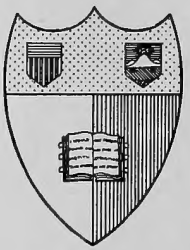

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STUDIES

FROM THE

MORPHOLOGICAL LABORATORY

IN THE

UNIVERSITY OF CAMBRIDGE.

EDITED BY

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[2] From the *Proceedings of the Cambridge Philosophical Society*, Vol. VII.
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ON THE EMBRYOLOGY OF THE ECTOPROCTA

BY

SIDNEY F. HARMER, M.A., B.Sc.,

Fellow of King's College.

With Plates I. and II.

THE opportunity of investigating the development of *Alcyonidium* was due to the kindness of Prof. H. de Lacaze-Duthiers, who permitted me to make use of the Zoological Laboratory at Roscoff during the summer of 1883. I desire to express my best thanks for the hospitality so courteously extended to me on that occasion, and to mention my agreeable recollections of the uniform kindness with which I was treated, during my stay at Roscoff, by Prof. de Lacaze-Duthiers himself and by all the members of his staff.

Alcyonidium polyoum is extremely abundant on the *Fucus serratus* which grows on the rocks exposed at low water in the Rivière de Penzé, near Roscoff; its embryos were obtained in abundance during the months of July and August.

The species was first described by Hassall (7), under the name of *Sarcochitum polyoum*, but is included by Hincks (8) in the genus *Alcyonidium*. The form which occurs in the Rivière de Penzé has been identified by Joliet (9) as *S. polyoum*, and I can depend on the accuracy of the statement made to me by M. Charles Marty, of the Zoological Laboratory at Roscoff, that my own specimens belong to the species described by Joliet from the same locality. I mention this fact, since the description given by Hassall and Hincks is in need of a few corrections, if their

species is really identical with that which is found near Roscoff,—of which, however, I am not entirely convinced.

My own specimens do not show the large papillæ mentioned by Hincks from which the polypides are said to issue. This, however, may possibly be due to contraction induced by the reagents in which they were preserved. The septa between the zoœcia are clearly seen from the surface of the colony, whilst the embryos are invariably aggregated into spherical clusters, each contained in the tentacle-sheath of an individual whose alimentary canal has atrophied, instead of being "scattered singly throughout the polypidom," as in Hassall's description. In spite of the fact that in these respects the Roscoff species does not conform to the diagnosis given by Hincks for *A. polyoum*, it does not appear to me desirable to give a new specific name to the Roscoff form until the correctness of Hassall's original diagnosis has been verified.

I have observed individuals with twenty tentacles, the number given by Hassall, although in my own specimens twenty-one tentacles are more commonly present. It should be noticed that these numbers are considerably higher than those which characterize most species of *Alcyonidium*.

Most of my observations on the development were made on sections of portions of the entire colony which had been preserved with corrosive sublimate. The best staining was obtained by using picrocarmine and washing successively with very dilute solutions of picric acid in water and various strengths of alcohol. By this method the nuclei were stained red and the yolk-spherules yellow. Hæmatoxylin followed by eosin and borax-carmine followed by hæmatoxylin were also used for differentiating the yolk-spherules from the nuclei.

The eggs, several of which develop simultaneously in the same zoœcium, are large and possess numerous yolk-spherules (similar to those figured in the embryos) distributed uniformly throughout their protoplasm. During the segmentation and early development of the embryo, these yolk-spherules are met with indifferently in all the cells, and do not in the slightest degree preponderate in the hypoblastic elements. The segmentation (which is preceded by the formation of polar bodies) is of the remarkable type which

appears to be characteristic of all the *Ctenostomata* and *Cheilostomata*, as described by Repiachoff (14), Barrois (1, 2) and others. The segmentation-cavity was first distinguished in embryos composed of sixteen cells, which are disposed in four longitudinal rows of four each, two rows belonging to the oral half of the embryo, and two to its aboral half. At the 48-cell stage, the aboral half is composed of thirty-two cells, and the oral half of twelve cells, whilst four cells are internal. In the aboral region, the arrangement is as follows:

(1) two longitudinal rows, of four cells each, disposed symmetrically, right and left of the median plane, and occupying the centre of the aboral surface,

(2) a ring of eight cells completely surrounding the central group of cells, and in its turn surrounded by

(3) a peripheral ring of sixteen cells, which are, as Barrois has shown, the commencement of the ciliated ring.

