals, there will be a tendency to carry the "anlage" of the trabeculæ backwards also, and consequently the upper ends of these will either have to take a sharp bend forwards to unite with the extremities of the parachordals, or have to fuse with their ventral surfaces.

It was long ago pointed out by Balfour that "the cranial flexure is least marked in Cyclostomata, Teleostei, Ganoidei, and Amphibia, while it is very pronounced in Elasmobranchii, Reptilia, Aves, and Mammalia" (**81**, p. 347). Consequently, if the views just expressed contain any truth, the former should exhibit the horizontal, and the latter the vertical position for the trabeculæ.

In his earlier paper Sewertzoff (**97**) recognised that in those cases in which the mesocephalic flexure of the brain is least marked the trabeculæ are approximately horizontal, and where it is greatly marked they are vertical; but he does not collate these cases. He points out (**99**) that in both Petromyzon and Acipenser the former position exists. From this and from Parker's figures and descriptions of Lepidosteus; from those of Stöhr on Siredon and Triton (**81**, p. 85), Rana (**82**, p. 85), and the salmon (**83**); those of Pouchet on Labrus, Gobius, Atherina, Syngnathus (**78**); those of Miss Platt on Necturus (**96**, p. 455); and from my own on Gasterosteus, it becomes evident that the horizontal position is exhibited by precisely those groups which, according to Balfour, have only a weak cranial flexure.

Amongst those fishes whose development has been fully worked out only the Elasmobranchs, viz. Acanthias (Sewertzoff, **99**, p. 285), Prestiurus (p. 300), Raia and torpedo (ibid., **97**, p. 417), exhibit the vertical position for the trabeculæ. The presence of a post-clinoid wall may be taken as a strong indication of the former existence of the same type in many of the other Elasmobranchs.

This may apply, but with diminished force, to the Chimæroids and Dipnoi.

There can be little doubt that the horizontal condition is the more primitive one, and that the vertical is secondary, due to a strong cranial flexure, which in its turn is explained by Balfour, probably correctly, "as being associated with an embryonic as opposed to a larval development;" and with some advantage to be "gained by a relatively early development of the brain" (**81**, p. 267).

In this respect, therefore, the Cyclostomata, Ganoidei, Teleostei, and Amphibia have retained a more primitive condition than the Selachii, and if their ancestral stock was in any way related to these, it must have been to some form whose fœtal life was not yet sufficiently lengthened out to permit the development of a strongly-marked flexure, and the associated ventral position of the trabeculæ.

The similarity in the condition of the brain and the trabeculæ in Amniota to that in Selachii must be regarded as due rather to convergence than to genetic affinity.

The Primordial Cranium.

As already mentioned, Gegenbaur's work on the cranium of Selachii led him to regard the chondrocranium of all the higher Vertebrata as derived from a similar type ; a conclusion to which he was guided mainly by a consideration of the cartilaginous condition in the former as opposed to the osseous condition in the latter. No doubt he was right as far as the mere substance of which the cranium was composed was concerned, but apparently it did not occur to him to inquire whether the chondrocranium of a higher vertebrate with its numerous fontanelles did in reality arise from a simple box-like Selachian cranium. Nevertheless, since he published his unique memoir, workers upon the piscine skull have largely assumed that such was the case; that the fontanelles of the one have arisen by fenestration of the other. Thus, beyond what has already been mentioned, Sagemehl in dealing with the Characinidæ, which have anterior and posterior fontanelles in the roof of the chondrocranium, regarded the former as the homologue of the Selachian "Præfontallücke," but the latter as an entirely new formation. More recently Pollard looked upon a small cartilage in the large supra-cranial fontanelle of Polypterus as the last remnant of an originally complete cartilaginous roof, and started a comparison of its cranium with that of Notidanus, with the "obvious postulate" that "the supra-cranial fontanelle be considered to have a complete cartilaginous tegmen cranii of which only the remains are now known" (**92**, p. 402).

Gegenbaur, comparing Alepocephalus with Salmo and Esox, concluded that mass of cartilage was no criterion of a lowly position, but the form and ossification of the same, and says : "Aus diesem Allen geht hervor, dass das reiche Maass von Knorpel in phylogenetischer Beziehung nicht verwerthet werden kann. Es wird nur auf die ontogenetische Anlage bezogen werden können,[1] und wird dann als eine Weiterentwickelung dieser Anlage gelten dürfen" (**78**, p. 27). Again, Huxley, as early as 1858, says : "There are discrepancies in the structure of the skull itself, which would forbid too close an approximation between the bony and the

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[1] The italics are not mine.

unossified crania if their adult forms alone were examined The study of the development of the ossified vertebrate skull, however, eliminates the difficulty, and satisfactorily proves that the adult crania of the lower Vertebrata are but special developments of conditions through which the embryonic crania of the highest members of the sub-kingdom pass" (p. 420).

Given a brain requiring protection, it is quite as reasonable to suppose that specialisation for this purpose would, in one case, show itself by an increase of cartilage, as in another by the accession of bone; and that the presence of bone would tend to preserve features belonging to the primitive cartilaginous cranium, which otherwise would be obliterated by excessive growth processes. But suppositions and assumptions must not displace facts.

Comparing the adult cranium of Amia with that of Heptanchus, it is seen that in the latter, except for nerve foramina, the ear cavity is completely shut off from the cavum cranii; and that the only fontanelle present is the "Præfontallücke," which lies at the anterior end of the roof, and, according to Sagemehl, in front of the epiphysis. In the former the cranial roof is massively cartilaginous, continuous, and unfenestrated; in the orbital region there is a "considerable vacuity" closed by membrane, and regarded by Sagemehl as a much enlarged optic fenestra (**84**, p. 202); and in the auditory region there is a gap, between the cavum cranii and the ear-capsule, which owes its existence, according to the same authority, to the enlargement of the labyrinth; and, finally, the floor is occupied largely by a well-developed pituitary fontanelle. Thus it becomes evident that, notwithstanding the presence of a bony covering, the one fontanelle present in the Selachian skull is absent in Amia; and those fontanelles which are present in this are represented, at the most, only by small nerve foramina in that.

In the advanced Amia larva (19 mm. long), as in the young salmon (fig. 62) and Lepidosteus (Parker, **81**), a large fontanelle certainly is present in the roof, but it cannot be homologised with the "Præfontallücke," for it lies entirely behind the epiphysis and between the sphenoidal and auditory regions. Again, it is not continuous cartilage which makes up the floor and the side walls, but fontanelles proportionately larger than those in the adult. In Lepidosteus and Salmo at least there is no sign at any later stage of a breaking down of walls to form fenestræ, but the mass of the chondrocranium goes on increasing into old age, and consequently, fontanelles may be reduced or even obliterated.

There is, in this connection, one feature about the development of the stickleback to which particular attention may be paid, viz. the fact that in it we have repeated ontogenetically a breaking down of pre-existing cartilaginous palatine process, suborbital bands, and trabeculæ, such as might have taken place phylogenetically. Consequently it is reasonable to expect that, if a fenestrating process ever did take place, such lowly forms as Lepidosteus and Salmo should show some developmental indications of it.

At still earlier stages Gasterosteus, Atherina, Engraulis, and Salmo also possess an anterior fontanelle homologous with the "Præfontallücke," and separated from the posterior one by the epiphysial cartilage.

Thus the whole course of development points to an ancestor whose cranium had two dorsal fontanelles separated by a band of cartilage usually related to the epiphysis; also lateral fontanelles for transmission of optic, trigeminal, facial, and auditory nerves; and a pituitary fontanelle.

Further evidence from independent sources is to be sought for in the Ostariophysi, in Polypterus, and the cartilaginous Ganoids.

The first constitute a branch of the bony fish series probably separate from that to which the forms we have so far considered belong, and they exhibit all those features just mentioned as probably characteristic of the ancestor. Sagemehl thought that the epiphysial bar had remained in order to serve as a support for the blood-vessels passing to the brain; but it could be said with equal plausibility that this was the cause of its first appearance.

In Polypterus Traquair describes a large supra-cranial fontanelle (**71**, p. 167) bounded laterally by the upper edges of the sphenoid. Pollard (**92**, p. 400) confirms him, but further remarks on the presence of a small sheet of cartilage in the middle of the fontanelle, which he says "may be regarded as indicating the former existence of a complete cartilaginous tegmen cranii;" and in a later paper (**95**, p. 414) he speaks of it as the homologue of the epiphysial cartilage, and of the space in front as homologous with Gegenbaur's "Præfontallücke." The true supra-cranial fontanelle, however, is the whole region enclosed by the supra-orbital band, and is much larger than the one described by Traquair under that name. The so-called sphenoid has not the same place relations as the alisphenoid and orbito-sphenoid, for in Teleosts these bones are continuous above with the supra-orbital band; in Polypterus, however, its upper border lies some distance inside of, and is separated by a wide space from this. Strictly speaking, therefore, the region between the trabeculæ and the supra-orbital band is unoccupied either by cartilage or bone, and in any case the existence of a wide space between it and the sphenoid betokens the existence of a large, morphologically lateral, fontanelle. The auditory capsule has no internal wall, and the cranial floor possesses an exceptionally well-developed pituitary fontanelle.

Among cartilaginous Ganoids the cranium of the adult sturgeon is so specialised in respect to the growth of cartilage that it is natural neither to expect nor to find any fontanelles. Nevertheless these do exist during development. The most instructive stage in this connection is that described by Parker (**82**) as Stage III. In this the cranium possesses a large fontanelle in the roof from end to end. The supra-orbital bands project towards each other in the region lying in front of the mid-brain, and thus indicate an epiphysial bar. In the side walls the "optic foramen is a fenestra" (**158**), and there seems to be a separate fenestra for the exit of the fifth nerve also. The pituitary fontanelle, though small, is present, and the auditory capsule lacks a cranial wall.

Polyodon (Bridge, **78**) retains this last feature, together with "Præfontallücke" and well-developed parietal foramina, representing post-cranial fontanelle, into the adult.

All definite reference to the orbito-sphenoid has been purposely omitted hitherto, but it should be remembered that whilst Allis states that it is a cartilage bone in Amia (**97**, p. 7), both Vrolik (**73**, p. 57) and Parker (**72**, p. 106) look upon it as a distinct membrane bone; if the latter are right, then to the already existing optic fontanelle must be added the space occupied by this bone.

According to Sewertzoff (**99**) young Acanthias possesses a large dorsal fontanelle, a large lateral one transmitting at first trigeminal and facial as well as optic nerves, and widely open auditory capsules. In Raia (Parker, **76**, p. 216) the dorsal fontanelle is divided by a transverse "cartilaginous beam."

Thus the development of Acanthias, as well as the adult anatomy and comparative ontogeny of Teleostomes, leads back to an ancestor with a fenestrated cranium.

In the light of all this it is interesting to read Parker's account of this region in the Marsipobranchs (**83**), especially in a moderately young lamprey. After mentioning the presence of a large pituitary fontanelle, he goes on to say the "side[1] walls of the chondrocranium of the lamprey are well developed," but "optic and trigeminal nerves pass out of considerable fenestræ, and not out of mere foramina." "The orbito-sphenoidal region is wider than the alisphenoidal, but the latter mounts up into the roof, and the two sides meet round the middle and fore-part of the hind brain. The occipital ring does not exist" (p. 414). He describes the presence in the front of this posterior sphenoidal "tegmen" of a "large pyriform fontanelle," and also states that the passage from the auditory capsule into the cavum cranii is large, especially in Myxine.

Apart from the absence of occipital region and of ossification, all that is required to complete the broad resemblance

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[1] The italics are not mine.

between the cranium of a lamprey and that of a Teleost is a close relation between the epiphysis and the sphenoidal "tegmen," which would then be the undoubted homologue of the epiphysial cartilage. Failing this, it will suffice to recall the fact that in the Cyprinoids and Characinoids this cartilage also arises directly from the sphenoidal region.

Parker himself considered that other types of fish, especially Lepidosteus, were descendants of primordial Marsipobranchs (**83**, p. 404), and the facts just put forward lend considerable support to this.

The possibility, of course, still remains that between this "primordial Marsipobranch" and the bony fish a form like a cartilaginous Ganoid, having bony scutes, as well as a box-like cartilaginous cranium, may have intervened; and that as the scutes became more closely related to this, the fontanelles present in the embryo were preserved, and the necessity for further growth in cartilage was obviated. It is equally possible that on the bony fish side bony specialisation appeared earlier, and was more rapid than in the Chondrostei, and resulted in a preservation of the fontanelles (with the possible exception of the roof) all through.

Again, the fontanelles always present during development might conceivably be explained as due to the relatively large size of the brain; but such an explanation would not apply to the condition of the Marsipobranch cranium.

The Relation of the Visceral Skeleton to the Cranium.

Great interest attaches to a study of the relationships of the so-called hyoid and mandibular arches, and such a study may best be commenced by briefly comparing the conditions found in the adult Heptanchus, as a primitive Selachian, and Gasterosteus, as a typical Teleost.

In the latter the hyomandibular articulates on the auditory capsule below and behind the post-orbital process, and the palatine process of the pterygo-quadrate articulates with the side of the ethmoid plate.

In the former the pterygo-quadrate cartilage is attached to the cranium at two points; the hinder one under the post-orbital process, by means of the otic process, and an anterior one between the exits of the second and fifth nerves, by means of the palato-basal process. In front of this the cartilage continues forwards as the "oberkiefersfortsatz" under the ethmoid region to unite with its fellow. The hyomandibular is slender, and has no articulation with the auditory capsule, and is fastened to this by ligament some distance behind the post-orbital process.

One glance at these two types suffices to show that the palato-quadrate of one possesses just those cranial attachments which are absent in the other, and vice versâ. To derive either condition from the other is therefore impossible.

The position of the hyomandibular relatively to the auditory region in Teleosts, together with other considerations concerning the associated muscles and the variations in the related nerve, led Pollard (**94**, p. 23) to conclude that the elements of that name in these two great groups of fishes were not homologous; and to seek for the Teleostean hyomandibular in the otic process of Heptanchus, and for that of the Elasmobranchs in the stylohyal of Teleosts. In view of his observation that in young Silurus the two sets of cartilages form a continuous whole, and that in Gasterosteus the broad head of the hyomandibular is formed by backward growth during development, it must be admitted that his case, though startling, is strong, and if true, at once puts all other Selachian types of suspensorium out of court as possible conditions for the derivation of the Teleostean type (cp. Gegenbaur, **72**, p. 175).

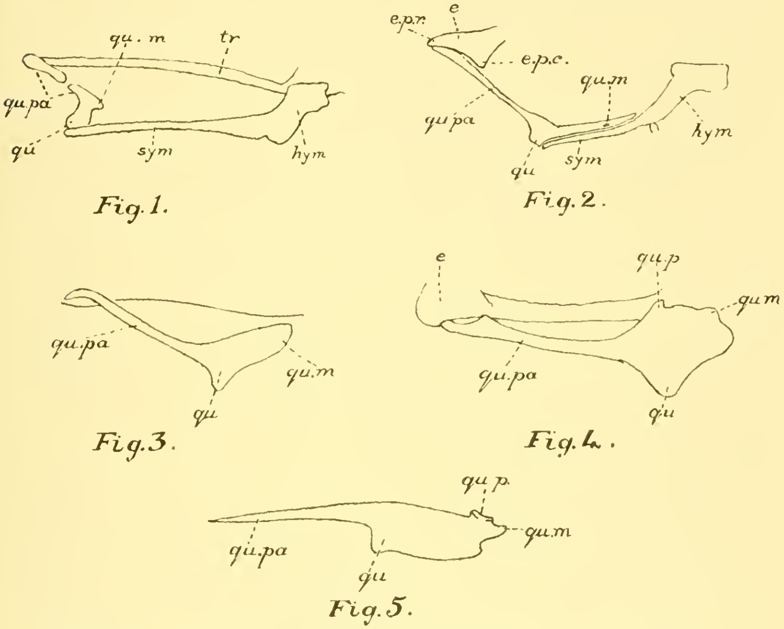
In 1876 Huxley introduced three useful terms—autostylic, hyostylic, amphistylic—to express the "manner in which the mandibular arch is connected with the skull." He regarded the second of these as "perfectly exemplified by Ganoids, Teleostei, and Plagiostomes," and characterised by the fact that the "palato-quadrate cartilage is no longer continuous with the chondrocranium, but is, at most, united with it by ligament" (p. 41). The condition presented by the Teleosts cannot, however, be completely described by any one of these terms, for whilst it is true that the hinder end of the palato-quadrate is suspended by a well-developed something, which may yet be shown to have no homology with the hyomandibular of Elasmobranchs, the fore-end is not merely suspended by ligaments, but articulates directly with the cranium, and may, as in Gasterosteus, Belone, and some Siluroids, be continuous with the ethmoid cartilage until a very advanced stage. This mode of suspension is therefore hyostylic only posteriorly, but autostylic anteriorly.

In the first stage in the development of Gasterosteus the palatine process does not reach the end of the trabeculæ. This cannot be interpreted as an approximation to the Selachian type, for the opposite processes are parallel. In early stages of Acanthias the homologues of these processes have not met, though the halves of the mandible are already united (Sewertzoff, **99**, p. 289). Similarly for other embryonic Elasmobranchs and for the adult Notidanus (Gegenbaur, **72**, p. 187).

It has already been pointed out that a line of advancement or retrogression can be recognised within the Teleostean class, in the gradual reduction of the metapterygoid region (Text-figs. 1—4). Reversing the order of procedure, and passing from forms without metapterygoid process (fig. 1) to those lowly forms in which it is strongly developed (fig. 4), other structures begin to appear. Thus, in the larval Amia (Pl. 31, fig. 60), the metapterygoid region, besides being large and plate-like, sends from its upper border towards the trabeculæ (*tr.*) a large process (*p.*), the pedicle. Below the exits of the optic and trigeminal nerves the trabeculæ, which are here pierced by the carotid artery (*ca.*), project slightly towards it.

In Salmo trutta (Text-fig. 4) the same condition prevails, and the pedicle is almost equally well developed. This is figured, but not referred to by Winslow (**98**).

These facts suggest that at some former time an actual connection or articulation must have existed between the pedicle and the trabeculæ. Such a condition exists in Lepidosteus (Text-fig. 5), in which, at all stages from the embryo two thirds of an inch long to the full-grown adult (Parker, **82**), the pedicle is strongly developed, and forms an articulation with the "basipterygoid process." This stands out from the same region of the trabeculæ as that just described for Amia. In the extinct Lepidotus also there is a stout process of the metapterygoid which bears a large facette, and which, according to Smith Woodward (**95**, p. 79),



Text-figs. 1—5.—Diagrams illustrating the various modifications exhibited by the quadrate and its processes in the larvæ of Bony Fishes.

Fig. 1, Syngnathus (after Pouchet); Fig. 2, Belone (orig.); Fig. 3, Zoarces vivipara (orig.); Fig. 4, Salmo trutta (modified from Winslow); Fig. 5, Lepidosteus osseus (after Parker). *e.* Ethmoid. *e. p. c.* Parethmoid cornu. *e. pr.* pre-ethmoid cornu. *hym.* Hyomandibular. *qu.* Quadrate. *qu. pa.* Palatine process of quadrate. *qu. p.* Pedicular process of same. *qu. m.* Metapterygoid process of same.

may have articulated with a lateral element in the cranium. I have no doubt that this is the homologue of the pedicle in Lepidosteus.

In Osteoglossum, Bridge (**95**, p. 309) describes a similar condition, but here it is a process of the parasphenoid, which supplies a surface of articulation for the process from the metapterygoid. He regards it as a "striking example of parallelism in evolution." May it not, however, be a case in which the pedicle has been retained, whilst the basipterygoid process has been lost and functionally replaced?

Whether this is so or not, the fact remains that the lowly Teleosts and Amia bring the bony fish type near to one having a pedicular articulation. This leaves little doubt that the condition found in Lepidosteus is not secondary, as Bridge supposed, but primary; and that in the ancestor the quadrate cartilage was attached, not merely to the edge of the ethmoid plate, but also to the posterior region of the trabeculæ somewhere between the exits for the second and fifth nerves.