The oral half consists of a central group of four large cells, surrounded by twelve peripheral cells.

The segmentation-cavity is at this stage fairly large, but is partially filled by four cells which are situated immediately above the central oral cells, and which have probably been derived from these latter. The four cells lying in the segmentation-cavity are the commencement of the hypoblast.

At a somewhat later stage I have observed the existence of a wide depression, the blastopore, situated in the middle of the oral surface and continuous with a somewhat irregular cavity surrounded by several large hypoblast cells.

At a subsequent stage, when the segmentation-cavity is partially filled by a large mass of cells (probably representing hypoblast *plus* mesoblast), the blastopore appears to have closed, whilst still later the segmentation-cavity is completely obliterated by the internal cell-mass, and the various organs of the larva are commencing to make their appearance.

In the first stage selected for figuring (Pl. I, fig. 1, a median longitudinal section through a young embryo) most of these organs are already partially established. The yolk-spherules are still to be found in all the tissues of the embryo. Two of the large cells

which compose the ciliated ring (*c.r.*) are to be seen at opposite ends of the section. The front part of the oral surface (within the area of the ciliated ring) is in the form of a depression, the "pyriform organ" of Barrois. This structure is developed as a cup-like involution of the epiblast, and there is no reason for believing that in *Alcyonidium* it makes its appearance in the interior of the embryo and subsequently fuses with the skin, as is stated by Barrois to be the case in *Lepralia* (2, p. 24). Not far behind the middle of the ventral surface is the aperture of the large sucker (*s.*) or "internal sac" of Barrois; this structure, like the pyriform organ, is developed as an invagination of epiblast, its aperture being much wider in earlier stages than in the embryo figured.

The alimentary canal consists of stomach (*st.*) and œsophagus (*œs.*). The stomach is lined by an extremely indefinite epithelium and has probably been developed by the hollowing out of the solid hypoblast-mass of earlier stages. The œsophagus (perhaps developed as a stomodæum) has a very fine lumen which can be traced as far as the stomach. The mouth (*m.*) is large and is far more conspicuous at this than at any of the later stages.

There is some slight reason for believing that the region immediately behind the aperture of the sucker (internal sac) represents, potentially, the anal region (*vide* fig. 1)[1]. If this is really the case, it is obvious that the embryo is *entoproctous*, and that the part of the body between the posterior end of the sucker and the ciliated ring represents the anal cone.

Figs. 2 and 3 are drawn from median longitudinal sections, the latter illustrating the structure of an embryo almost ready to be hatched, whilst the former explains the condition of the various organs in the period intermediate between the stages represented in fig. 1 and fig. 3 respectively. In fig. 2 the alimentary canal is seen to have acquired its maximum development. The lumen of the stomach (*st.*) is very conspicuous, although the epithelium which bounds it is by no means distinct, at this or at any other stage. This epithelium may consist of a mass of yolk-spherules

[1] The distinctness of the anal region has unfortunately been exaggerated in the figure.

embedded in a small quantity of protoplasm, with a few nuclei at intervals, or it may have the form of a very thin protoplasmic layer, in which nuclei are sparingly developed; but it is in any case extremely unlike an ordinary secreting epithelium, and this taken in conjunction with the facts (1) that the lumen of the stomach becomes progressively smaller as development proceeds, and (2) that there is probably, in the later stages, no communication between the stomach and the exterior, leads me to the belief that in *Alcyonidium* the alimentary canal is a rudimentary structure. A reference to fig. 3 will show that food could hardly, by any possibility, pass through the œsophagus at this stage of the development. Owing to the large supply of food-yolk in the eggs, to the fact that development proceeds within the body-wall of the adult, to the extremely short free larval life and to the degeneration of many of the embryonic organs during the metamorphosis, the alimentary canal is no longer required in its functional form.