Huxley's comparison between the subocular arch of the frog and the hyosuspensorial apparatus of the Teleosts (**58**) on the one hand, and the cranio-facial skeleton of Petromyzon (**76**) on the other, implied a resemblance between the latter two, which, as pointed out by Pollard, he ceased to recognise later. Nevertheless, this resemblance does exist, and in no respect is this more clearly shown by Petromyzon than in the fusion of the arch, anteriorly with the ethmoid and posteriorly with the trabeculæ, between the exit of the optic nerve and below that of the trigeminus (Parker, **83**, p. 401). Nor is continuity of substance to be regarded as an important difference, for, as shown above, it exists between the palatine and ethmoid in the latest developmental stages of some Teleosts, and has been also observed by Parker in his earlier stages of Lepidosteus (**82**, p. 450). Moreover, in my Stage III, the hyomandibular forms a continuum with the auditory capsule. Again, in Myxine all these points are marked by the presence of a different kind of cartilage from the rest.

If Pollard was right in regarding the hyomandibular of Teleosts as part of the same cartilage to which the quadrate belongs, then this has a third connection through the auditory capsule with the cranium, and increases the resemblance to the Marsipobranch, for both Myxine and Bdellostoma possess an otic attachment in addition to the palatal and pedicular ones.

Turning to Elasmobranchs, and descending from the more specialised to the less specialised forms, it is noticeable that, apart from the hyomandibular, in the former, e. g. Scyllium, the palato-quadrate is suspended only by ligament; in intermediate forms, e. g. Acanthias, a palato-basal process or pedicle is present; and in the latter, e. g. Heptanchus, which is undoubtedly a lowly type, suspension is by means of both otic and pedicular processes. There are some forms, e. g. Cestracion, which do not conform to this, but the constant recurrence of the pedicle amongst Selachii points back to an ancestor which certainly possessed that feature. Whether an otic articulation was also present must, in view of Huxley's (**76**, p. 44) and Sewertzoff's (**99**, p. 299) opinions that it is secondary, and Gegenbaur's (**72**, p. 186) and Pollard's (**94**, p. 23) that it is primary, be left undecided until the homology of the Teleostean hyomandibular is definitely determined.

Sewertzoff considers that the palato-basal process was the primary attachment for the mandibular arch (**99**, p. 299), because at a very early period in the development of Acanthias it is united with the trabeculæ by dense tissue. The fact that in Petromyzon the facial skeleton commences as an outgrowth—the pedicle—from the trabeculæ (Parker, **83**, p. 441), that in Lepidosteus the pedicle appears very early, and that in Teleosts the palatine process always grows out from the quadrate (Stöhr, Pollard, and above in Stage I), strongly supports this view, and points to a remote time when neither palatal nor otic processes existed.

Systematic Position and Affinities of Gasterosteus.

The present views of the relationships of the Gasterosteidæ can be best stated by entering briefly into the history of their growth.

On account of the presence of spines in the fins, and of the union between the suborbital bone and the pre-operculum, Cuvier and Valenciennes (**29**) classified this family with the mail-cheeked Acanthopterygii, which included the Triglidæ and Cottidæ. Thirty years later Günther (**61**), whilst still retaining it among the Acanthopterygii, separated it from the mail-cheeked forms; and because of its spinous anterior dorsal fin and the abdominal position of the pelvics, put it with the Fistularidæ in a separate division, the Acanthopterygii Gastrosteiformes, and indicated his ideas of the affinities of this by placing the Mugiliformes and the Centrisciformes on either side. In a paper, which has since formed a basis for much recent systematic work, Cope, because of the position of the pelvic fins (**70**, p. 456), separated these three divisions from the Acanthopterygii, creating for the Mugiliformes the distinct order Percesoces, and for the other two, the Hemibranchii. The latter he regarded as annectant between the former and the Lophobranchii; looking upon the weak branchial apparatus, the presence of interclavicles, the simple post-temporals, the prolongation of the muzzle, and the presence of ganoid plates on the body, as approximations to the Lophobranch type; and upon the character of the dorsal spines as an indication of relationship to Nematocentris, one of the Atherinidæ. Later systematists have followed Cope more or less closely. Gill (**93**) placed the Hemibranchii next the Lophobranchii, and considered it as equivalent not merely to the Acanthopterygii, but to an order—the Telocephali—containing these and the Haplomi, Scomberesocidæ, and Percesoces. Jordan and Evermann (**96**) acknowledge that it is closely allied to the Lophobranchii, and that though well marked off from the Percesoces and other Telocephali, it descended from the ancestors of these groups. In this they are followed by Kingsley (**00**), who adds to it the extinct Dercetidæ (Hoplopleuridæ) which "show relations towards Belone." This year Boulenger (**01**, p. 378) remarks on their close affinity with the Lophobranchii, more especially through the Fistularidæ and the fossil Pseudosyngnathus.

It may at once be stated that there is nothing to support Parker's (**68**) suggestion of Siluroid affinity for Gasterosteus.

In order to see how far these views are supported by the study of the head skeleton, we may now briefly compare that of Gasterosteus with that of Syngnathus, a typical Lophobranch, and of Fistularia, a typical Hemibranch. McMurrich's paper (**83**), supplemented and confirmed by my own observations, is my authority for details concerning the former. Klein (**84**, **86**) on the cranium, and Rutter (v. Jordan and Evermann) on the branchial skeleton, are the only workers who, so far as my knowledge goes, have dealt with the latter. To attempt to explain the why and the wherefore of Klein's tangle in describing the auditory region would be of no use for my present purpose; I shall therefore give the results of my own examination without reference to his.

Taking the various parts in the same order as in the former part of this paper, the consideration of the hinder region of the cranium comes first.

That of Gasterosteus is not so compressed dorsi-ventrally as the other two, but all are alike in the absence of an opisthotic and basisphenoid, the even upper surface, the sculpturing of the roofing bones, the simplicity of the post-temporal, the essential shape of the ethmoid, and the great size of the supra-occipital, which separates the parietals widely, and appears to separate the hinder portion of the frontals. In Gasterosteus the exoccipital extends forwards between the pterotics and basioccipital to the pro-otic. In the others the pterotic extends ventrally to the basioccipital, and also part of the way into the large membranous space between this and the pro-otic, thus separating the exoccipital widely, and the basioccipital partially, from the pro-otic. In Gasterosteus the space just referred to is represented by an area of cartilage (Pl. 29, fig. 21). In the sphenoidal region of Fistularia the pro-otic completely encloses the foramen for the exit of part of the fifth nerve, and forms the hinder boundary of the other exit. The large alisphenoid forms the front boundary for the rest. No eye-muscle canal is present, consequently the parasphenoid lies flat against the floor of the cranium. Laterally it sends out processes up to the sphenotic. In Syngnathus McMurrich was doubtful about the presence of an alisphenoid, but the enclosure of the trigeminal nerve exit by the pro-otic, and the absence of the eye-muscle canal, furnish points of resemblance to Fistularia; whilst in the union of parasphenoid and frontal processes it is similar to Gasterosteus.

Thus the last named is more normal in the occipital region and more advanced in the sphenoidal than the other two, and, on the whole, differs more from them both than they do from one another.

In the anterior portion of the cranium, Fistularia and Syngnathus present the same features as those given above for the Gasterosteus, but it is greatly elongated, and almost completely ossified. In the first this region is proportionally much wider, because the narrow pre-ethmoid is supplemented laterally by the nasals. Apart from this, and the presence of teeth on the vomer, it bears a much closer resemblance to the second than to the last, for though Gasterosteus spinachia has an elongated ethmoid, this is still almost wholly cartilaginous.

In the visceral skeleton all are alike in the tendency towards a weakening of the branchial apparatus, in the great forward slant of the hyomandibular, in the great elongation of the symplectic, in the great reduction or complete suppression of the metapterygoid cartilage, in the absence of an ectopterygoid, and in the possession of the acrartete condition.

In Fistularia the reduction of the branchial skeleton has advanced much further than in Syngnathus, for all the basibranchials and the fourth epibranchial are absent. The pharyngobranchials of the second to fourth arches are present, but, unlike those of Gasterosteus, the first two are fused; the third is free, and all are rod-like, and lie one behind the other. In Syngnathus the first and second basibranchials and the second hypobranchial alone are present; the fourth epibranchial has gone, but the edentulous pharyngobranchials, though rod-like, occupy the same position relatively to one another as in Gasterosteus.

In the hyoid arch the basihyal, though present during development, is absent in the adult Syngnathus, but attains a great length in Fistularia.

Of the bones immediately concerned in the gill-cover and branchiostegal membrane, the operculum alone survives in Syngnathus, but are all present, together with five branchiostegal rays, in the Fistularia. The interoperculum, which McMurrich failed to recognise as such, bears, by reason of its position, a superficial resemblance to the gular plates of Polypterus, and was mistaken for such by Parker (**68**). Otherwise, as in Fistularia, it is quite normal in its relationships.

In describing the other suspensorial bones, McMurrich mistook the pre-operculum for the infra-orbital, and consequently went wrong in his identification of the rest. The true infra-orbital, or rather the first bone of the suborbital series (fig. 50, *so.*^{1}), articulates with the parethmoid (*e. p. b.*) above, and forms the lower border of the narial opening. Ventrally it appears to divide into two laminæ, lying on the outer and inner sides respectively of the cheek muscles, and is attached by its lower border to the combined symplectic and pre-operculum (*sym.* + *o. pr.*). In front of the latter lies the greatly extended quadrate (*qu.*), of which only the small part indicated by the dotted line originated by ossification of cartilage. Along its upper and anterior borders lie three bones, *a*, *b*, *c*, whose homologies are uncertain; *b* and *c* together have all the relationships of the pterygoid in the stickleback, but as *b* is developed in relation to the vestigial metapterygoid process, it must be the metapterygoid bone. *a* is probably the nasal. The palatine is insignificant and edentulous. In Fistularia the inner lamina of the suborbital bone alone remains, the quadrate is much larger posteriorly, and the pterygoid bone bears a close resemblance to that of Gasterosteus. Between the hinder process of the last-named bone and the suborbital is the undoubted metapterygoid, which thus occupies a similar position to, but is much smaller than, *a* in Syngnathus.

Thus once more this fish exhibits a much closer resemblance to Syngnathus than to Gasterosteus. At first sight one is inclined to think that this may be in some way associated with the long snout. That the formation of such a feature does not, however, of necessity produce the same characters, is well shown by the differences which existed in the pterygoid and metapterygoid of the two fishes. Again, the long-snouted Mormyroids do not possess the acrartete condition, but one which might be most aptly described as an elongated panartete condition.

Add to this the fact that forty years ago Kner and Steindachner (**63**, p. 28) were driven to conclude that the extinct Pseudosyngnathus was intermediate between Lophobranchs and Fistulariidæ, and to prophesy that these two groups would some day have to be relegated to the same order.

Again, consider the latest diagnoses of these two orders (Jordan and Everman, **96**, pp. 741, 759). After the elimination of those characters common to both; those mentioned as characteristic of one, though equally characteristic of the other, e. g. bony plates; those based upon error, e. g. condition of branchial apparatus in Syngnathus; those not common to all members of the order, e. g. for Hemibranchs, the elongated anterior vertebræ, which are not even indicated in Aulorhynchus and Gasterosteus; the only distinctive features left are the tufted gills and single opercular bone for the one, as opposed to the pectinate gills for the other.

To retain these two groups of fishes as distinct orders in the face of these considerations would savour too much of unnecessary conservatism.

On the other hand, when put together they form a compact and natural group, clearly marked off from the Acanthopterygii by the reduced condition of the metapterygoid, the shape of the ethmoid, and the abdominal position of the pelvic fins; and further from the Percesoces and Haplomi by the acrartete condition, the elongated symplectic, the strong tendency to the reduction of the branchial apparatus, and the possession in the trunk of so-called interclavicles and of bony scutes, which may either form a more or less complete armature, or be developed merely along dorsal, ventral, and lateral lines.

There is some difficulty in determining what degree of importance must be attached to this last feature. Sagemehl (**85**, p. 3) has brought forward a number of valid arguments against its reliability; but when, in a natural group of fishes such as this, all the members, including even the scaled forms, possess bony scutes, generally arranged in definite order, it can only be regarded as something more than a superficial similarity. That a group of Teleosts should have arisen in which the ganoid plates along some lines were retained, instead of being converted into scales, is a possibility which receives an air of probability from the fact that in Gasterosteus the plates of the lateral series are provided with that peg-and-socket arrangement (Parker, **68**, p. 41) so characteristic of ganoid plates.

Other features there are—such as the sculpturing of the roofing bones in the less specialised members; the simple post-temporal; the absence of opisthotic; the general absence of maxillary process and the teeth in the palatine; the single pterygoid bone; the complete withdrawal of the cranial cavity from the orbit, even in the lowest members; the general shape of the body; the elevated pectorals; the position of dorsal and ventral median fins relative to one another—to which much importance cannot be attached singly, but which, when taken together, help substantially to strengthen the conviction that these forms should be referred to a separate sub-order. I propose, therefore, that these fishes, hitherto placed in the sub-orders Hemibranchii and Lophobranchii, should be put together in one sub-order, having the name Thoracostei,[1] as expressive of the presence in all of a more or less complete bony armature, and especially of infraclavicles.

The two old sub-orders might still be provisionally retained as divisions until such forms as Solenostoma and Aulorhynchus have been thoroughly examined; but, in view of the facts already put forward, the sticklebacks should certainly be referred to a separate division, the Gasterosteoidei.

One feature of great interest about the Thoracostei is the possession of undoubted highly specialised characters side by side with primitive ones, which indicate that they branched off from lowly physoclistous, or even physostomous fishes. We may now briefly inquire into their relationships to other fishes.

To the best of my knowledge, the nearest approach to this order among living fishes is made by the Scomberesocidæ. Indeed, so close is this approach that on a consideration of the head skeleton alone one would be almost obliged to place Belone in the same sub-order with Gasterosteus. Give its cranium an arched instead of a flattened roof, replace its alisphenoid by overlapping frontal and parasphenoid processes, shorten the premaxillæ and mandible to a normal length, elongate the symplectic still further, and it would be extremely difficult to find any feature of importance in which the two crania differed, for in the Belone all the roofing bones are sculptured; in spite of its lowly affinities, its opisthotic is absent; the ethmoïd, though more cartilaginous, is of the same type; the branchial apparatus is an exact replica of that in Gasterosteus in the number and nature of the basibranchials,

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[1] Since the above was written, Smith Woodward has published his much-needed fourth volume of the 'Catalogue of Fossil Fishes in the British Museum.' In this he has united the two old sub-orders under the one name Hemibranchii.

in the number, shape, and proportional size of its pharyngobranchials, and in all other features except the fusion of the vestigial elements of the fifth arch. Again, the hyomandibular is of the same shape, though its articulations are more generalised; the metapterygoid is equally reduced; one pterygoid line alone is present; the palatine is small, edentulous, and lacks a maxillary process; finally it presents the acrartete condition.

The similarity is so great that one may say with considerable truth that the little stickleback is but a slightly specialised Belone.

In the trunk region, however, though the pectorals are raised, the pelvics, abdominal, and the arrangement of the other fins is the same as in Thoracostei; yet the complete absence of bony plates and infra-clavicles gives some excuse for not including the Scomberesoces in the new sub-order.

Boulenger (**01**) has recently placed them as a family of the Percesoces, and the possession of a reduced metapterygoid in Atherina supports this view. It is interesting to note that, at least so far as the head skeleton is concerned, they depart from the other members of that sub-order in just those features in which they approach the Gasterosteoidei; for all the other Percesoces I have examined possess a suspensory pharyngeal, a well-developed opisthotic (Starks, **99**), and the acrartete condition.

If this is their true position, it would strongly tend to show that the acrartete condition was derived from a lowly disartete by loss of the post-palatine articulation. If it is not, then the most convenient way would be to keep the Scomberesoces in a separate sub-order as before, and to speak of them and the closely allied Thoracostei collectively as the Scomberesocine series. For my own part, I do not like the word Scomberesoces, because it implies relationships which do not exist. On the other hand, the term Synentognathi of American writers is equally inapplicable.

Klein has shown (**79**, p. 120) that the opisthotic may be absent in very diverse families of Teleosts, and that even in those forms in which it is constantly present its relationships are extremely variable. Nevertheless it cannot be a mere coincidence that all the forms belonging to the Scomberesocine series, including so lowly a form as Belone, should be lacking in this bone. It must therefore be lacking also, or much reduced, in their immediate ancestors and allies.

Turning now to the palæontological side of the question, we find the Thoracostei well represented by forms differing but little from those of the present day as early as the Eocene.

There seems at present much more to be said against than for Kingsley's suggestion concerning the relationship between these forms and the extinct Dercetiformes or Hoplopleurides (Pictet, **54**, p. 215). Smith Woodward, to whom I am indebted for the opportunity of examining a number of the original fossils, places Belonorhynchus, with considerable show of reason, among the Chondrostei (**95**), and the remaining forms in two families, the Dercetidæ and Enchodontidæ (**01**). Despite the presence of rows of bony scutes along dorsal, lateral, and ventral lines, the condition of the cranial roof and mandibular suspensorium alone make it very improbable that they have anything to do with the Thoracostei.

One other group of bony fishes—Zanclidæ, Acronuridæ (Teuthididæ), and Plectognathi—demands a reference because it possesses the acrartete condition. Jordan and Evermann (**96**) place the first two families together with the Ephippidæ and Chætodontidæ in one sub-order, the Squamipinnes, and say that "The Teuthididæ and Balistidæ are as nearly related to each other as the Ephippidæ are to the Chætodontidæ;" and again: "There can be no doubt of the common origin of the Balistidæ and Teuthididæ, and that the divergence is comparatively recent." For this reason they subordinate the Plectognathi to the Acanthopterygii, and place them as an offshoot of the Squamipinnes.

What has already been said concerning this ethmoid and suspensorial region in Teuthis and Balistes tends to support the statements (just quoted) of these authors very strongly, but tells with equal strength against the relationships of these forms to the Chætodontidæ and Ephippidæ. In Chætodon plebeius (fig. 46), the ethmoid region is an extremely specialised one of the Pagellus type, for though the palatine lies against the parethmoid, it is united to that exclusively by ligaments, and the articular surfaces have aborted. The palatine, moreover, has the large maxillary process so characteristic of the Acanthopterygii, and mobility for the suspensory apparatus is gained, as in Cyprinoids, by articulation between the palatine and pterygoid bones. Judging by the character of the ethmoid region, and its relation to the palatine alone, the relationships of the Plectognathi, and the undoubtedly closely allied Zanclidæ and Acronuridæ, must not be sought within the Acanthopterygii; nor, judging by the well-developed metapterygoid, and presence of both pterygoids, must they be sought in the Scomberesocine series, but somewhere lower down.

V. Summary and Conclusions.

1. The cranial flexure, together with other features in the shape of the embryonic head skeleton in Teleosts, is probably a mechanical effect due to differences in the degree of distensibility between the dorsal and ventral surfaces of the brain, and to the presence of skeletal structures in close association with the latter (pp. 507—509).

2. The presence of an epiphysial bar, with consequent division of the large dorsal, cranial fontanelle into an anterior and a posterior portion, is a common feature among Teleosts during development (pp. 516, 517).

3. The Ostariophysi differ from all other Teleosts in the retention of this early developmental condition of the cranial roof in the adult (pp. 525, 526).

4. The intra-cranial notochord, so far from undergoing reduction, never at any stage ceases to grow (pp. 513, 516, 523).

5. In Gasterosteus, during embryonic life, those skeletal

elements immediately concerned in the support of the jaws and operculum, and in the attachment of associated muscles, seem to undergo a considerable acceleration in the rate of development as compared with the rest of the head skeleton (pp. 534, 535).

6. Among Teleosts and the immediately related Ganoids, three types of palato-ethmoidal relationship exist (pp. 538, 539, 551—557).

(*a*) The Panartete, in which the palatine cartilage or its derivatives is attached to the ventral surface of the ethmoid for the whole length of this, from the parethmoid to the pre-ethmoid cornua, e. g. Amia, probably presented also by many Malacopterygii (Isospondyli).

(*b*) The Disartete, in which the attachment is at the parethmoid and pre-ethmoid cornua, but not at any intermediate point, e. g. Esox, also presented by the Salmonidæ, Cyprinodontidæ, Acanthopterygii, and probably some Malacopterygii (Isospondyli).

(*c*) The Acrartete, in which the attachment is confined solely to the pre-ethmoid cornua, e. g. Gasterosteus, and also presented by the Thoracostei, Scomberesoces, Plectognathi, Zanclidæ, Acronuridæ, and in a modified form by Lepidosteus.

7. The study of the adult anatomy and comparative ontogeny of the head skeleton in Elasmobranchs and Teleostomes seems to point to a common ancestral stock for these two great divergent branches of fishes. It presented among other features the following:

A short embryonic life; weak cranial flexure; trabeculæ united to the extreme anterior end of the parachordals.

A wholly cartilaginous cranium, possessing trabecular, parachordal, and occipital portions (pp. 560—562).

A cranium having a large dorsal fontanelle, which may or may not have been divided by a transverse epiphysial bar. Also two lateral fontanelles for the passage of the optic, and possibly also the trigeminal and facial nerves. Also a ventral or pituitary fontanelle. Also a large opening between the cavum cranii and auditory capsule (pp. 562—568).

A quadrate cartilage supporting a lower moveable jaw, formed by the union of two cartilages in the middle line, and bearing dorsally two, possibly three processes; an anterior one, parallel to its fellow, and not united with it, but with the ethmoid plate, so that a moveable upper jaw did not exist; a middle one articulating with the trabeculæ, in the region lying between the optic and trigeminal nerves; a posterior one articulating with the auditory capsule (pp. 568—573).

A branchial apparatus consisting of at least five arches, already segmented into four parts.

Balfour's term Prolognathostomata (81, p. 271) would be sufficiently expressive of such a type.

8. The manner of mandibular suspension in Teleosts is insufficiently described by the term Hyostylic (pp. 569, 570).

9. The Lophobranchii and Hemibranchii should no longer be kept in separate orders, for they together constitute a natural group, which may be designated the Thoracostei (pp. 575—579).

10. The Scomberesoces, through the Gasterosteoidei, approach more closely to the Thoracostei than do any other living Physoclisti, and seem to form with them a compact series, which may be provisionally spoken of as the Scomberesocine series (pp. 580, 581).

11. As judged by the study of the ethmoid and suspensorial regions, the Zanclidæ and Acronuridæ are closely allied to the Plectognathi, but the affinities of these forms must not be sought amongst living Physoclisti (pp. 582, 583).

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EXPLANATION OF PLATES 28—31,

Illustrating Mr. H. H. Swinnerton's paper, "A Contribution to the Morphology of the Teleostean Head Skeleton, based upon a study of the Developing Skull of the Three-spined Stickleback (Gasterosteus aculeatus)."

List of Reference Letters.

a. b. c., see page 577. *a. f.* Anterior cranial fontanelle. *an.* Angular. *ar.* Articular. *au. c.* Auditory capsule. *au. c'.* Pillar round which the horizontal semicircular canal runs. *b.* Brain. *b. f.* Fore-brain. *b. h.* Hind brain. *b. m.* Mid-brain. *br.* Branchial arch. *br. b.* 1—4. Basibranchials 1—4. *br. c.* 1—5. Ceratobranchials 1—5. *br. e.* 1—4. Epibranchials 1—4. *br. h.* 1—3. Hypobranchials 1—3. *br. p.* 2—4. Pharyngo-branchials 2—4. *br. r.* Branchiostegal ray. *ca.* Foramen for internal carotid artery. *ch.* and *ch'.* Notochord. *d.* Dentary. *e.* Ethmoid region. *e. m.* Mesethmoid. *e. m. c.* Mesethmoid cartilage. *e. p. b.* Parethmoid bone. *e. p. c.* Parethmoid cornu. *e. pr.* Pre-ethmoid cornu. *e. pr. b.* Pre-ethmoid bone. *ep.* Epiphysis. *ep. c.* Epiphysial cartilage. *ep. f.* Epiphysial foramen. *ep. s.* Connection between epiphysis and supra-occipital region. *ey.* Eye. *ey. c.* Eye-muscle canal. *fe'.* Fenestræ in the floor of the auditory capsule. *fe''.* Fenestræ in the side wall of the auditory capsule. *fr.* Frontal. *fr'.* Process from frontal. *g.* Gape. *hy.* Hyoid arch. *hy. b.* Basihyal. *hy. c.* Ceratohyal. *hy. c'.* Process of the ceratohyal. *hy. e.* Epihyal. *hy. h.* 1, 2. Hypohyal 1, 2. *hy. i.* Stylohyal. *hym.* Hyomandibular. *hym'.* Opercular process of the hyomandibular. *hym''.* Articular processes of the hyomandibular. *hym'''.* Articular facets for the hyomandibular. *inf.* Infundibulum. *l.* Labial cartilage. *l.* Labial fold. *m. e.* External rectus muscle. *mk.* Meckel's cartilage. *mx.* Maxilla. *na.* Nasal. *na'.* Process of nasal bone. *o. e.* Epiotic. *o. p.* Pterotic. *o. pr.* Pro-otic. *o. pr'.* Pro-otic process. *o. pr''.* Anterior end of the parachordal. *o. sp.* Sphenotic. *oc. a.* Occipital arch. *oc. a'.* Small process on the occipital arch. *oc. b.* Basioccipital. *oc. c.* Occipital chondrification. *oc. e.* Exoccipital. *oc. n'.* First occipital nerve. *oc. n''.* Second occipital nerve. *oc. s.* Supra-occipital. *op.* Operculum. *op. i.* Interoperculum. *op. pr.* Pre-operculum. *op. s.* Suboperculum. *p. ch.* Parachordal. *p. ch'.* Interparachordal fossa. *p. f.* Posterior cranial fontanelle. *p. t.* Post-temporal. *pa.* Palatine. *pa'.* Pre-palatine articular facet. *pa''.* Post-palatine articular facet. *pa. m.* Maxillary process of the palatine. *par.* Parietal. *pg. ec.* Ectopterygoid. *pg. en.* Entopterygoid. *pg. m.* Metapterygoid. *pmx.* Premaxilla. *pmx'.* Cartilage on the ascending process of the premaxilla. *ps.* Parasphenoid. *ps'.* Median process of the parasphenoid. *ps''.* Lateral process of the parasphenoid. *pt.* Pituitary body. *pt. f.* Pituitary fossa. *qu.* Quadrate. *qu'.* Process of quadrate. *qu. m.* Metapterygoid process of the quadrate. *qu. pa.* Palatine process of the quadrate. *qu. pd.* Pedicular process of the quadrate. *r.* Rostrum. *sb. b.* Supra-orbital band. *sb. p.* Post-orbital process. *so.* 1—3. Suborbitals 1—3. *sym.* Symplectic. *tg.* Tegmen cranii. *tr.* Trabeculæ. *tr'.* Point of union of the trabeculæ with the parachordals. *vo.* Vomer. *x.* Infra-symplectic cartilage. I—X. Nerve foramina. * Boundary between the head and body. ** Curve of the egg-shell. † Articulation between palatine and pterygoids.

Fig. 1. Stage I.—Dorsal view of the chondro-cranium of a larva, 3·6 mm. long. × 70.

Fig. 2. Stage II.—The same of a larva, 5·7 mm. long. × 60.

Fig. 3. Stage III.—The same of a larva, 6·6 mm. long. × 50.

Fig. 4. Stage IV.—The same of a larva, 16·0 mm. long. × 16.

Fig. 5. Stage IV.—Dorsal view of the skull with the membrane bones. × 16.

Fig. 6. Stage I.—Lateral view of the chondro-cranium. × 70.

Fig. 7. Stage II.—Lateral view of the chondro-cranium. × 60.

Fig. 8. Stage III.—Lateral view of the chondro-cranium. × 50.

Fig. 9. Stage IV.—Lateral view of the chondro-cranium. × 16.

Fig. 10. Stage IV.—Lateral view of the skull with the membrane bones. × 16.

Fig. 11. Stage IV.—Posterior view of the skull with the membrane bones. × 16.

Fig. 12. Stage IV.—Ventral view of the posterior region of the chondro-cranium. × 16.

Fig. 13. Stage IV.—Internal view of the mandibular and hyoid arches with the mandible removed. × 16.

Fig. 14. Stage II.—Ventral view of the hyoid and branchial arches. × 60.

Fig. 15. Stage III.—Ventral view of the hyoid and branchial arches. × 50.

Fig. 16. Stage IV.—Ventral view of the hyoid and branchial arches. × 16.

Figs. 17—24 are all of the adult;

Fig. 17.—Side view of the cranio-facial skeleton. × 3½.

Fig. 18.—Dorsal view of the cranium. × 3½.

Fig. 19.—Side view of the cranium. × 3½.

Fig. 20.—Internal view of the cranium. × 3½.

Fig. 21.—Ventral view of the cranium. × 3½.

Fig. 22.—Ventral view of the hyoid and branchial arches. × 3½.

Fig. 23.—External view of the mandibular and hyoid arches with the mandible removed. × 4.

Fig. 24.—Posterior view of the cranium. × 3½.

Fig. 25.—Sagittal section of the intercranial notochord of a larva, 6·3 mm. long. × 80.

Fig. 26.—The same of a young stickleback, 21·0 mm. long. × 80.

Fig. 27.—The same of a full-grown adult, 47·0 mm. long. × 80.

Fig. 28.—Transverse section through the labial cartilage of the adult. × 35.

Fig. 29.—The same, but 30 sections behind. × 35.

Fig. 30.—Transverse section through the pre-ethmoidal and pre-palatine regions of larva belonging to Stage IV. × 140.

Fig. 31.—Transverse section through the same region of the adult. × 30.

Fig. 32.—Transverse section through the parethmoid region. × 30.

Fig. 33.—Transverse section through the anterior ends of the parachordals of a larva, 9·0 mm. long. × 140.

Fig. 34.—The same of a young stickleback, 16·0 mm. long. × 70.

Fig. 35.—The same of an adult. × 35.

Fig. 36.—Transverse section through the basi-occipital of the adult. × 27.

Fig. 37.—Median sagittal section through the basis cranii of the adult. × 27.

Fig. 38.—The same of a young stickleback, 14 mm. long. × 70.

Fig. 39.—Transverse section through the region of the infra-symplectic cartilage of a young stickleback, 16 mm. long. × 70.

Fig. 40.—Ventral view of the same region. × 37.

Fig. 41.—Transverse section through the auditory capsule and hyomandibular of an embryo, 3·6 mm. long. × 400.

Fig. 42.—Sagittal section through the ascending process of the premaxilla of the adult. × 30.

Fig. 43.—Lateral view of the ethmoid and quadrate regions of the adult Esox lucius. × ½.

Fig. 44.—Lateral view of the ethmoid and palatine regions of the adult Scomber scomber. × 1½.

Fig. 45.—The same of the adult Pagellus centrodontis. × $\frac{8}{10}$.

Fig. 46.—The same of the adult Chætodox plebius. × 4.

Fig. 47.—The same of a larval Salmo salar, 20 mm. long. × 25.

Fig. 48.—Projection of the chondrocranium of a young Siphonostoma typhle, 22 mm. long. × 15.

Fig. 49.—Lateral view of the ethmoid and quadrate regions of the adult Belone acus. Not size.

Fig. 50.—The same of Syngnathus. × ½.

Fig. 51.—Lateral view of the ethmoid and palatine regions of the adult Gasterosteus aculeatus. × 5.

Fig. 52.—The same of Zanclus cornutus. × 2.

Fig. 53.—The same of Balistes maculatus (young?). × 2¾.

Fig. 54.—Diagrammatic transverse section through the head region of a sixth-day embryo of Gasterosteus aculeatus; killed within the egg. × 80.

Fig. 55.—The same; killed after being released from the egg. × 80.

FIG. 56.—Diagrammatic sagittal section through the head region of a sixth-day embryo of Gasterosteus aculeatus; killed within the egg. × 80.

FIG. 57.—The same; killed after being released from the egg. × 80.

FIG. 58.—Diagrammatic sagittal section through the head region of a just-hatched larva of Gasterosteus aculeatus of the ninth day. The dotted outline represents parts belonging to an eighth-day embryo which was killed within the egg. × 80.

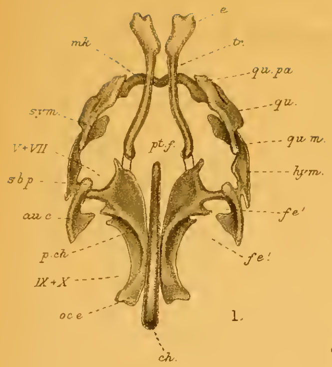
FIG. 59.—Diagrammatic sagittal section through the head region of an adult of Gasterosteus aculeatus. × 6.

FIG. 60.—Dorso-lateral view of the trabecular and quadrate portions of the head skeleton of a larval Amia calva, 19 mm. long. × 8.

FIG. 61.—Projection of the chondrocranial roof of a larval Salmo salar, 20 mm. long. × 20.

FIG. 62.—Projection of the chondrocranial roof of a larval Salmo salar, 25 mm. long. × 17.

NOTE.—Figures 1—16, 40, 47, 60, were taken from wax models. In all except Figs. 47 and 60, the uncoloured portions represent pro-cartilage; those coloured blue, cartilage; those coloured green, ossifying cartilage; those coloured yellow, bone without cartilage.



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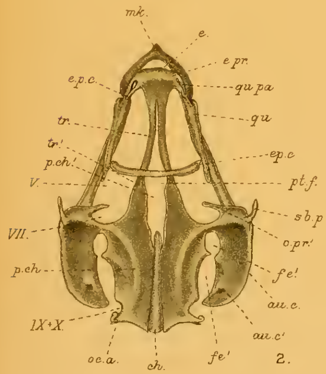

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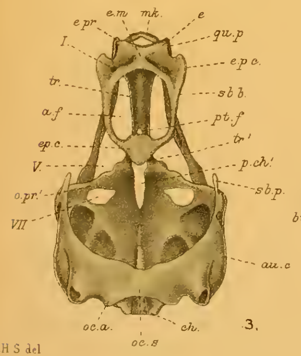

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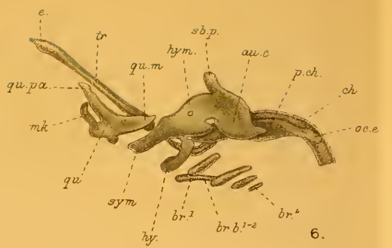

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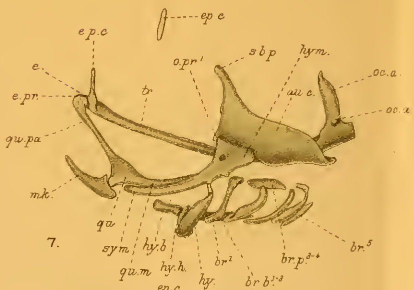

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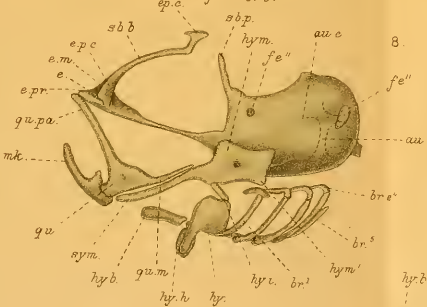

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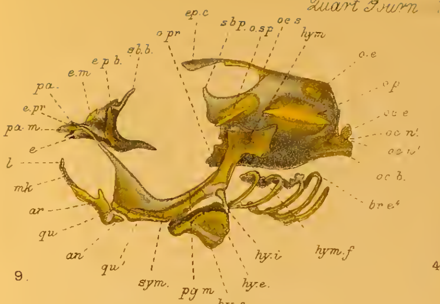

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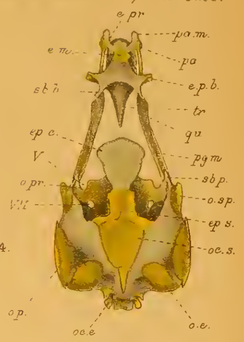

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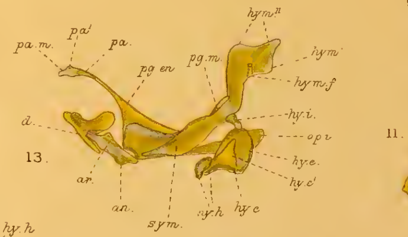

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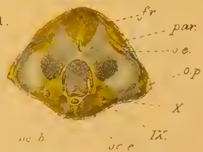

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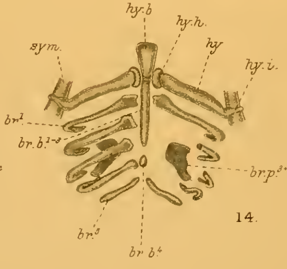

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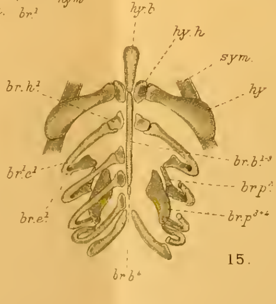

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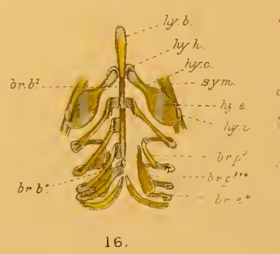

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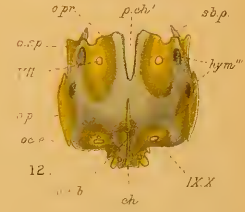

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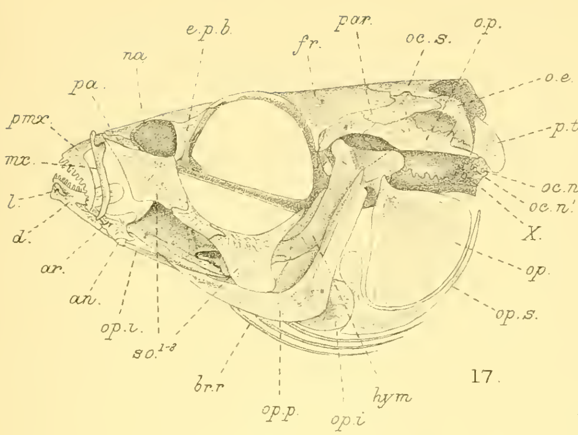

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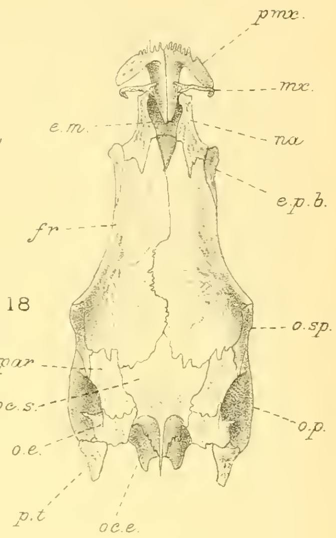

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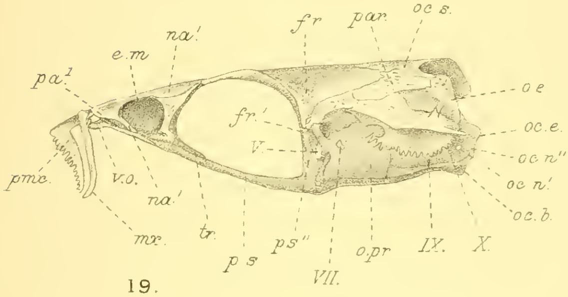

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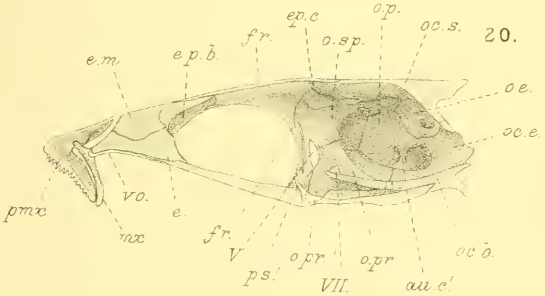