The mouth (*m.*) is unmistakeable in fig. 2; the œsophagus, whose walls contain large numbers of yolk-spheres, has, however, no obvious lumen except near its junction with the stomach; the supposed anal region is now provided with a few cilia. The sucker is loaded with less yolk than in the preceding stages, although a few spheres still remain in its walls. A deep groove (*m.c.*), running round the aboral region of the embryo, has appeared on the dorsal side of the ciliated ring, with which it is concentric. This groove is already distinguishable in fig. 1, and is the structure which has been described by Barrois and others as the mantle-cavity. Its function is probably to render possible the revolution of the ciliated ring into the interior of the vestibule which is formed on the ventral side of the larva during the process of fixation.

The changes which subsequently take place in the alimentary canal, sucker and mantle-cavity may be understood by referring to fig. 3. The œsophagus is, at this stage, somewhat difficult to distinguish at the middle part of its course, whilst the stomach has thicker walls and a less conspicuous cavity than before.

The sucker has a very small lumen, and is further characterized by the almost complete absence of yolk from its long, columnar

cells. It extends into the lateral regions of the embryo, where it passes further forwards than in the middle line; its anterior border is thus markedly concave, as figured by Barrois (1) in many genera of *Cheilostomata* and *Ctenostomata*. The mantle-cavity is lined by a very high epithelium.

The function of the pyriform organ is by no means clear. Repiachoff (15) states that in *Tendra* a mass of cells is segmented off from the embryonic hypoblast in front of the mouth, and supposes that this mass represents the hypoblastic vesicle described by Hatschek in the embryos and stolons of *Pedicellina*. It appears to me probable, however, that the region which corresponds in *Alcyonidium* to that including Repiachoff's supposed hypoblastic vesicle in *Tendra* is occupied by a mass of nervous tissue which constitutes the brain of the larva. In spite of this, it is still possible to compare this region with the "dorsal organ" of the *Entoprocta*, since there are reasons (*cf.* 5 and 6) for doubting the existence of hypoblastic elements in the "dorsal organ" and for regarding it, on the contrary, as an important nerve-centre.

Fig. 4, which illustrates the structure of the region in question in *Alcyonidium*, is a transverse section through the anterior part of an embryo of about the same age as that represented in fig. 3, the ciliated ring (*c.r.*) and mantle-cavity (*m.c.*) having precisely the same arrangement as in that figure. In the middle of the ventral surface is seen the cup-shaped depression which constitutes the pyriform organ; at the sides of the latter, as far as the ciliated ring, the epiblast is thick, with finely granular protoplasm and few yolk-spheres.

As in the preceding figures, there is no definite body-cavity, although certain irregular spaces occur at intervals in the mesoblastic structures. The middle of the section is occupied by a large development of fine fibrils, bounded laterally by masses of nucleated protoplasm without yolk-spheres, and these masses appear to be continuous with the dorsal epiblast at the two sides of the middle line. I shall provisionally assume that the structures just described are of nervous nature, and that they represent the brain of the embryonic *Alcyonidium*.

The pyriform organ has at first sight the appearance of a mucous gland, owing to the presence in it of large spaces filled with a transparent substance, which does not readily take up staining materials. A more careful examination seems, however, to show that the organ is composed of a series of cells closely packed together at their outer ends, and prolonged internally into fine processes between which occur other cells filled with vacuole-like spaces. The nuclei of the latter cells are situated, for the most part, at their inner ends. It is important to notice that there is no sharp line between the pyriform organ and the central mass of nerve-fibres, which can in fact be traced into the cells of the pyriform organ. It seems to me probable, from the facts just described, that the principal function of the organ in question is a sensory one. The larva ordinarily swims with its pyriform organ directed forwards, and it is possible that this structure may be of use in estimating the character of the substance on which the animal desires to fix itself. The intimate connection of the pyriform organ with the central nervous system, together with the ciliation of the organ as a whole, is in favour of the view that the structure in question is of nervous rather than of glandular nature: I am unable to say whether all the cells of the pyriform organ are ciliated[1].