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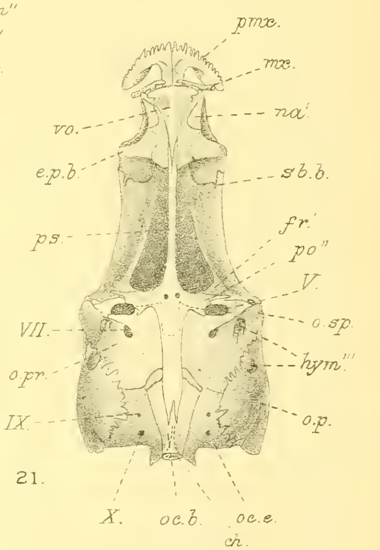

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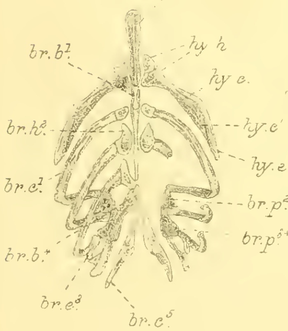

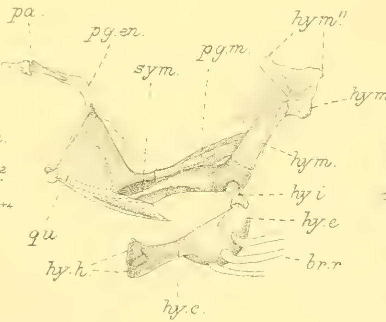

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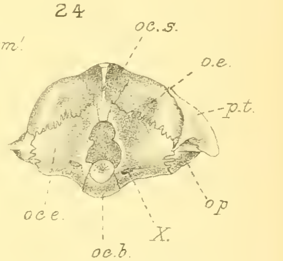

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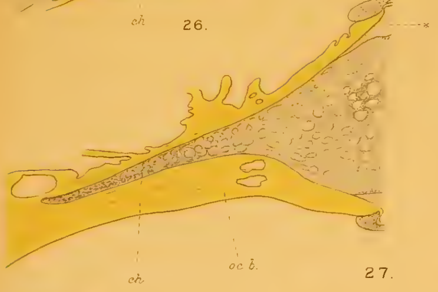

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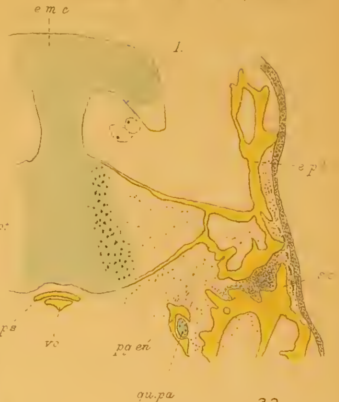

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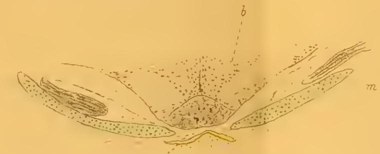

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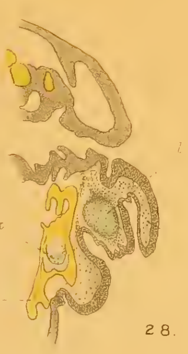

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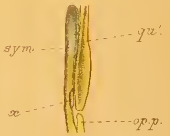

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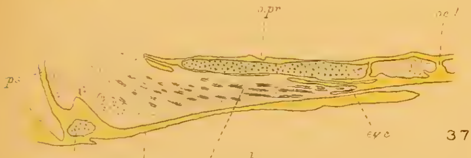

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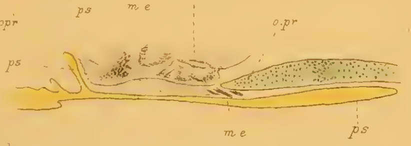

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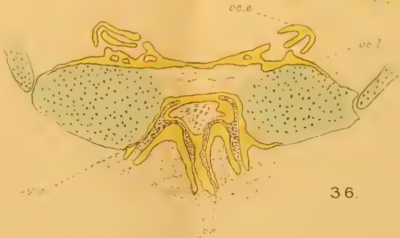

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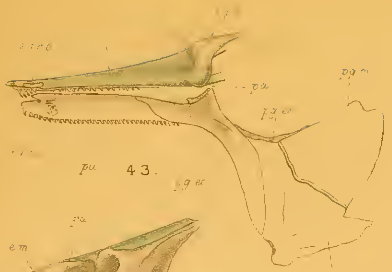

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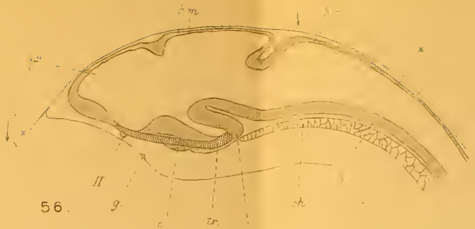

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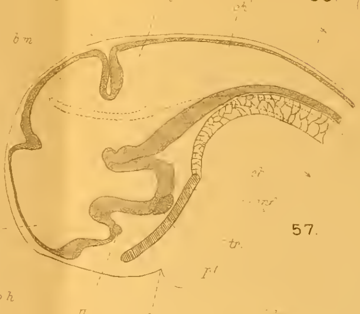

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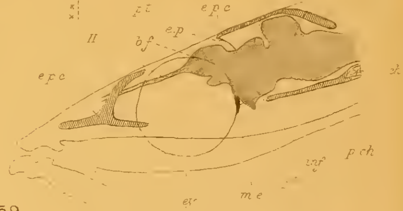

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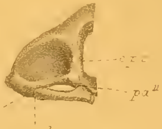

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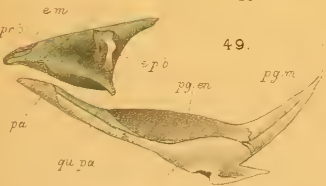

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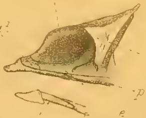

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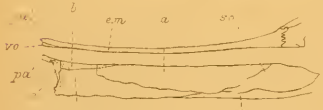

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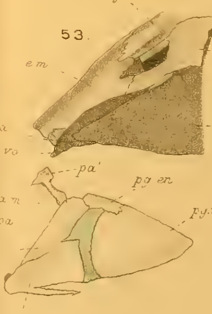

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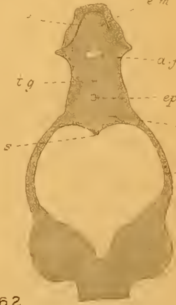

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A. S. Huth, Lith^r London.

The Development of Admetus pumilio, Koch: a Contribution to the Embryology of the Pedipalps.

By

L. H. Gough.

With Plates 32 and 33.

Introduction.

I began my investigations of the development of Admetus pumilio in November, 1899. During the previous year I had been studying the development of spiders under Prof. A. Goette, in Strassburg.

Through the kindness of Prof. R. Burckhardt I received materials to examine, which he had obtained from Dr. Goelde, in Para. These materials consisted of two females of Admetus pumilio, each of which carried a batch of eggs, which will be described under Stages II and V.

In January, 1900, I received two further batches of eggs, this time through the kindness of Dr. G. Hagmann, also in Para; unfortunately only one of these batches was of use; from it I procured Stages I, III, and IV; the other had been deserted by the mother animal, as Dr. Hagmann stated. Cuts through embryos coming from this batch only show an inner mass of yolk surrounded by a thick and dense layer of bacilli. I was not able to procure any further material.

At this place I must also express my thanks to Prof. F. Zschokke, Director of the Zoological Institute of the

University of Basle, in whose laboratory this paper was prepared, and to Prof. R. Burckhardt, to whom I am much indebted for the help he rendered me during my studies, and more especially whilst working at this paper.

I must also express thanks publicly to Dr. Goelde and Dr. Hagmann for having procured me the materials, and to my friend and fellow-student Oscar Huber, for some of the drawings given in this paper.

Technical Remarks.

It was at first very difficult to obtain good cuts through the eggs, because of the presence of the great amount of yolk which they contained. When embedded in paraffin the yolk always crumbled away before the knife of the microtome.

The following is the method I usually used :—The embryos were brought through successive degrees of alcohol into absolute alcohol. Next they were left in celloidin for some days. They were then taken from the celloidin and put directly into chloroform. This has the double effect of making the celloidin firm, and of rendering the embryos ready to be transferred into paraffin. After having been treated thus, the embryos were cut as ordinary paraffin objects. The cuts were attached to the object-glass with water; when all the cuts were arranged on the glass, the water was quickly removed with a piece of blotting-paper, whereupon very fluid celloidin was poured over the cuts; they were then allowed to dry, but being still enclosed in paraffin the cuts could not shrink in any way. When quite dry the coating of celloidin became very thin indeed.

To remove the paraffin I again always used chloroform. Afterwards the cuts were treated in the usual manner. In this way I managed to obtain several perfect series, the yolk remaining in its place without being liable to crumble.

The staining was always done with eosin and hæmatoxylin, and invariably after cutting, the outer cuticle of the embryos being impermeable to the reagents used.

LITERATURE.

The object of this paper is to supply, as far as the materials at my disposal permit, a gap in the literature of the embryology of the Arachnids. Only three papers have as yet appeared treating the development of the Pedipalps. Of these one is on the development of the Thelyphonidæ, the other two treating the development of the Phrynidæ. Their titles are—(1) Dr. Strubell (**42**), 'Zur Entwicklungsgeschichte der Pedipalpen' (Vorläufige Mittheilung); (2) Sophie Pereyaslawzewa (**37** and **38**): (*a*) 'Les premiers stades du développement des Pedipalpes;' (*b*) 'Les derniers stades du développement des Pedipalpes;' (3) M. Laurie (**31**), 'On the Morphology of the Pedipalpi.' Of these three authors only the two last mentioned treated of the Phrynidæ.

When we compare the ages of the embryos I intend to treat about, we find that my first two are younger than Pereyaslawzewa's youngest, my third one is of the same age as her second, and my fourth corresponds to her third. My fifth stage is younger than both Pereyaslawzewa's last stage and Laurie's embryos.

PRELIMINARY REMARKS.

I intend to divide the description of the embryos into five parts, giving each stage in my possession a section to itself. In each stage I will first consider the general superficial appearance, and then the details found in the sections.

STAGE I.

The earliest stage at my disposal was obtained out of a batch of well-developed eggs, the rest of which had already undergone reversion. The egg in question had for some reason or other, probably pressure, stopped growing very soon after fertilisation.

It was perfectly spherical before being cut into sections, and was enclosed in a loose outer membrane. Superficially no differentiation whatever could be discovered.

After having cut it I found it to contain about eight nuclei; these were all situated near each other, not far from the surface. The rest of the egg consists of yolk, the whole being surrounded by a delicate inner membrane.

The position of the nuclei in a group near each other, under the surface, makes it seem probable that the fertilisation of the egg took place in the middle of the egg, and that the first cleavages took place there too; the cells resulting from these cleavages then wandering towards the surface, just as they do in spiders. The pressure of the two membranes also points to a resemblance with most of the other orders of Arachnids, whose eggs are also regularly enclosed in two membranes.

The yolk itself consists of at least two different kinds of yolk elements. The first of these tinges very freely with eosin, and is not influenced by hæmatoxylin. It consists of larger and smaller spherules measuring between ·09 mm. and ·02 mm.; they form the greater bulk of the yolk. The other yolk element is much more irregular in shape, and helps to fill the spaces between the spherules of the element first described, to which it adheres, thus becoming crescent-shaped in cuts, and in reality forming convex-concave lenses. It also differs in tinction from the first described kind of yolk, staining both with hæmatoxylin and eosin to a light purple.

The size of these yolk-bodies varies between ·036 mm. and ·05 mm. The distribution of the yolk elements does not seem to follow any definite rule, unless, perhaps, that the yolk elements last described are more numerous in the interior of the egg. I shall not again refer to the yolk or to the membranes, excepting where I have to point out a change in them.

STAGE II.

The next stage at my disposal is only a little further developed than the one just described. It is derived from a batch of eggs which are all at about the same stage of development.

Surface views of these eggs show that the blastoderm is already formed. It appears as a long white ribbon covering about one third of the surface of the egg in length and one sixth in breadth. At one end the white patch seems much thicker, being more opaque in reflected light. The blastoderm is not of the same breadth throughout its length, but is somewhat narrower in the middle, and rounds out at both ends. The margins are not distinct or abrupt, but gradually fade away until at last they become invisible.

It is not possible to distinguish any further details superficially, the material having, unfortunately, been kept too long in alcohol.

Sections through the egg at this stage show that the blastoderm already consists of the three germinal layers.

The ectoderm consists of a continuous epithelium or layer of cells covering the surface of the egg. The walls of these cells are distinctly visible. The cells themselves are rounded, their nuclei fairly large and somewhat oval; they measure ·01 mm. in length by ·007 mm. in breadth. The chromatin is not evenly distributed, but forming a number of small particles, gives the nuclei a spotted appearance. This layer is sometimes as much as three cells deep.

The mesoderm lies directly under the ectoderm. The cells forming it are disconnected; whether they form a continuous layer in life or not I am not able to decide, as the cells may have shrunk in alcohol. Between the cells of the mesoderm yolk particles are often to be seen, which makes it probable that the mesoderm never consisted of a continuous layer. The nuclei of the mesoderm cells are larger than those of the ectoderm, and also rounder; they measure ·014 mm. in diameter.

The cells of the mesoderm seem to be engaged in rapid reproduction, karyokinetic phenomena being very frequent, and the centrisomata very often visible.

The entoderm consists of single cells, lying deeply embedded in the yolk. Generally only the nuclei of these cells are to be seen. The nuclei are of about the same size as those forming the ectoderm, measuring ·01 mm. by ·012 mm. Their shape is sometimes convex-concave. Their chromatin is very evenly distributed, but still presents a slightly granular appearance.

These three germ layers correspond in appearance and position very closely to the same three of spiders, as described in the handbook of Korschelt and Heider (**26**).

The yolk only differs from the description given in the first stage in the parts nearest to the blastoderm. Where the yolk penetrates the mesoderm, and in all parts adjacent to the same, the yolk spherules have become very small indeed; which would lead one to think that the mesoderm is causing the yolk to break up.

The outer membrane shows no difference from that described in Stage I. The inner has, however, changed since the first stage, having risen above the surface of the egg in the region of the blastoderm, leaving a free space between itself and the ectoderm.

Stage III.

The third stage at my disposal is considerably more advanced than the last. The reversion of the embryo has already taken place, and the extremities have begun to grow. I have only found one egg at this stage; it comes from the same batch as the eggs described under Stage I and Stage IV. Its growth had evidently been stopped by the pressure of the surrounding eggs, which also caused the embryo to develop in two disconnected halves, only held together by the yolk. The embryo also showed several other signs of not having developed normally.

My sections through this egg are, unfortunately, not all that I could wish, but still they are good enough to make out several details. For this reason I shall only attempt to describe a few of the organs.

The brain is already divided into its three parts, the commissures and the two kinds of nuclear tissue, the difference of which will be explained in full in Stage IV. These two tissues are chiefly characterised by the size, tinction, and density of the nuclei they contain, the smaller being closely packed, and stained darker. They measure ·005 mm., the larger, lighter stained, and less dense nuclei, on the other hand, measuring as much as ·009 mm. to ·01 mm.

The ventral ganglion-cord has not yet begun to appear. Those parts of the abdomen and cephalothorax which are bent upon each other at the time of the reversion of the embryo are devoid of any cellular integument, although lined by a thick cuticle. It is in this part that the ventral ganglion-cord takes its origin in the next stage.

It is interesting to observe that, as in spiders, the legs are full of yolk, only the tips being free. The yolk seems to get pushed backwards during the growth of the legs pari passu with the growth of the muscles and nerves. Neither the median nor the lateral eyes have yet begun to appear, nor are the lungs, heart, coxal gland, lateral organs, or alimentary canal in any degree traceable.

It is in the yolk that the chief peculiarity is to be seen. The neighbouring eggs have, through pressure, caused a deep semicircular impression on one side of the embryo, and at the same time caused it to develop in two halves. The pressure has also influenced the yolk, causing several of the yolk-spherules to amalgamate and to form a mass without any regular shape. The appearance of this fusion necessitates the conclusion that the living yolk particles were of a fatty nature, and that they were suspended in a watery lymph, forming a kind of emulsion.

Stage IV.

The next stage which I possess is only a little more mature than the one just described. The reversion of the embryo has taken place long ago, the cephalothorax being separated from the abdomen. The extremities are much further advanced than those of the third stage and, except at their bases, are devoid of yolk. In surface views one sees the Anlage of the brain as two white spots at the front end of the cephalothorax. On the sides may be seen, at the base of the fourth pair of extremities, a horseshoe-shaped excrescence; this is the lateral organ, first described by Laurie as occurring in Phrynus; it is always covered by a shred of some dark substance.

The joints of the legs can already be distinguished, the embryo at this stage greatly resembling the one given in the drawing (figs. 1 and 1 *a*) less the eyes, and with a much smaller amount of brain.

There are six pairs of extremities to be observed. The first pair, the cheliceræ, now lie before and on both sides of the mouth, and under the fold which carries the median eyes; their bases lie fairly wide apart. They are double-jointed, the second joints pointing towards each other, not as in adults, parallel and pointing downwards; this becomes still more conspicuous in the fifth stage.

The pedipalpi, too, begin near the same fold, to which, indeed, their bases are attached. At their bases they give off a branch, the endopodite, which forms a kind of mandible. As yet no thorns are to be found on the ectopodite; they first begin to appear in the fifth stage. The ectopodite is much larger than the endopodite.

The third pair of extremities corresponds to the first pair of walking legs in spiders; here they are developed into long whip-like legs, with probably only a sensory function. They lie doubled up upon themselves, surrounding the pedipalpi, and with their tips reaching as far as between the cheliceræ. At the bases of this and the next posterior extremity I have been able to find the coxal gland. The next three pairs of extremities are the walking legs; they are all of about the same length, and shorter than the whip-legs. They are likewise doubled upon themselves, and their free ends are tucked under the preceding legs, only the sixth pair making an exception, the tibia and tarsus of which run along the under side of the other legs.

The whole embryo is enclosed in a loose outer skin, which follows the contour of the whole body, extremities included, without ever actually touching it, except, perhaps, in the region of the lateral organ, and in parts of the dorsal side of the abdomen. This cuticle is covered in parts with numerous wart-like processes, as mentioned by Pereyaslawzewa (**37**) and Laurie (**31**). On surface views nothing further is to be seen; we will therefore proceed to the description of the organs as seen in cuts.

(1) The Skins.—The outer cuticle just mentioned is seen in cuts to consist of several exceedingly thin strata; it is otherwise perfectly structureless. The embryo itself is covered by a thin epidermis, which in most places consists of a single layer of cells. It does not as yet extend over the entire surface of the embryo, patches on the sides of the abdomen being still void of this covering.

(2) The Cœlom.—I have not been able to follow out the development of the cœlom. In my younger embryos it was, of course, not to be found. At this stage it has already reached a high development. I consider two layers of cells found under the epidermis, which send folds into the interior of the yolk, to be the cœlom, from their resemblance to the cœlom of Spiders and Scorpions. The cœlom also enters the bases of the legs. With the folds the Anlagen of the future dorso-ventral muscles of the cephalothorax and abdomen also enter the yolk. Between cœlom and epidermis are also found the first Anlagen of the segmental muscles, which arise from the somatic cœlom layer.

(3) The Lateral Organ.—The lateral organ of the Pedipalps has already been described by Laurie (**31**) and Strubell (**42**); it has also been described by Bruce (**9**) and Pereyaslawzewa (**37**).

In the stage which we are now considering the lateral organ seems to be at the height of its development. It appears as a horseshoe-shaped excrescence on the base of the coxa of the fourth extremity, which it covers on both sides. It is always covered by shreds of some dark substance, which is probably secreted by it. Cuts show that the lateral organ is a more complicated structure than it seems to me to have been considered as yet.