The supposed brain of the embryo of *Alcyonidium* consists then of a mass of nerve-fibres partially surrounded by ganglion-cells (as I identify the masses of nucleated protoplasm seen at the sides of the fibrous mass in fig. 4). The ganglion-cells are connected with the dorsal epiblast, except near the middle line, where a wedge-shaped mass of tissue characterized by the abundance of yolk-spheres intercalates itself into the nervous system. The fibrous mass of the ganglion sends off a pair of strong nerves (one of which is shown on the right side of fig. 4, *nv.*), which can be traced, in

[1] The pyriform organ has certain obvious resemblances with the structure described by Kleinenberg (*Zeits. f. wiss. Zool.*, T. XLIV, 1886, p. 61) in the larva of *Lopadorhynchus* as the *Kopfschild*, although as the latter belongs to the præoral region it is probably not to be regarded as the homologue of the former. The *Kopfschild* is said to be composed of vacuolated cells, which, although not themselves of nervous nature, are in the most intimate connection with the nervous system; the organ is moreover in relation with a ciliated sense-organ.

the sections, as far as the ciliated ring. These two nerves probably regulate the action of the cilia of the latter, and appear further to give off fibrils to the thick ventral epiblast at the sides of the pyriform organ.

In fig. 3 may be seen the supposed nervous structures of an old embryo in longitudinal section, the brain being connected with the dorsal epiblast, as in fig. 4.

In fig. 1, the region of the future brain is indicated by *br*. It is difficult to assert that any nervous structures are at present developed, but it may be noticed that the dorsal epiblast is very much thickened above the pyriform organ. This character is still obvious in embryos of the age of fig. 2, where it can usually be seen (and often more distinctly than in fig. 2) that the dorsal thickening of epiblast is so intimately connected with the ganglion-cells of the brain that it can hardly be doubted that these cells have been derived from the dorsal thickening itself. The origin of the nerve-fibres is more difficult to ascertain. It is possible that they may be developed from the dorsal side, and subsequently enter into relation with the pyriform organ and other parts of the ventral surface—or that they are developed partly from the dorsal and partly from the ventral surface. Such sections as figs. 3 and 4 seem to show that the nerve-fibres are not entirely derived from the ventral surface, and it appears to me probable, on the whole, that the greater part of the nervous system is developed from the dorsal epiblast.

If it can be admitted that even a portion of the "brain" has this origin, it then follows that we have in the larvæ of the *Ectoprocta*, as in those of the *Entoprocta*, a development of nervous tissue from the dorsal side of the ciliated ring, in the anterior part of the embryo. The region just described as "brain" in *Alcyonidium* will thus be the homologue of the "dorsal organ"—the supposed endodermic vesicle—of the *Entoprocta*. It would be interesting, in this connection, to know whether the pigment-spots described by Nitsche (11) and others in the larva of *Bugula* are in any way connected with this 'dorsal organ', as is the case with the eyes of the larva of *Loxosoma*.

The above conclusions do not altogether agree with the

statements of previous observers, to which we must now devote our attention.

It is practically certain that the separation of a mass of endoderm-cells from the alimentary canal does not take place, in *Alcyonidium*, in the region of the pyriform organ, as described by Repiachoff (15) in *Tendra*. The œsophagus is sharply distinguished, except in the earlier stages, from the tissues immediately in front of it by the large number of yolk-spheres present in its walls (*vide* figs. 2 and 3), and it is hardly to be supposed that the fibrillar tissue in front of the œsophagus could in any case be derived from the latter. I feel myself obliged to doubt the accuracy of Repiachoff's statements on this part of the development of *Tendra*, although it will be noticed that in other respects the description I have given agrees very closely with that of Repiachoff.

Vigelius (16) has published certain figures of sections of *Bugula*-embryos which suggest the possibility of the occurrence, in that genus, of a nervous system similar to that of *Alcyonidium*. In fig. 49 of Pl. XXVII Vigelius shows a layer of fibrils running round the pyriform organ in exactly the same position as the nerve *nv.* in my own fig. 4. Vigelius does not, however, in his description call any attention to the existence of these supposed nerve-fibrils. Again in fig. 14 of Pl. XXVI, Vigelius shows that the structure of the "calotte" of the larva is almost identical with that represented in the dorsal region of fig. 4 of the present paper;—i.e. that an internal proliferation of epiblast cells on each side of the middle line apparently takes place in this part of the larva. These cells may perhaps correspond with the structure identified as the brain in *Alcyonidium*, and the similarity between this genus and *Bugula* is rendered still more striking by the existence, in the latter (as is shown by the figure of Vigelius), of a central region which does not take part in the proliferation, and which projects as a wedge-like mass into the supposed nervous tissue (*cf.* my own fig. 4). Vigelius does not, however, show that there is any connection between the cells proliferated off by the "calotte" and the fibres round the pyriform organ.