I am not able to state anything as to the origin of this structure, as I possess only embryos without the lateral organ, or with it in later stages of development.

Cuts show that the lateral organ consists of an outer layer of cells, forming the external wall of the sac; the interior of the sac contains two cavities filled with yolk, which are separated from each other by a second internal wall of cells, running nearly parallel to the external wall. The cells forming the outer wall of the lateral organ (fig. 5) are deeply stained with eosin; they protrude into the processes of the cuticle, at whose bases a dark substance is being deposited. The nuclei of these cells are oblong, and take a deep stain from hæmatoxylin.

The internal walls of cells resemble the external in its histological elements, with the difference that its cell walls are not visible, and that the cells have no distinct outline, so that it is almost impossible to determine their boundaries. On the side of this wall nearest to the body of the embryo protoplasmic processes of these cells are seen enveloping yolk particles.

The yolk in the one cavity does not resemble that in the other. In the outer cavity, enclosed by the external and internal wall, this yolk consists of very minute particles, which appear to have had to pass the internal wall before having reached the external cavity. The yolk in the internal cavity still in every respect resembles that filling the abdomen, and is in direct communication with it.

At the base of the lateral organ, where it is attached to the base of the fourth extremity, the epidermis has begun to grow inwards, forming a partition between the lateral organ and the leg. This partition has still an opening in the middle, through which the inner cavity of the lateral organ communicates with the yolk of the embryo. Later on this opening closes, after which the lateral organ becomes functionless and drops off.

The lateral organ of the Thelyphonidæ has been described by Strubell (**41**), and there is no doubt that it is identical with that of Admetus. In other orders of Arachnids we only find the lateral organ in Solpugids and Pseudo-scorpions.

Croneberg (**10**) described the lateral organ of Galeodes. This also seems to be very similar to that of Admetus. I have also been able to find a similar organ in a young adult Chelifer; it seems to me to have already become functionless, and much resembles that described for Admetus in the fifth stage. The possession of a lateral organ seems to me to point out a nearer relationship between these three groups.

(4) The Coxal Gland.—There is in Admetus, as in all Arachnids, a so-called coxal gland. I have found it, like the authors already cited, Miss Pereyaslawzewa excepted, at the base of the third extremity; I am also able to prove its existence, if only as a rudiment, at the base of the fourth extremity. This last atrophies very soon. At this stage the coxal gland consists of a perfectly straight tube, running from the under surface of the coxa inwards, and lying immediately on the surface of the brain itself. It is easily distinguishable from the brain by the lighter tinction of its nuclei. It is everywhere surrounded by connective tissue. Whether it is still in open communication with the cœlom or no I am not able to decide. The occurrence of the coxal gland at this stage in the fourth extremity as well as the third makes it appear probable that it was originally segmental, as in scorpions, and it is likely that it would be discoverable in every segment in earlier stages of growth.

(5) The Nervous System and Sense-organs.—The nervous system at this stage consists of the cerebral ganglia and of the ventral ganglion-cord; this last extends far into the abdomen.

Of sense-organs only the median eyes and the coxal sense-organs have as yet made their appearance.

The præoral part of the brain consists, as in Stage III, of two distinct tracts, distinguishable by size, colour, and number of nuclei. The more anterior part consists of closely packed, small and darkly stained nuclei, averaging ·0034 mm. in size. Nowhere in the rest of the brain are the nuclei so small, so densely packed, or so darkly stainable. We shall call this part of the brain the accessory brain. In all other parts of the brain the nuclei are less densely packed; they average ·01 mm. in diameter. The brains of adult Admetus also show the same division.

These two parts of the brain, following Laurie (**31**), who has briefly referred to the difference, are also said to be distinguishable in Scorpions.

I am in a position to give more notes about the development of the ventral ganglion-cord. This last extends on the one hand from the cerebral ganglia, into which it merges imperceptibly, and runs along the ventral side of the cephalothorax and ends in the abdomen. In the latter it merges into the ectoderm so continuously that it is impossible to say where the ventral ganglion-cord begins and the ectoderm of the abdomen ends.

As all the different stages of the embryonic development of the brain are to be found in the ventral ganglion-cord of one embryo, it will be as well to give an account of it, beginning, for the sake of simplicity, with the distal and least differentiated part of the cord (see fig. 8).

If we examine the epidermis covering the median ventral line of the abdomen at the part where it is thinnest, we find that it consists of two layers of cells, surrounded by much protoplasm. The cell walls are not visible. The nuclei are oblong and tinge deeply with hæmatoxylin; the chromatin not being equally distributed, but collected in small masses, gives the nuclei a spotted appearance. The micro-nucleus is conspicuous in several of the nuclei.

The nuclei of the two layers lie with their axes pointing in different directions, the rounder nuclei of the outer layer, which measure ·01 mm. in length and ·008 mm. in breadth, being mostly inclined at an angle of about 75° to the surface; the more oblong nuclei of the inner layer, measuring ·01 mm. in length and ·004 mm. in breadth, lie parallel to the outer surface of the embryo. This inner layer is continued forwards, and forms a skin covering the inner surface of the brain; it is of mesodermatic origin.

The first step towards the differentiation of the brain out of the epidermis just described consists of a rapid thickening of the outer or germ layer, through the multiplication of its cells. It soon becomes six to seven cells thick, and the nuclei have no longer any common direction. Through the thickening of the outer layer the surface of the embryo has here become a little arched. After this the outer or germ layer again becomes thinner, and only consists of one layer of cells. The inner layer also thickens till it becomes two or three cells deep; but as it does not take part in the construction of the brain I shall refer to it again as little as possible.

After proceeding forwards a short distance, probably corresponding to one abdominal segment, the cell-mass of the germ layer becomes again reduced to a single layer of cells; then it thickens again as before.

When the germ layer has reached its former thickness we observe several important changes. In the first place a new element has begun to develop. The cells of the germ-layer nearest to the surface have changed the direction of the axes of their nuclei. The nuclei themselves have become much elongated, measuring now ·015 mm. in length by ·004 mm. in breadth; they have also become poorer in chromatin. In this manner a new outer integument, the definite epidermis, has been formed.

The cells forming the germ-layer were till now equally distributed throughout the whole of the layer; this now ceases to be the case. A little space void of nuclei is formed on the surface of the germ-layer. This is filled with plasm; just above it there is a gap in the epidermis. For convenience, sake I shall call such superficial masses of un-nucleated protoplasm "surface pits;" this name I give only with reference to their appearance, and not to their structure, and I desire that this may be distinctly borne in mind. The nuclei of the cells of the germ-layer adjacent to this "surface pit" are beginning to arrange themselves radially around the centre of the hollow. Further on, again proceeding forwards, the germ-layer again presents its former appearance. Still proceeding towards the cephalothorax, we meet with another new change. Just before the next thickening containing a "surface pit" is reached, the mesodermatic inner skin begins to lift itself from off the nuclei of the germ-layer. The space between both is now filled with nerve-fibres, the longitudinal fibres being the first to appear, as in Scorpions (Brauer [7]). This "surface pit" only distinguishes itself from the last by the presence of a slight depression on its surface.

After the next "surface pit" has been reached, the germ-layer loses its continuity and breaks up into a number of groups of cells, each lying in front of its corresponding "surface pit." The space around these groups is filled with nerve-fibres, forming the commissures; they seem to run in every direction. A change has also taken place in the epidermis; its nuclei are no longer so elongated, having become more rounded; they now measure ·01 mm. by ·005 mm.

The first of the groups of brain-germ cells met with measures ·08 mm. in length by ·02 mm. in breadth, and lies ·02 mm. from the surface of the embryo. It is composed of nuclei lying about three deep and twelve broad, measuring between ·009 mm. and ·01mm. They all lie with their long axes pointing towards the surface. The nuclei of these groups are all connected with the centre of the "surface pit" by radial fibres, which all converge towards it. The fibres probably belong to the neuroglia, and serve as a supporting tissue.

The epidermis is discontinued just at this "surface pit," as it was in the last. The "surface pit" also resembles the last described in having a slight depression on its surface. The cells of the epidermis also take an active part in the building up of the groups, by forming a funnel-like sheath around the radial fibres. The nuclei of the cells forming this sheath measure about ·018 mm. in length by ·005 mm. in breadth. Karyokinetic figures are sometimes to be found in them.

The next such collection of germ-cells is, perhaps, even more typical. It lies just at that point where the abdomen forms an angle to the cephalothorax (fig. 8). Although more advanced than the last its dimensions are not larger.

The length and breadth are the same as those of the last group, the length of the radial fibres being ·02 mm., as in the last case; the group, however, now lies ·037 mm. from the surface.

The cause of the group lying deeper than the last described is an ingrowth of the epidermis in the shape of a narrow tube. Its bore is ·007 mm., and its length ·01 mm. The walls of this tube are formed by a single layer of cells, whose nuclei are but lightly stained, and which contain very large micro-nuclei. One nucleus I measured was ·01 mm. long by ·004 mm., its micro-nucleus, however, actually measuring ·004 by ·003 mm.

The nuclei of the cells forming this tube are all arranged with their long axes lying at right angles to the axis of the tube. The tube ends in an expansion, forming a nearly spherical sac, whose diameter is about ·01 mm. The walls of this sac are formed by the ends of the radial supporting fibres. The sac just described lies within the funnel-shaped sheath, which encloses the radial supporting fibres. The next group of cells so much resembles the last described that it is not necessary to go into any details about it.

Still proceeding forwards, we now meet with a group which half retains its original form and independence, and is half connected with and converted to the ventral ganglion-cord in its definite form. The original germ-group lies ·1 mm. from the surface; its inner surface abuts on the commissures. On the side of the group which is turned towards the abdomen, the sheath covering the radial supporting-fibres and the germ-cells forming the group are as before, but the cells forming the tube have multiplied rapidly, and now reach as far as the cells forming the group. On the anterior side all parts of the group have multiplied their cells to such an extent that they build a solid mass of nuclei, reaching from the surface to the commissure. In this mass only the nuclei of the sheath can be distinguished from the others. The interior of the epidermis-tube is now filled with supporting fibres.

From the interior surface of the nucleiferous mass are seen in parts nuclei wandering through the commissural part of the brain, the "Punktsubstanz;" these afterwards form a cellular layer on the dorsal side of the commissures, which had been hitherto only covered by the mesodermatic inner skin mentioned at the beginning of this description. That the whole of the post-oral ventral ganglion-cord is formed in the manner just described is proved by the presence of numerous remains of tubes, filled with tangled masses of supporting fibre, in the brain-mass. Each such tube denotes the place where there was such a group of cells during the earlier development of the cord. Later on the tubes become entirely obliterated. These groups of cells, with their radial supporting fibres, their sheaths and tubes, possibly represent what Patten (**34**) compares to ommatidia in his description of the development of the brain of Arthropods. The comparison with sense-organs is certainly very good. I find, however, more resemblance with the "Hügelorgane der Seitenlinie," as described by Leydig for fishes, and by the Sarasins (**40**) for the larvæ of Amphibians. Judging by Patten's figures, however, I must conclude that he saw a phenomenon in part different to that which I have just described. In his drawing one sees that each segment of the brain is composed of several sense-organs, with larger ones in the middle line.

I have only been able to find one in each neuromere. This probably corresponds to the larger sense-organs in Patten's figures. It is to be regretted that Patten did not publish any drawing of a transverse section of such a sense-organ, or a description of their development. Kishinouye (22) also states that the nervous system of Limulus consists at one period of peculiar cell-groups resembling ommatidia. According to the drawings he gives, he must have cut them at right angles to the direction in which I have cut them in the embryo described.

According to the description just given, we find that the brain is derived in all its parts from the ectoderm, as follows:

(i) Directly, as regards the germ groups.

(ii) Indirectly, through the epidermis, as regards the sheaths surrounding the radial supporting-fibres and the tubes.

In more mature portions of the brain the cell-elements have reached a higher development. We find in the ventral ganglion-cord the two usual kinds of nerve-cells, lying the one amidst the other.

(i) Cells with smaller, generally oblong nuclei, measuring ·01 mm. by ·007 mm., without visible protoplasm; these form the chief part of the brain behind the accessory brain. It is impossible to distinguish these nuclei from those of the germ-layer or from the neuroglia.

(ii) Cells with larger, generally round nuclei, measuring ·015 mm. in diameter; these nuclei do not generally stain so deeply with hæmatoxylin. They are usually surrounded by protoplasm, and often have very distinct micro-nuclei. They are usually to be found near the commissural substance. They much resemble the ganglion-cells of other animals.

The real meaning of the just-described process of development becomes clearer when we compare the development of the central nervous system of the Arachnids with that of other classes of animals. Since the Arachnid brain has reached such a high degree of perfection, we must look for analogies chiefly in classes of similar development of brain. First we may look to the Vertebrates.

In the central nervous system of Vertebrates and Arachnids the grey and the white matter seem to have totally different relative positions; the white substance surrounding the grey in Vertebrates, and being almost surrounded by it in Arachnids. This seeming dissimilarity is soon explained. Since the central nerve-tube of Vertebrates becomes folded inwards during its development, it is clear that its innermost walls, which abut on the canalis centralis, are that part of the wall which was originally outermost. Thus we would in both cases have the grey substance outermost, the white substance lying under it.

His (**16**) describes the spinal cord of Vertebrates as arising out of "Zwei Kernfrei Zonen, eine äusserste und eine innerste, und eine die kerne enthaltende Mittelzone." He terms the outer of the two zones without nuclei the "Randschleier," the inner the "Säulenschicht." These three layers or "Zonen" are all to be met with in Arachnids, though somewhat modified, having in part become discontinuous. The columnal layer, "Säulenschicht," could be compared to the "surface pits;" but it, of course, no longer forms a continuous layer in Arachnids as it does in Vertebrates. The "Mittelzone" can be compared, as regards position and structure, to the nuclei groups in the developing ventral ganglion-cord of Admetus, and the "Randschleier," which gives rise to the white matter in Vertebrates, is evidently equivalent to the commissural substance, or "Punktsubstanz" of the brain of Admetus, also as regards position and structure.

The ganglion cells of Admetus are almost always to be found in the depth of the grey matter, just below the Punktsubstanz or white matter, as is also the rule with Vertebrates. In the latter all nerves proceed out of the white substance. Even this has an analogy in Arachnids, as all the nerves I met with in my cuts left the ventral ganglion-cord just above the grey matter, at places where the nucleiferous covering of the "Punktsubstanz" was very thin. These were the chief points of resemblance. The chief points of difference are—in Vertebrates the origin of the neuromeres is evidently secondary; nerves issue from the spinal cord only in those places where the vertebral sheath leaves them spaces to pass through; in Arachnids the neuromeres appear, in Admetus at least, to be primary in origin, and at the same time to be segmental. This does not point to any fundamental difference in the whole process; on the contrary, it is only to be expected that the segmentation which occurs in Arthropods should be more constant and more early in appearance than that of Vertebrates. In these the segmentation is disappearing everywhere, and in all systems of organs.

According to a theory of von Kupffer and others, the sense-organs of the Vertebrates are derived from a hypothetic primitive form of sense-organs, the so-called placods. The placods remain in their least changed form as the "Hügelorgane der Seitenlinie" of Leydig, and as papillæ of the organ of taste. These sense-organs much resemble those just described as building part of the Anlage of the ventral ganglion-cord of Admetus. A similar feature is that the epidermis of the branchial region of Vertebrates gives rise to the epibranchial ganglia,—that is to say, in Vertebrates, as in Arachnids, primitive sense-organs take part in the building up of the ganglia.

The Sarasins (**41**) have also pointed out the resemblance of small sense-organs of Helix Waltoni to the "Hügelorgane" of Ichthophis. Here the sense-organs also seem to take part in the building up of the ganglia. A peculiar coincidence is to be found when we compare the brain of Helix Waltoni with that of Admetus. The Sarasins mention that the most anterior portion of the brain of Helix Waltoni consists of very small, darkly stained, and closely packed nuclei, containing no Punktsubstanz and no ganglion-cells; this portion of the brain of Helix Waltoni they call the accessory brain. The process of the development of the accessory brain of Helix Waltoni resembles the same process in Admetus very closely and conspicuously. According to the Sarasins the accessory brain of Helix Waltoni takes its origin out of the so-called cerebral tubes; by analogy with Scorpions, it is perhaps possible to prove the same for Admetus, though I can only find it by comparing the papers of Brauer (**7**) and Laurie (**29**). Laurie says that the median eyes of Scorpions arise out of an invagination, which takes place just in front of the Anlage of the brain; he describes the cells forming it as resembling brain-cells, but having smaller, darker stained and more densely packed nuclei; in another paper (**31**) he states that the brain of Phrynus resembles that of Scorpions inasmuch as in both cases we find a division of the brain in a part containing smaller, darker, and more densely packed nuclei, and a part with lighter, larger, and less dense nuclei. According to Brauer the median eyes arise on a small projection, which lies beyond the invagination mentioned by Laurie, this invagination becoming deep, and giving rise to an accessory part of the brain. Brauer, however, omits to mention whether he found the nuclei composing this part to differ from those forming other parts of the brain.

According to Kleinenberg (**25**) part of the nervous system of Lopadorhynchus is also formed out of primitive sense-organs, which afterwards become converted entirely into ganglion-masses.

We are thus led to suppose that the central nervous system of Arthropods to some extent corresponds in origin and structure to that of Vertebrates; namely, as regards the origin of the three layers ("Saulenschicht," "Mittelzone," and "Randschleier" "surface pit," germ-group, and commissural substance), and as regards the conversion of sense-organs into ganglia. To some extent it corresponds to that of Molluscs, namely, as regards the origin of ganglia out of sense-organs, and perhaps in possession of an accessory brain. Lastly to that of Worms, namely, as regards the origin of ganglia out of sense-organs.

The Median Eyes.—As yet only the median eyes have begun to make their appearance. Being unpigmented they are not visible on surface views. The lateral eyes are first met with in more mature stages. Just above the cheliceræ, on the front of the cephalothorax, we meet on each side with a lappet-like excrescence, the bases of which have already begun to unite with each other where they meet in the median plane; thus they form a kind of mask in front of the embryo, covering its mouth. The space beneath this mask remains hollow till much later.

These folds are the Anlagen of the median eyes; they consist of two simple thickenings of the ectoderm, which have probably been inverted in the way described by Brauer for Scorpions.

The front wall of the eyes still only consists of a single row of cells; in the posterior wall the cells have begun to multiply. The space between the anterior and posterior walls of the eyes contains no nuclei, being only filled with cell-walls and plasm.

The eyes measure in length ·1 mm.; they are ·04 mm. thick.

Besides the eyes there is only one other set of sense-organs to be found. These are the segmental sense-organs first described by Patten (**34**) as occurring at the base of the legs of Spiders; they were also described by Brauer (**7**), who found them in Scorpions. The description and drawings given by Brauer accord with those which I could give for Admetus.

(6) The Alimentary Canal.—The alimentary canal is at this stage still very incomplete, only the most anterior part existing as yet. It consists of a simple tube which just pierces the brain. Its outer anterior end does not project beyond the brain, the posterior end doing so for about one third of its length. From the point where it leaves the brain it is slightly bent in a ventral direction. The cells forming the walls of the alimentary canal form a thick layer at both ends of the tube. No muscles are as yet observed in connection with the alimentary canal.

In transverse sections it otherwise presents a similar appearance to that of more advanced stages.

The cavity of the alimentary canal is **Y**-shaped; the cells composing its walls are high and cylindrical. The nuclei chiefly lie at the end of the cell nearest to the cavity. A thin cuticle has been secreted by these cells.

The whole is surrounded by a thin layer of mesoderm cells, which form a skin round the tube. The nuclei of these cells have begun to elongate, and will probably form the ring-shaped muscle found later on in this part.

(7) The Heart.—The circulatory organs are at present represented by the heart alone. The origin of the heart seems to me to be the same as in Scorpions (Brauer [7]) and other Arachnids. It is evidently formed by the cœlom on both sides of the embryo meeting, leaving a space between the walls on either side, which, although surrounded by cœlomatic walls, does not belong to the cœlom itself. The heart causes a slight ridge on the surface of the embryo.

(8) The Lungs.—At this stage the lung-books are just beginning to make their appearance. They belong to the first and second abdominal extremities. Laurie (**31**), however, has located them on the first and third. They differ neither in development nor in appearance from the lungs of other Arachnids.

(9) The Muscles.—Typical muscles are as yet nowhere to be found. In the extremities, and also in the abdomen, we find the cells which give rise to the future muscles. These are distinguishable by their long, granular nuclei. Though already spindle-shaped, they do not as yet stain with eosin, as the muscles in more advanced embryos always do.

(10) The Genital Organs.—The genital organs have not as yet begun to make their appearance.

STAGE V.

The two illustrations (figs. 1 and 1 *a*) of the embryo at this stage will give a very good idea of the general superficial appearance of these embryos. They appear in almost every respect similar to the embryos of the fourth stage, and the description of those embryos only requires a few additions to be perfect for the embryo of the fifth stage.

In the first place we must remark the median eyes. They are now very deeply pigmented, except in a narrow line which separated the two eyes.

The lateral eyes are now also visible; they resemble Y-shaped marks on both sides of the median eyes. This is caused by the pigment being deposited between the single ocelli, which are three in number. The margin of the fold carrying the median eyes is also more distinctly visible than in the fourth stage.

1. The Skins.—No important change can be observed in the skins since Stage IV.

2. The Cœlom.—The cœlom has undergone many changes since Stage IV. It has, for instance, given rise to the muscles, of which at least two sets are to be distinguished. A dorso-ventral muscular system has followed the foldings of the cœlom, and now consists of a paired muscle in each segment, running from the carapace to the ventral side, except perhaps in the first two segments of the cephalothorax. The other set consists of the intersegmental muscles. These run parallel to the surface, from segment to segment. The walls of the cœlom also take part in building up the mid-gut. On the ventral side of the abdomen we also find the genital cells lying inside the cœlom, as will be described further on.

3. The Lateral Organ.—The lateral organ is still to be found, but it seems to me to have ceased to have any function. Superficially it seems to be in the same state as it was in the fourth stage; it is only on cuts that the difference is remarked.

Sections show that the lumen of the lateral organ is no longer directly connected with that of the rest of the body, and with the base of the fourth extremity in particular.

The cells which at a less mature stage formed the walls of the lateral organ have died off, and it is only here and there that traces of them are found. With the drying up of the wall cells their plasma has been withdrawn from the interior of the wart-like processes of the cuticle.

In the fourth stage the outer cavity of the lateral organ was filled with very small yolk particles; these have now conglomerated and form a solid mass, staining deep red with eosin. The partition that had begun to form between the base of the lateral organ and the base of the fourth extremity is now complete.

A remarkable fact is that a substance resembling the filling of the lateral organ is to be found in the adjacent parts of the base of the fourth extremity.

The shreds of dark substance covering the lateral organ in the fourth stage have become much thicker (they have been removed in the drawing [fig. 1 *a*], so as not to hide the lateral organ). This makes it appear more probable that they have been secreted by the lateral organ.

4. The Coxal Gland.—At this stage the coxal gland is at the height of its development. Only the gland belonging to the third extremity is still to be found. It occupies all the space between the cerebral ganglia and the ventral ganglion-cord that is not occupied by the muscle-stomach. Bulging over the sides of the ventral ganglion-cord, it now lies in at least four segments, namely, the third, fourth, fifth, and sixth, its opening lying at the base of the third extremity.

There are two different parts of the gland which can be distinguished, namely, the mouth end and the gland proper. The mouth end is composed of cells in every way resembling those that form the epidermis. Its nuclei are oblong, and stain deeply with hæmatoxylin. In this part I observed no trace of cell-walls. The second part builds up the chief bulk of the gland itself. It consists of an unbranched tube, much convolved at its inner end. The tube runs nearly straight from the surface up to near the brain; next it bends backwards and runs in almost a straight line till it reaches the sixth segment; then it begins to twist and turn so much that it is impossible to follow it further. As I have nowhere been able to observe a branching of the tubes, I suppose that it must be simple in its whole length, as in other Arachnids.

The cavity of the gland is about ·01 mm. wide. The cells composing the tube have very distinct cell-walls, the cell-plasm being very clear and staining very slightly. The nuclei are perfectly round, and do not stain very deeply; their diameter is ·007 mm. They lie almost always on the side of the cells nearest to the lumen of the gland, leaving, however, a space between themselves and the cell-walls. In this space the plasm seems at its thickest. The length of the cells, measured from outside the gland to the cavity of the gland, is ·02 mm.

The tube forming the gland itself is enclosed in a sheath of flat cells, of mesodermatic origin, as in other Arachnids. The space between the windings of the tube is filled out by connective tissue. The whole gland is likewise covered by an outer skin, the elements of which somewhat resemble those forming the sheath of the tabule.

5. The Central Nervous System.—The nervous system now consists of the cerebral ganglion, the ventral ganglion-cord, and the nerves.

When compared with the fourth stage, the ventral ganglion-cord appears much contracted. In the fourth stage it was continued far into the abdomen, now we only meet with it in the cephalothorax.

A great advance on the fourth stage is also to be observed in the development of the ganglia. In Stage IV it was impossible to distinguish them from each other; now they are very distinct. The whole brain has become very similar to that of the adult.

The outer form is to be seen in the illustration (fig. 2), made after a model constructed by me from a section-series. I will begin by a description of the superficial appearance of the brain.

A glance at the illustration will show that the brain consists of two parts, a smaller dorsal and a larger ventral. It is pierced by the alimentary canal in the region where the two parts are joined to each other.

Five pairs of nerves issue from the ventral or post-oral part of the brain; these belong to the pedipalpi and the legs. The nerves and ganglia belonging to the cheliceræ are præoral.

No other nerves as yet leave the dorsal portion of the brain, though two swellings on each side of it, just behind the ganglion of the cheliceræ, denote the optic ganglia. They are not yet connected with the eyes by nerves, these being very late to appear. The dorsal portion of the central nervous system contains the accessory brain, the four cerebral ganglia, and part of the ventral ganglion-cord, containing the ganglia of the cheliceræ.

The ventral ganglion-cord consists of eighteen ganglia, six belonging to the extremities. The other twelve are very small; although lying in the cephalothorax they really belong to the abdomen.

The elements forming the brain and ventral ganglion-cord are histologically mostly the same as those described in the fourth stage. We now remark, however, small masses of darker stained fibres in the commissural parts of the central nervous system, the origin and structure of which it is difficult to understand. They are not to be found in the adult brain.

6. The Eyes.—The median eyes have become much further developed since the fourth stage. This can best be described in connection with the drawing (fig. 6). The median eyes are still situated on a fold in front of the mouth. The mouth opens into the cavity (*c.*) formed between the fold carrying the eyes and the cephalothorax. We can distinguish between three distinct layers of the fold—the corneal, the retinal, and the subretinal layer. This last is separated from the retinal by a fissure.

The stratum corneum (*co.*) consists of a layer of nuclei, two or three deep. In front it has begun to deposit chitin, the future lens (*l.*).

Under the cornea lies the retina (*r.*). It is deeply pigmented in its anterior half. One can distinguish thicker and thinner lines of pigment (*p.*) in front. The retinæ of the two eyes are very distinctly separated from each other by a light unpigmented line (*s.*).

The post-retinal layer (*pr.*) resembles the epidermis elsewhere.

I am not in a position to say how the eye has developed out of the Anlage described in the fourth stage.

There are three lateral eyes on each side of the cephalothorax. They lie in groups in a line with the median eyes. The lateral eyes originate out of simple ectoderm thickenings, as Laurie stated, as will be seen in the drawing (fig. 7). Pigment is as yet only deposited in the spaces between the single eyes. The lateral eyes of the adult also consist of three facets.

7. The Alimentary Canal.—Since the fourth stage the alimentary canal has made very rapid progress. It now forms a nearly complete tube, only the foremost part of the midgut remaining absent. The alimentary canal now consists of the following parts:—mouth, pharynx, œsophagus, muscle-stomach, midgut, and rectum. The mouth is situated on a small protuberance, which projects into the subocular cavity, and lies between the bases of the pedipalpi. Just behind the mouth we find the pharynx; that has an I-shaped cavity, the walls of which are lined with a thin chitinous membrane. The cavity measures ·1 mm. by ·01 mm.

The cells forming the walls of the pharynx have very distinct cell-walls; the nuclei are small, oblong, and stain very deeply with hæmatoxylin; they measure ·007 mm. by ·004 mm. Besides the lateral and dorsal muscles attached to this part of the alimentary canal, described by Laurie, I must draw attention to another set of muscles connected with the pharynx. This set is a ring-muscle, which runs round the pharynx; it evidently acts as the antagonist of the lateral and dorsal muscles, and serves to close the cavity when it has been distracted by the other muscles.

The pharynx goes over into the œsophagus, when it enters the brain-mass. Its hollow is now Y-shaped. The cells forming its walls are similar to those of the pharynx. A distinct cuticle is still to be seen. It is no longer enclosed in a ring-muscle, but is only covered with connective tissue. After having passed through the brain, the alimentary canal again changes its character and becomes muscular once more. Its cavity is much wider here, and is X-shaped in transversal sections. The cells forming this part much resemble those of the parts already described.

The musculature of the muscle-stomach can be divided into two systems, similar to those of the pharynx. The first of these consists of radial muscles, the longest of which runs dorsally towards the carapace; the two others are much shorter, and insert laterally in a cartilage, which also serves to support the coxal gland.

The other system again consists of a ring-muscle, which is much stronger than that in the region of the mouth.

As yet the muscles are all smooth, in the adult they are striated. The dorsal and lateral muscles pierce the ring-muscle and insert in the walls of the stomach itself.

The alimentary canal has a break in its continuity, just behind the muscle-stomach; we next meet with it in the abdomen.

Through in-foldings of the cœlom the yolk is divided into several distinct masses. The walls of the midgut are in part formed by the cœlom. At its anterior end it is wide, open, and funnel-shaped, and it tapers towards its posterior end. It is everywhere filled with yolk. On the interior side of the funnel formed by the cœlom the entoderm cells have built up an epithelium. This epithelium seems to be separated by a membrane from the walls composing the cœlom.

The cells forming the lining of the midgut have distinct cell-walls; their nuclei stain lightly with hæmatoxylin; they are perfectly round, and measure ·01 mm. in diameter. A micro-nucleus is often to be found in them.

The end of the midgut is not in open communication with the rectum, being closed by a plug of entoderm cells.

The rectum is formed by an invagination of the ectoderm. At its exterior end its cells quite resemble those forming the epidermis; at its interior (proximal) end the cells are vacuolarised. The rectum, as also the most anterior parts of the dilators, canal, is supplied with powerful muscles; one set, the alimentary, runs from its walls to the skin of the abdomen; the contractors being ring-shaped, as in the pharynx and muscle-stomach.

As in Scorpions the Malpighian tubes are without doubt of entodermatic origin, as they enter the alimentary canal near the posterior end of the midgut. In this stage they are already well developed; they are very long and run parallel and juxta-apposed to the alimentary canal.

8. The Heart.—The heart of the Pedipalpi has been best described by Pereyaslawzewa as yet.

The heart at this stage consists of a long tube, lying dorsally, immediately beneath the skin, in the median plane of the abdomen. Its walls are thick, but do not contain many muscle elements.

At each segment the heart widens, and seems to me to give off a pair of small arteries. A large artery leaves the heart at its anterior end, this runs into the cephalothorax; following the outer surface of the embryo and reaching the cerebral ganglion it suddenly bends downwards; soon afterwards it divides into two branches, which run forwards on both sides of the muscle-stomach till they reach the central nervous system, when they terminate abruptly.

My embryos not being so advanced as Pereyaslawzewa's (**37**), I am not in a position to state anything about the other arteries and veins which she has seen; at the same time I consider her statement that the heart terminates "par une artère post-abdominale" as at all events not perfectly correct, since, as is hardly necessary to state, the Phryniscidæ have no post-abdomen, either as embryos or as adults.

Inside the heart the blood-cells are to be seen. These are large cells, staining red with eosin. They are usually nearly spherical, measuring up to ·036 mm. in diameter, and seem to be surrounded by a thin membrane. The nuclei of the blood-cells always lie on the surface of the cell, and are oblong. Each cell contains many nuclei, of which one is always remarkable as being several times larger than the others; this one measures ·007 mm., and is often in a state of mitosis. These cells are possibly the same as the fat-cells seen by Kishenonye (**23**) in spiders, but are here confined to the interior of the heart. Besides these larger blood-cells, smaller ones are also to be seen in the cavity of the heart. These have only one nucleus, and are poor in plasma; they resemble those found in the heart in the fourth stage. There the larger, spherical blood-cells are missing.

9. The Lungs.—It is not necessary to follow the development of the lungs, as it follows the same type as most other Arachnids.

10. The Genital Organs.—I am not in a position to state anything new about the genital ducts, Pereyaslawzewa (**38**) having given a fuller account of them than can be made out of my embryos. I have only been able to find the genital germ-cells. These are the largest cells in the whole embryo. They are situated in the remains of the cœlom, on the ventral side of the abdomen, in the region of the second, third, fourth, fifth, sixth, and seventh abdominal segments.

The shape of the genital-cells is always more or less oval (fig. 4), the nucleus resembling the cell in shape. The genital cells are surrounded by a thin cell-wall; the plasma stains red with eosin, and is granular in appearance. It often contains as many as three vacuoles; one at all events seems never to be wanting.

The nucleus stains only a little darker than the plasma, and is little influenced by hæmatoxylin. The chromatophores are distinctly visible in the shape of bands of darker stained substance. The nucleus also seems to be separated from the cell-plasm by a thin membrane.

The micro-nucleus is very conspicuous; it is always perfectly round, and stains very deeply with hæmatoxylin. It is almost always surrounded by a clear space containing little stainable matter. It is always found inside the nucleus.

The average measurements of the genital cells are:—Length of cell ·07 mm., breadth of cell ·03 mm., length of nucleus ·03 mm., breadth of nucleus ·02 mm., diameter of micro-nucleus ·004 mm.

11. The Muscles.—The two chief systems of muscles have already been referred to under the heading Cœlom. They are at this stage very well developed, and are composed of smooth fibres only.

Pereyaslawzewa (**38**) declares that the muscles of the cephalothorax are all striated, those of the abdomen being all smooth. It is hard to understand why this should be the case, and I think that the statement requires further confirmation, especially as all the muscles are derived from the same segmental sources, both in cephalothorax and abdomen.

12. The Yolk.—It is now only necessary to state that pari passu with the development of the central nervous system, and with the contraction and withdrawal of the ventral ganglion-cord into the cephalothorax, the chief bulk of the yolk has been forced back into the abdomen, as is the case with all Arachnids.

Conclusions.

On the whole the development of the Pedipalps follows the types prevalent among other Arachnids, sometimes leaning more towards the one, sometimes more towards the other class. It resembles—

(1) That of Spiders:
- *a.* In the first cleavages (probably).
- *b.* In the egg-envelopes.
- *c.* In the general build of the blastoderm.
- *d.* In the development outside the mother animal.

  - *e.* In the development of the lungs, heart, alimentary canal, and coxal gland.

(2) That of Solpugids and Pseudo-scorpions :

  In the development of the lateral organ.

(3) That of Scorpions :

  - *a.* In the development of the central nervous system.
  - *b.* In the presence of an accessory brain.
  - *c.* In the development of the median and lateral eyes.
  - *d.* In the development of the lungs, heart, coxal gland, and parts of the alimentary canal and Malpighian tubes.

The mode of development of several of the organs is the same in Spiders as in Scorpions,—for example, heart, lungs, etc.

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EXPLANATION OF PLATES 32 & 33,

Illustrating Mr. L. H. Gough's paper on "The Development of Admetus pumilio: a Contribution to the Embryology of the Pedipalps."

[N.B.—It must be borne in mind that the descriptions in the text are made from whole series of sections, but that the drawings were each made from one cut only.]

PLATE 32.

FIGS. 1 and 1 *a*.—Embryo of Stage V; explanations in the text. Magnified 12 times.

FIG. 2.—Reconstruction of brain of embryo of Stage V. The parallel lines are to demonstrate the position of the cavity caused by the alimentary canal, otherwise as in text. Magnified 18 times.

FIG. 3.—Sagittal section of lateral organ of embryo of Stage IV. Magnified 165 times. *c.* Cuticle. *d.* Deposit. *e. w.* External wall. *i. w.* Internal wall. *p.* Partition. *o. c.* Outer cavity. *i. c.* Inner cavity. *y.* Yolk.

FIG. 4.—Sagittal section of part of the abdomen of embryo of Stage V, with genital cells. Magnified 220 times. *v.* Vacuole of germ-cell. *mn.* Micronucleus of germ-cell. *n.* Nucleus of germ-cell. *c. p.* Cell-plasm of germ-cell. *a. e.* Fifth abdominal extremity. *c.* Remains of cœlom.

FIG. 5.—Sagittal section of a portion of the heart of embryo of Stage V. Magnified 330 times. *w.* Walls of heart. *b. c.* Blood-cells. *y.* Yolk. *e.* Epidermis.

FIG. 6.—Sagittal section through cephalothorax of embryo of Stage V. Magnified 60 times. *c. g.* Coxal gland. *o. c. g.* Opening of coxal gland. *d. v. m.* Dorso-ventral muscles. *a. b.* Accessory brain. *b.* Brain.

FIG. 7.—Horizontal section of rectum and mid-gut of embryo of Stage V. Magnified 220 times. *e.* Epidermis. *re.* Rectum. *en.* Entoderm cells forming mid-gut. *m.* Muscles forming sphincter and dilators. *y.* Yolk.

PLATE 33.

FIG. 8.—Sagittal section through embryo of Stage IV, showing Anlage of part of ventral ganglion cord, and development of ganglia out of small sense-organ-like structures. Magnified 280 times. *s.* Surface pit. *tu.* Tube.

s. f. Supporting fibre. *g.* Ganglion cell. *c. o. m.* Punktsubstanz. 1—9. Sense-organ-like structures in different stages of development.

Figs. 9 and 9 *a*.—Sagittal sections through lateral eyes of embryo of Stage V. Magnified 420 times. 1, 2, 3. First, second, and third eye.

Fig. 10.—Horizontal section of median eye of embryo of Stage V. Magnified 280 times. *l.* Lens. *co.* Stratum corneum. *p.* Pigment. *R.* Retina. *F.* Fissure. *P.R.* Post-retinal layer. *c.c.* Subocular cavity.

Fig. I.

Fig. Iª.

Fig. 4.

Fig. 6.

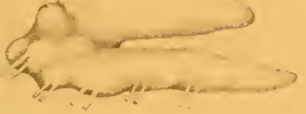

Fig. 2.

Fig. 3

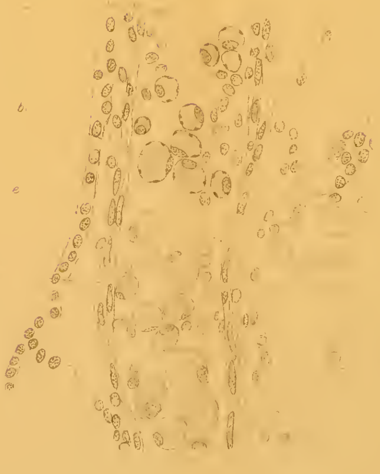

Fig. 5.

Fig. 7.

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Fig 9.ª

Fig. 9.

Fig 8

Fig 10.

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On the Teeth of Petromyzon and Myxine.

By

Ernest Warren, D.Sc.,

Assistant Professor of Zoology, University College, London.

With Plate 34.

THOSE observers who regard the Cyclostomata as a degenerate offshoot from a gnathostome ancestor would naturally desire to look upon the horny teeth as degenerate structures, and they would endeavour to find in them remains of parts homologous to those of an ordinary vertebrate tooth.

In 1889 Dr. Beard[1] published an investigation on the teeth of the Marsipobranchii. The teeth of Bdellostoma, Myxine, and several species of Petromyzon were examined, and the results arrived at seemed conclusive as to the degenerate nature of the teeth. In the young tooth of the Hag-fishes a more or less complete enamel epithelium, with perhaps a trace of enamel, was identified; also semi-calcified odontoblasts were described, forming a conical mass beneath the enamel epithelium. More recent observers, however, have thrown doubts on these interpretations. In 1894 Prof. Howes[2] expressed his opinion that the "odontoblasts" exhibited no calcification, and in the same year Ayers[3] stated that he was unable to find a trace of enamel or dentine.

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[1] "The Nature of the Teeth of the Marsipobranch Fishes," 'Zoologische Jahrbücher,' iii, 1889. A bibliography is there given.

[2] 'Nature,' Nov., 1894, Review of the Wood's Holl Lectures.

[3] Biological Lectures at Wood's Holl, 1894.

In making a series of preparations illustrating a course of lectures on odontology I was led to the Cyclostomes, and I have cut sections through the heads of young specimens of Myxine glutinosa (L.) (about five inches long), and of Petromyzon marinus (L.). These sections have not confirmed the views of Dr. Beard, and there can be no doubt that the cone of "odontoblasts" is purely epidermal in origin, and is, in fact, a successional tooth developing beneath the functional tooth.

The heads were stained with borax carmine, and treated with acid alcohol. They were then slowly impregnated with chloroform and paraffin, and ultimately were passed into pure paraffin (58°). In the case of Myxine it was necessary to paint the surface of the block with a solution of celloidin and gum mastic before cutting every section. Good sections were thus obtained, and they were counter-stained on the slide with picro-nigrosin. With this stain anything of the nature of horn becomes bright yellow, while connective-tissue fibres become blue.

Petromyzon marinus (L.).—Fig. I (A, B, C) illustrates the development of a horny tooth situated near the edge of the mouth. In fig. A the tooth follicle, if it may so be termed, has already been formed by the downgrowth of the epidermis into the corium. A small mesodermal papilla, like that of a hair, is present. The first sign of the developing tooth occurs a little above the mesodermal papilla. The cells at this place proliferate, gradually expand, and become granular. The cells of the epidermis above the developing tooth become flattened by the pressure exerted.

In fig. B the young tooth is more definitely marked out; the cells of which it is composed are considerably larger than before, and the granular nature of the protoplasm is still more evident. With picro-nigrosin staining these cells become faintly yellowish. The mesodermal papilla has become more or less hollow, and constitutes a kind of pulp-cavity. The whole structure is strikingly like that of a developing hair.

The cells of the young tooth gradually cornify, the process proceeding from the apex downwards. Cornification may continue for a considerable time around the base of the tooth, and the nuclei which resist the process longer than the rest of the cell may sometimes be seen embedded in the horn near the growing edge. The tooth breaks through the cells above, and soon projects above the surface, and like a hair it is purely ectodermal in origin (fig. C). Even before the tooth has broken through the surface a new tooth may be seen developing below on the same site as was occupied by the first.

A pulp-cavity cannot be found to all the teeth. Those situated at some distance from the edge of the mouth become differentiated simply out of a thickening of epidermis.

Myxine glutinosa (L.).—Fig. II represents the tooth of Myxine in vertical section. Some little distance beneath the horny tooth can be seen a cone of peculiar cells with large nuclei. This cone must be the "odontoblast cone" of Dr. Beard. The large cells stain yellowish, just like the cells of the developing tooth of Petromyzon. The granules tend to be arranged in lines, and this gives the margin of the cone a distinctly striated appearance. As in the case of Petromyzon, the base of the tooth is firmly fixed in a deep groove of the epidermis, and cornification continues here until the tooth is shed.

The main mass of the tooth projecting out of the epidermis is formed by the cornification of the cone of large granular cells with large nuclei, while the remainder is produced in the horn-producing groove out of comparatively flat unaltered epidermal cells. In thin sections through the horny substance of the functional tooth this difference in origin can be made out. In the upper part of the tooth transformed large nuclei, and also hollow spaces, can be observed. Towards the base the transformed nuclei are small and flat. The hollow spaces just mentioned gradually develop as the large cells of the cone become converted into horn, and in a partially cornified tooth they are very conspicuous.

The epidermal cells lining the pulp-cavity are distinctly columnar, and would correspond to the enamel epithelium of an ordinary tooth.

In the case of the ctenoid lingual teeth the tooth-germs have fused together, and the cones of large granular cells, which will be converted into the succeeding horny tooth, are continuous with one another, although small separate pulp-cavities can be distinguished to each cone or originally distinct tooth-germ.

The structures described do not lend support to the idea that these horny teeth are degenerate calcified teeth, but if they actually are degenerate they must be regarded as having reverted to a condition that probably preceded the placoid scale of an Elasmobranch.

The placoid scale is of very great antiquity, being found amongst the oldest organic remains, and living and fossil forms give us little information as to its origin. The stages in the evolution of a placoid scale must, therefore, be surmised rather than actually observed.

A rough skin was undoubtedly of some use to the ancestors of Elasmobranchs, and the simplest condition conceivable would be where the general surface of the body and jaws was covered with little horny warts. As the warts were gradually converted into more pronounced structures they would come to possess a pulp-cavity, in response to the need of a supply of blood-vessels, etc., to the proliferating epidermis. Such specialised warts where cornification was very complete would result in structures like the horny teeth of Petromyzon and Myxine.

Calcification of the outer portion of the pulp would add strength to the horny scale, and there is no improbability against supposing that such a variation arose. The shape of the resulting calcified mass would be moulded by the overlying Malpighian layer of the skin (enamel epithelium), just as the shape of the future tooth is prefigured by the enamel organ.

If the horny teeth or warts were useful to their possessors, then a projecting cone of calcified substance would certainly be more efficacious, and it would probably not be difficult for natural selection to replace the horny tooth by its calcified core. This would be the primitive dentine.

We can imagine that at a later period the calcification which first originated in the mesoderm of the pulp-cavity of the wart afterwards extended into the Malpighian layer of the epidermis, and this would constitute the primitive enamel.

In support of such a view it should be remembered that among the dentines of the teeth of living and fossil forms we can meet with every transition from the most irregular calcified mass of vaso-dentine to the highly organised, fine-tubed varieties. Also among enamels there can be found every transition from the thinnest varnish-like layer of apparently homogeneous calcareous matter, to thick layers of enamel, consisting of striated prisms and interprismatic substance.

The teeth of the jaws in the primitive condition would originate by a separate ingrowth (diagram 1) of epithelium from the surface for every tooth. Such ingrowths are frequently indicated externally by slight swellings, which perhaps represent the horny tooth, which according to the hypothesis advanced phylogenetically preceded the calcified tooth. An advance on this condition can be seen in the case of the Pike, where frequently an enamel-germ buds out from an older enamel-germ instead of from the general epidermis.

If the ingrowths of epidermis for the individual teeth occurred close together or in contact along a single line around the edge of the upper and lower jaws we should have the beginning of the tooth-band (diagrams 2, 3, 4).

If, now, all the new enamel-germs for the successional teeth were regularly budded off from the preceding germs, instead of only a few, as in the Pike, we should arrive at the condition well seen in the lower jaw of embryo Scyllium catulus (diagrams 5, 6).

In an older embryo, and especially in the lower jaw, the distinction between the individual tooth-germs becomes lost dorsally (diagram 7), but ventrally it is retained.

On the enamel-cups being pinched off on separate stalks ("necks") we should arrive at the typical condition of the tooth-band seen in a reptile (diagram 8).

EXPLANATION OF PLATE 34,

Illustrating Dr. Ernest Warren's paper "On the Teeth of Petromyzon and Myxine."

Fig. I, A—C.—Vertical sections of developing teeth from the margin of the mouth of Petromyzon marinus (L.). × 280 diameters.

In C the successional tooth is beginning to cornify at its apex beneath the functional tooth.

Fig. II.—Vertical section through the median tooth of Myxine glutinosa (L.). × 140 diameters.

Diagram 1.—Tooth-germs budded off separately from the surface; irregularly scattered.

Diagram 2.—Tooth-germs arranged in a single row.

Diagram 3.—Tooth-germs in contact.

Diagram 4.—Tooth-germs fused together to form a dental lamina (*d. l.*); *r* = dental ridge.

Diagram 5.—Vertical section through tooth-germ of embryo Scyllium catulus. B is a young tooth-germ being budded off from the preceding germ.

Diagram 6.—Three tooth-germs (1, 2, 3) and bud B. Above and below there are indentations marking off several germs.

Diagram 7.—In a somewhat older embryo the distinction between the individual germs tends to disappear on the upper surface.

Diagram 8.—Enamel cups pinched off on stalks ("necks").

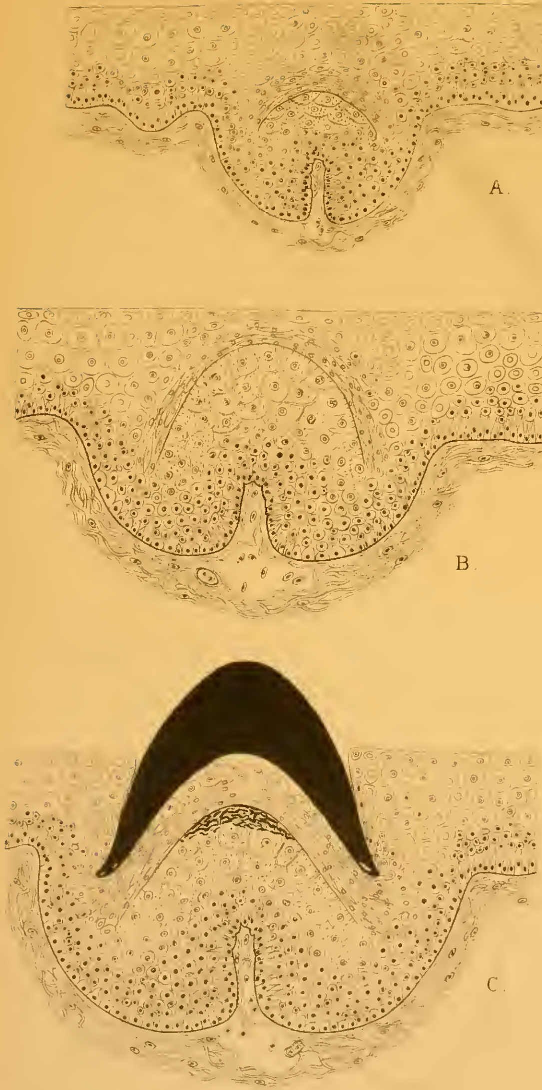


Fig. I.

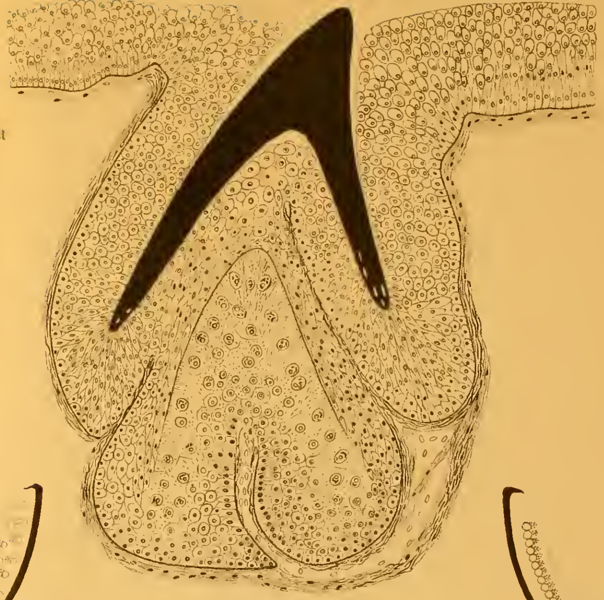
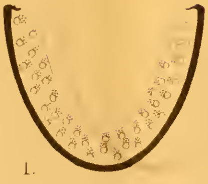


Fig. II



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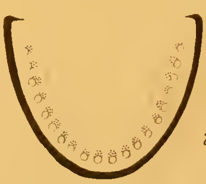

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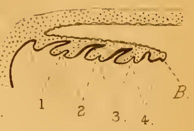

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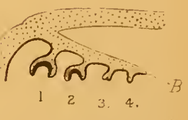

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A.S. Huth, Lith^r London

Typhlorhynchus nanus: a New Rhabdocœle.

By

F. F. Laidlaw, B.A.

With Plate 35.

The small Rhabdocœle described below was found by Mr. Goodrich at Naples, living on the body of the Polychæte worm Nephthys scolopendroides, Delle Chiaje. He sent a number of specimens preserved with Lang's reagent to Dr. Gamble, who was good enough to hand them over to me for examination. I am indebted to Mr. Goodrich for a further series of specimens, some fixed with corrosive sublimate and acetic acid, others with Lang's reagent; also for figs. 2, 6 *a*, *b*, drawn from life. I have, unfortunately, been unable to study living specimens; hence my account, especially as regards the genital organs, is necessarily somewhat incomplete. The work was done in the Zoological Laboratory at Owens College.

The external appearance and general characters are shown in Pl. 35, fig. 1.

The total length of the body varies from ·7 mm. to 1 mm. In size, therefore, it is quite comparable to a large infusorian such as Stentor polymorphus, Mull. The variations in length between different specimens depend largely on the amount of extension or contraction of the body, especially of that part of it constricted off to form the snout or proboscis.

The body is spindle-shaped (see Pl. 35, fig. 1), the anterior end more pointed than the posterior. The front fifth of the body is constricted off to form a kind of proboscis or preoral lobe (*Pr.*), which is non-retractile. Immediately behind this constriction lies the "mouth" mid-ventrally (*M.*). There are two genital openings, also mid-ventral, lying close together at about a fifth of the total length of the body from its hinder end; the male opening (♂) is in front of the female (♀).

The surface of body is evenly ciliated throughout. In some cases there is a disc-like flattening at the hinder end, but this is only exceptionally present. On the sides of the proboscis are papillæ which resemble in appearance those figured by von Graff for Proxenetes tuberculatus, v. Gr. [2]; a few of these papillæ are present at the hinder end of the body.

The mouth leads through a well-developed pharynx (*Ph.*) into the spacious gut cavity (*En.*), which sends forward a median diverticulum (*A. d.*) into the proboscis, terminating immediately behind the brain (*Br.*), which lies at about the middle of the proboscis. On either side of this anterior diverticulum lies a rounded testis (*Te.*). There is a well-developed penis provided with a complicated armature (*Pe.*) lying in front of the male opening. Into the penis open a pair of vesiculæ seminales (*V.s.*) and a number of unicellular glands (*Gl.*). The female aperture leads into a bursa seminalis (*B. s.*) provided with a chitinous appendage (*Ch. a.*). The single ovary (*Ov.*) lies at the hind end of the body nearly in the middle line; it is somewhat curved, and the eggs are progressively riper from behind forwards. In front of the ovary is a structure which may be called the receptaculum seminis (*R. s.*).

The pigmented eye-spots found in many Rhabdocœles are here absent, and there is no otolith.

In several respects this little creature differs from any known forms; its nearest allies appear to be found amongst the Mesostomidæ and Proboscidæ as defined by von Graff [2], but as it cannot well be referred to any known genus of either of these families I have found it necessary to create a new genus for its reception under the name of Typhlorhynchus. The species may be called Typhlorhynchus nanus.

Habits.—Typhlorhynchus nanus, as already stated, is found on the body of Nephthys scolopendroides, to which it attaches itself by its hinder end. From Mr. Goodrich's figures (figs. 2 *a*—*c*) it appears to use its proboscis as a tactile organ. In no specimen that I have examined is there any food substance in the gut space, but in the protoplasm of the gut wall are numerous fine food granules. Its epizoic habit does not seem to have produced any marked degeneration of the organs of the body. The loss of the eye may be due to this, but a number of species belonging to the genus Mesostomum which are free-living (*e.g.* M. Cuenoti, recently described by Dörler [5]) are also without eyes.

The other known parasitic Rhabdocœles belong to the family Vorticidæ, and include a number of forms parasitic in Echinoderms, on the kidneys and gills of Molluscs, etc.

Method.—Mr. Goodrich obtained specimens of Typhlorhynchus by putting Nephthys scolopendroides into sea water with about 10 per cent. of alcohol (70 per cent.), when the parasite fell off in considerable numbers. No eggs were found. They were then treated with corrosive sublimate and acetic acid or with Lang's reagent. Those treated with the latter yield on the whole the best results in sections, the protoplasm being beautifully preserved. Those hardened with the former reagent have shrunk to some extent, but in them the gland cells and rhabdites stain more readily. I have examined a number of series of sections both transverse and longitudinal, as well as specimens mounted whole. For the sections I obtained excellent results with brazilin; I also employed the iron-hæmatoxylin method of staining. Whole preparations were stained with borax carmine.

Structure: Integument.—The body-wall is made up of a layer of ciliated epithelium lying upon a double muscle layer. The epidermis is equally ciliated over the whole surface of the body. A number of irregularly arranged papillæ formed by the bulging out of the epidermis occur on the proboscis (fig. 5, *T.*), and some few at the hind end of the body. The flattening observed at the hind end of several specimens is undoubtedly connected with the mode of attachment observed by Mr. Goodrich.

The average thickness of the epidermis is 5 μ. No cell limits can be discerned in it. In sections of specimens preserved with Lang's reagent small clusters of nuclei, four or five in each cluster, are scattered at considerable intervals through the epidermis. The outer limit of the epidermis is seen as a delicate line, which under high power resolves itself into a row of exceedingly fine dots, recalling exactly the appearance figured by Böhmig for Monoophorum striatum, Böh.; whilst the clusters of nuclei suggest the "Tastkörperchen" of the same species (**3**, pl. xx, figs. 17—19), except that there is no break in the cilia above them. In the case of sections of specimens fixed with corrosive sublimate and acetic acid numbers of small deeply stained rhabdites are visible in the epidermis. Assuming that the clusters of nuclei referred to above are to be regarded as connected with sensory organs, the question arises as to the whereabouts of the true epithelial nuclei. The nuclei in the clusters are the only ones occurring in the epidermis so far as my sections show.

The basal membrane is thin, about 1 μ thick or rather less. The muscle layers consist of an outer circular and an inner longitudinal layer, evenly developed all over the body (fig. 7, *Cir.*, *Lon.*). Special sphincter muscles, derived apparently from the circular layer, lie round all the three openings in the body-wall (figs. 4—7, *Sp.*). But few gland-cells are developed in connection with the surface of the body. A few cells with granular deeply staining protoplasm lie here and there immediately under the muscle layers of the body-wall, and doubtlessly come into this category; they are more numerous in the proboscis than elsewhere (fig. 5, *Gl.*).

Parenchyma.—The space between the various organs of the body and the body-wall is occupied by the parenchyma, This consists of a reticulum of delicate fibrillar protoplasm containing round finely granular nuclei; the protoplasm is without cell limits, and the nuclei are few and widely scattered. Most of the body organs, e.g. yolk glands, penis, etc., lie in perfectly definite spaces in this parenchyma, but in two cases, viz. the gut wall and the bursa seminalis, this is not so. The lining of the gut space consists of protoplasm without cell limits, of precisely the same character as that of the parenchyma, and it is not marked off from the latter in any way. The only characters which serve to distinguish the gut wall (endoderm) from the parenchyma are, firstly, the nuclei, which in the endoderm are oval, and contain coarse darkly staining chromatin granules (fig. 7, *Nuc.*), whilst those of the parenchyma, as stated above, are round and finely granular (fig. 7, *P. N.*); and secondly, the presence in the endoderm protoplasm of numbers of fine granules, which are probably food granules, but these only disappear gradually in passing from the endoderm to the parenchyma.

In the case of the bursa seminalis the protoplasm forming its walls, though denser and more hyaline than the general parenchyma protoplasm, nevertheless merges quite imperceptibly into it.

Owing to the spaciousness of the enteron and the size of the yolk glands in the middle regions of the body, the parenchyma in those regions is much reduced.

In the proboscis the parenchyma is densest immediately under the body-wall; below this it is spongy and scarcely distinguishable, especially towards the tip of the proboscis.

Alimentary Canal.—The mouth opens on the mid-ventral line just behind the constriction at the base of the proboscis. As already stated, there is a sphincter muscle arrangement around the mouth opening, developed from the muscles of the body-wall, most probably from the outer circular layer, but possibly from both; my sections do not bring this point out clearly.

The mouth opens into the pharyngeal pouch ("Pharyngealtacshe," von Graff). This pouch is at first narrow, but as it passes dorsally it widens into a chamber of small size, into which the lower part of the pharynx projects (fig. 3, *Ph. T.*, *Ph.* T_1.), so that the roof of the chamber is formed by the pharynx itself. The pouch agrees very closely with that figured by von Graff [2] for Mesostomum Ehrenbergii, and, as in the latter, it is provided with a few muscle-fibres attached to the walls at its widest part, running to the body-wall. Neither the epithelium lining the wider part of the pouch nor that on the exposed part of the pharynx is ciliated, the cilia only extend to the narrow part of the pouch. With this should be compared the condition found in Mesostomum Ehrenbergii, v. Graff, in which the pouch is ciliated throughout. In Mesostomum Cuenoti, recently described by Dörler [5], on the other hand, only the roof of the pouch, i.e. the projecting wall of the pharynx, is ciliated. The pharynx itself has its principal axis a little elongated, and running nearly dorsiventrally. It is pyriform, its narrow end being ventral and the broader dorsal. The larger size of the dorsal part is due to the greater size in that region of the pharyngeal cells (fig. 3, *Ph. C.*).

The pharynx conforms to the type called by von Graff "pharynx rosulatus," characterised by the numerous large gland cells which in sections appear as coarsely granular cells, and also by the arrangement of the muscle-fibres. The latter consist of a double outer layer, forming, as it were, a muscular capsule, and a double inner layer lying immediately under the epithelium lining the lumen of the pharynx. Between these two definite layers run numerous radial fibres (fig. 3, *R. M.*). The outer layer consists first of longitudinal fibres (*O.L.*),—that is to say, of fibres running parallel to the principal axis of the pharynx; and immediately below these, of stouter circular fibres (*O. Cir.*). The inner layer consists of a number of fine circular fibres (fig. 4, *I. c.*), lying immediately on the outside of the epithelial lining of the lumen (*Ph. E.*), and outside these of longitudinal fibres (fig. 3, *I. L.*), which like the inner circular fibres are but feebly developed. The radial muscles are most numerous in the ventral part of the pharynx.

The epithelium lining the lumen (*Ph. E.*) is very much reduced, excepting at the lower end of the pharynx, where it is continuous with the epithelium on the exposed surface. It is quite devoid of nuclei (cf. Mesostomum Cuenoti).

In addition to the intrinsic muscles of the pharynx a large number of fibres run from the body-wall to become attached to its anterior wall, apparently fusing with the outer longitudinal fibres of the pharynx itself. It is the insertion of these fibres into the body-wall which causes the constriction that cuts off the proboscis from the rest of the body (fig. 4, *A. M.*).

There is no well-marked œsophagus; a few unicellular glands lie in the neighbourhood of the upper end of the pharynx.

The gut is spacious; posteriorly it extends as far back as the level of the female aperture. That part of it running into the proboscis is best described as an anterior unpaired diverticulum (fig. 1, *A. d.*). This diverticulum is often occluded to a considerable extent by pseudopodial processes sent out by the endoderm, but can always be distinguished in transverse sections. The characters of the endoderm have been sufficiently described in dealing with the parenchyma.

Nervous System.—The brain lies in the proboscis at about its middle, and consists of a quantity of ganglion cells (fig. 5, *G.*) lying about a transversely elongated mass of "Punktsubstanz," apparently composed of exceedingly fine fibrillæ (fig. 5, *br.*).

The Punktsubstanz, or central mass, is divided into two lobes by a slight median constriction, and from each of the lobes a group of nerve-fibres runs outward for a short distance towards the wall of the proboscis, and then turns backwards (fig. 5, *N.*). A group of fibres also runs from the ganglion cells lying in front of the central mass to each lobe of the latter close to the middle line, and a similar group of fibres passes into the central mass from ganglion cells lying behind it. These posterior fibres do not form such compact groups as the anterior pair, and enter the central mass more laterally.

The ganglion cells stain very darkly, and appear to be bipolar; the nucleus is finely granular and rather large, and there is a small black nucleolus.

The arrangement of ganglion cells lying on the anterior side of the central mass is remarkable. On either side of the middle line a group of them extends forwards like a horn from the main body of ganglion cells, and curves slightly inwards at its anterior extremity, ending some distance from the tip of the snout. The cells constituting these two horns are identical in character with the other ganglion cells. Numerous nerve processes run forwards from them to the tip of the snout, others run down to join the groups of fibres entering the brain anteriorly (fig. 1, *H.*).

The tip of the proboscis then appears to have a very rich nerve supply, and we may conclude that the proboscis is the chief seat of the tactile sense. Possibly with this is correlated the presence on the proboscis of the papillæ already referred to, although such papillæ are not entirely confined to it.

Organs of Reproduction.

(a) Female.—The ovary is single, and lies at the hinder end of the body nearly in the middle line; it is short and somewhat curved (fig. 1, *Ov.*), its length is about ·12 mm., and it contains from twelve to fifteen eggs, which are progressively riper from behind forwards. The eggs are oblong, closely pressed against each other, and have large nuclei. Their protoplasm is finely granular. The nuclei have a deeply staining capsule; immediately below this a number of coarse, dark granules, and inside these a relatively clear space in which lies a large black nucleolus (fig. 8, *Ov.*). As already stated, the ovary lies in a space hollowed out in the parenchyma, and is surrounded by a protoplasmic membrane containing flattened nuclei.

In front of the ovary this membrane is apparently attached to a short funnel-shaped structure which ends blindly in the parenchyma, and has its wider end next the ovary (fig. 8, *R. s.*). In the space enclosed by this body, which may be called the receptaculum seminis, lies a small mass composed of spermatozoa (fig. 8, *S.*), which are thus immediately in front of the ripest, most anterior egg.

There is a pair of unbranched yolk glands which extend from the level of the front end of ovary as far forward as the pharynx, lying close along the lateral wall of either side of the body in a cavity of the parenchyma, which here is not much developed.

These yolk glands are built up of elongated cells lying parallel to one another and closely pressed together, with their long axes roughly dorsiventral. Each cell has a nucleus at about its middle; each nucleus contains a nucleolus lying in a clear space in the centre of the nucleus, surrounded by a finely granular ring when seen in section. In each cell are two, three, or several small black refringent bodies, which tend to group themselves together in a ring. Amongst these black bodies are found small refringent yellow globules of yolk matter.

The female aperture is furnished with a sphincter muscle arrangement (fig. 7, *Sp.*), and opens into a small chamber (fig. 7, *B. s.*). The ciliated epidermis of the body-wall extends to the walls of this chamber. Into it the bursa seminalis (fig. 7, *B. s.*) opens dorsally through a narrow neck. Above the neck, which is quite short, the cavity is transversely widened, but narrow antero-posteriorly. Dorsally it extends to a point just below the front end of the ovary, but does not communicate with the latter directly. The cavity is bordered by a chitinoid lining substance which stains deeply; beyond this lining the walls are built up of clear hyaline protoplasm, which merges quite gradually with the protoplasm of the parenchyma. A small number of muscle-fibres lie in the walls of the bursa, running from the neighbourhood of the neck of the cavity to the body-wall, or in some cases to the capsule of the penis (fig. 7, *M.*). The hinder wall of the bursa at about its middle is produced to form a kind of spout or short tube, which is blocked up by a small chitinous plug (*Ch. A.*). This latter agrees with the "Chitinanhang" described by von Graff for Hyporhynchus coronatus, v. G. [2], and with a similar organ found in many other forms.

Owing to the way in which the walls of the bursa seminalis merge into the parenchyma in whole preparations it is only possible to determine the position of the lumen. In sections some distinction, as pointed out above, can be drawn between the tissue immediately surrounding the lumen and the parenchyma proper. In no case that I have examined does the bursa seminalis contain spermatozoa.

I have found considerable difficulty in interpreting the funnel-shaped organ which I have called the receptaculum seminis; the explanation here put forward of this organ was suggested to me by an examination of a figure of Byrsophlebs Graffii (Jens.) in Jensen's work 'Turbellarier ved Norges Vestkyst' [1].

In Byrsophlebs Graffii the riper end of the single ovary is posterior, and immediately behind it lies an organ which Jensen calls the receptaculum seminis. This receptaculum opens to the exterior, and contains spermatozoa which do not, however, according to Jensen in his account of this species, reach it directly, but pass through the opening into a bursa copulatrix (the receptaculum and bursa having a common opening), and from the bursa travel along a long convoluted duct, called by him the ductus longus, into a receptaculum. Now it is evident that, so far as its position goes, the receptaculum bears the same relation to the ovary of Byrsophlebs Graffii, as does the funnel-shaped organ to the ovary of Typhlorhynchus nanus. Both, moreover, contain spermatozoa.

The organ called by Jensen bursa copulatrix would, then, be homologous with the organ which I here call the bursa seminalis. My reason for adhering to the latter name is that it is used by von Graff to designate a comparable organ in Hyporhynchus and other genera.

If, then, we may suppose that the receptaculum seminis in

Typhlorhynchus has lost its opening to the exterior, we can readily compare the female organs in this creature with those of Byrsophlebs. The spermatozoa may reach the receptaculum (funnel-shaped organ) by a duct similar to the ductus longus of the latter; such a duct would scarcely be discernible save in the living state and when full of spermatozoa.

It should be remarked that the walls of the bursa are much folded, so that the lumen is quite irregular.

(b) Male: Testes.—There is a pair of compact spherical testes, one on either side of the proboscis immediately behind the brain (fig. 5, *Te.*), each enclosed in a very delicate membrane, which often is hardly distinguishable. In every specimen that I have examined I have found apparently mature spermatozoa lying for the most part on the dorsal and anterior surface of either testis. The rest of the testis is composed of sperm mother-cells in various stages of development. I have not found it practicable to follow out the history of the development of the spermatozoa. The appearance of the cells composing the testes agrees very closely with that of the germ-cells of Plagiostoma Girardi figured by von Graff (l. c., Taf. xvi, figs. 11—14). I have also compared sections of the testes of Typhlorhynchus with some of Mesostomum tetragonum, O. Sch., and find there, too, a strong resemblance. Cells in a morula state are always present (fig. 5, *Mo.*). The position of the testes is hardly paralleled amongst the Mesostomidæ and Proboscidæ.

In Macrorhynchus Naegelii, as figured by von Graff (loc. cit., Taf. xi, fig. 7), they extend as far forward as the level of the brain and pharynx, but in no case do they lie in the retractile proboscis. In most Mesostomidæ and Proboscidæ the testes lie in the middle region of the body, and are continuous with the vesiculæ seminales. In Typhlorhynchus, however, I have not been able to find any communication between them, although the two vesiculæ always contain spermatozoa in my specimens. These vesiculæ (fig. 1, *V. s.*) are narrow tubes, with thin chitinous-looking walls, opening close together into the penis at their posterior end, and each ending in a small swelling at their forward extremities. They have a total length of about ·15 mm.

The penis is about ·1 mm. long, backwardly directed, pyriform, with its apex curved ventrally. Close to the point at which the vesiculæ seminales open into it there open also a number of gland cells, which lie immediately ventral to the penis, and pour a secretion into it. The penis itself consists of an outer muscular capsule composed of muscle-fibres running parallel to the long axis of the penis (fig. 7, *Ex. M.*). There is an inner muscle layer also composed of a cylinder of longitudinal fibres, attached at one end to the outer capsule at its widest part, and by the other to the eversible part of the penis (fig. 7, *I. M.*). The outer capsule is continuous with the lining of the cavity immediately within the male aperture. The armature of the penis is very remarkable, and quite unlike that of any previously described form. Its appearance is well shown in Mr. Goodrich's figures (figs. 6*a*, *b*). When evaginated the penis is mushroom-shaped, with a convex head. From the margin of the disc of the head extend two lobes, one on either side [**4**]. From the centre of the head projects a long chitinous spine, whose proximal end is sharply crooked and embedded in the penis (fig. 6, *Ch.*). The convex surface of the head is covered with meridionally arranged rows of short, slender, slightly curved spines (*C. S.*). There appear to be some eighteen of these rows, each with ten or twelve spines.

The large central chitinous spine is tubular at its proximal end, but the tube distally appears to open out into a groove. This spine is an impregnating organ homologous with the "Chitinrohr" described by von Graff [**2**] for Proboscidæ and Mesostomidæ. The spermatozoa probably pass into its tube by an aperture at its proximal end (cf. Proxenetes gracilis, v. Gr. [**2**, Taf. viii, fig. 12]). A few muscle-fibres are apparently attached to its base.

Affinities.—The character of the pharynx is sufficient to indicate that the Rhabdocœle under consideration is allied to the families Mesostomidæ and Proboscidæ, and there are no features in the structure of Typhlorhynchus which forbid us to refer it to one or other of these families. Which of the two is to be selected depends chiefly on the importance attached to the proboscis. This in Typhlorhynchus differs sharply from a typical proboscis, such as is found in Macrorhynchus or Gyrator, but not so greatly from that of Pseudorhynchus. In all the genera referred by von Graff [2] to this family, however, the proboscis is retractile to some extent. Further, in none of them do the brain or the testes occupy a position similar to that found in Typhlorhynchus, and in Pseudorhynchus alone is the proboscis invaded by the gut space.

On the other hand, Byrsophlebs amongst the Mesostomids is characterised by the presence of two genital apertures, the male in front, the female behind—a character that only occurs in this genus and in Typhlorhynchus amongst the whole of the Rhabdocœla (*s. str.*), leaving out of account the Prorhynchidæ. Further, as I think I have shown, the female genital apparatus of Typhlorhynchus may be compared in detail with that of Byrsophlebs.

A bursa seminalis provided with a chitinous appendage very like that of Typhlorhynchus occurs in Hyporhynchus amongst the Proboscidæ and Proxenetes amongst the Mesostomids.

The penial apparatus, whilst differing greatly in detail from any of those figured for these families by von Graff, resembles them in a general way, especially in being provided with a chitinous tube or spout (Chitinrohr—cf. von Graff's figures of Hyporhynchus coronatus and Proxenetes gracilis).

It is, on the whole, I think, most convenient to place this new genus amongst the Proboscidæ in the neighbourhood of Pseudorhynchus. It differs sufficiently from other Proboscidæ to warrant the creation of a sub-family to receive it. In some respects, e. g. the female organs, it shows an approximation to Byrsophlebs, and may be regarded as to some extent intermediate between the Mesostomidæ and Proboscidæ. It is particularly of interest as being the only member of either of these families that has adopted an epizoic habit.

The character of the parenchyma should be specially remarked. This, in the way in which it merges into the endoderm, shows a distinct approach to the condition found in the Alloiocœla.

The genus Typhlorhynchus may be defined briefly as follows:

Body provided with a non-retractile pre-oral lobe or proboscis. Gut not clearly separated from the parenchyma, provided anteriorly with a median diverticulum extending into the pre oral lobe. Pharynx rosulate, no genital atrium, male opening in front of female. Penis (when evaginated) with meridionally arranged rows of spines, and in addition a long chitinoid tube. The single pair of testes lie in the pre-oral lobe; ovary single, at hind end of body; yolk glands paired. Accessory female organs consist of—(1) a bursa seminalis opening to exterior by the female aperture; (2) a receptaculum seminis.

In conclusion, I wish to thank Dr. Gamble very sincerely for the kind way in which he has assisted and advised me in preparing this account.

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EXPLANATION OF PLATE 35,

Illustrating Mr. F. F. Laidlaw's paper "On Typhlorhynchus nanus.

FIG. 1.—Typhlorhynchus nanus, diagrammatic, seen from above. × 90. *Pr.* Pre-oral lobe, snout, or proboscis. *M.* Mouth. *Ph.* Pharynx. *En.* Gut space. *A. d.* Anterior gut diverticulum. *Br.* Brain. *H.* Horn-shaped process. *Te.* Testis. *Pe.* Penis. *Gl.* Glands opening into the penis. Gl_1. Glands lying about the male aperture. ♂. Male aperture. *V. s.* Vesicula seminalis. *Ov.* Ovary. *R. s.* Receptaculum seminis. *B. s.* Bursa seminalis. *Ch. a.* Chitinous appendage. *Y. gl.* Yolk gland. ♀. Female aperture.

FIG. 2.—Various attitudes assumed in life. × about 10 times.

FIG. 3.—Long. sec. through the pharynx. × 400. *Ph. c.* Pharynx cells. *O. L.* Outer longitudinal muscles of pharynx. *O. Cir.* Outer circular muscles, and *I. L.*, inner longitudinal muscles of the same. *Ph. E.* Epithelium lining the lumen of the pharynx. *Ph. T.* Pharyngeal pouch. *Ph.* T_1. Narrow part of pharyngeal pouch. *R. M.* Radial muscles of pharynx. (The inner circular muscles are seen as a row of dots immediately to the inside of the inner longitudinal fibres.) *Sp.* Sphincter muscle of the "mouth" aperture. *A. M.* Muscles running from the anterior side of the pharynx to the body-wall. *Ex. M.* Other extrinsic muscles of the pharynx.

FIG. 4.—Trans. sec. through the pharynx region showing the gut diverticulum (*A. d.*). *I. c.* Inner circular muscles of the pharynx. Other lettering as in Fig. 4.

FIG. 5.—Horizontal section through the pre-oral lobe. *G.* Ganglion cells. *Gl.* Integumentary gland cells. *Mo.* Cells in morula stage in testis. *N.* Nerve. Other lettering as in Fig. 1.

FIG. 6 *a.*—Penial armature closed.

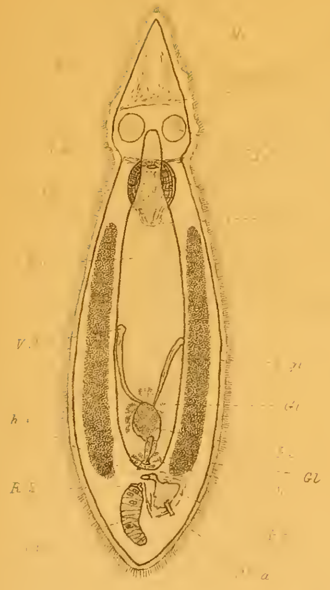
FIG. 6 *b.*—The same evaginated, "much enlarged, drawn from life." *Ch.* Chitinous tube. *C. S.* Chitinous spines. *L.* Lobes.

FIG. 7.—Long. sec. through the penis and bursa seminalis (drawn from two sections and combined). *Cir.* Circular muscle-fibres of body-wall. *Lon.* Longitudinal fibres of body-wall. *En.* Endoderm. *Ex. M.* External muscular capsule of the penis. *I. M.* Inner muscular layer of the same. *M.* Muscle-fibres. *Ar.* Penial armature. *Sp.* Sphincter muscle-fibres of female aperture. *B. s.* Chamber into which the bursa seminalis opens. *B.* s_1.

Bursa seminalis. *Nuc.* Endoderm nucleus. *P. N.* Nucleus of parenchyma. Other lettering as in Fig. 1.

Fig. 8.—Optical section through the bursa seminalis, receptaculum seminis, and ovary of a specimen mounted whole. *Ov.* Ovum showing the large nucleus. *S.* Mass of spermatozoa in the receptaculum. Other lettering as in Fig. 1.

(The position of the "mouth opening" is drawn rather too far back in Fig. 1.)



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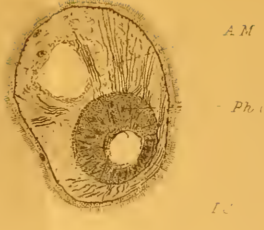

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