It is believed by many writers that there is no fundamental difference between the larvæ of the *Ectoprocta* and those of the *Entoprocta*, and that the latter belong to the true Trochospheral type. This view is now adopted by Barrois (4), who admits that the alimentary canal, the oral and aboral surfaces and the ciliated ring are of essentially similar construction in the two groups of larvæ, and that the internal sac of the larva of the *Ectoprocta* is the homologue of part of the vestibule of the larva of the *Entoprocta*[1]. I am in complete accord with this view, but would myself push the agreement between the two types of larvæ somewhat further, in endeavouring to establish the homology of a part of the embryo of *Alcyonidium* with the "dorsal organ" of the *Entoprocta*.

Although it is true that in my paper on *Loxosoma* (5) I suggested that the pyriform organ itself might be the homologue of the brain of the *Entoprocta*, Lankester, in his article *Polyzoa* in the *Encyclopædia Britannica* (10), has somewhat misrepresented the view then expressed by me.

In Lankester's fig. 20 (from Balfour, after Barrois), *m*? is the pyriform organ, whilst *st.* (said to be considered by me as the cephalic ganglion) is the sucker or internal sac, the larva being turned with its dorsal surface downwards.

By reference to one of Repiachoff's figures[2] of *Tendra*, one of the *Cheilostomata*, it will be seen that the structure of the embryo of this genus is, as has been already explained, extremely similar to that of the larval *Alcyonidium*. The pyriform organ (*x.*), the alimentary canal (*o.*, *g.*) and the internal sac (*v.*) correspond with those of *Alcyonidium*. The dorsal thickening of epiblast, *y.*, which I formerly supposed to represent the cement-gland of the

[1] The work just quoted was published simultaneously with my paper *On the Life-History of Pedicellina* (6), and some of the figures in the latter would not have been required had the memoir of Barrois appeared at an earlier date. It will be hardly necessary to consider in detail Barrois' criticisms of my previous results, since certain modifications of the views formerly held by me (especially with regard to the nature of the metamorphosis) which I have explained in my paper referred to, bring me into moderately complete agreement with Barrois on the more important points on which he does me the honour of noticing my results.

[2] Reproduced in Pl. XX, fig. 22 of my paper on *Loxosoma*.

Entoprocta, is more probably the equivalent of the dorsal thickening of epiblast connected with the formation of the brain in *Alcyonidium*. The cells *e.*, identified by Repiachoff as hypoblastic in nature, are perhaps part of the brain-tissue itself.

In fig. 24 (*Cyphonautes*) of the plate just referred to, I reproduced one of Repiachoff's figures which was in some respects wrongly interpreted, owing to my previous inability to read Repiachoff's description. I now find that the structure *z. c.* is merely the anterior part of the ciliated band, that *x.* is the pyriform organ and that *e.* is the supposed endoderm-bud. This latter structure is not said by Repiachoff to give rise to the first polypide, as I formerly supposed.

It has recently been proved by Ostroumoff (12) that the organ shown in Repiachoff's figure just in front of the rectum ("l'organe énigmatique de Schneider") is in reality the sucker or internal sac, by which fixation is effected. The structure of *Cyphonautes* is hence more similar to that of other *Ectoproct*-larvæ than was formerly imagined to be the case.

It is difficult to assert at present that the cement-gland of the *Entoprocta* is represented in the *Ectoprocta*. Further investigations are needed to show whether the calotte of the latter is to be regarded as the homologue of the cement-gland, of the dorsal organ or of any other structure possessed by the larvæ of the *Entoprocta*.

The alimentary canal of the larvæ of the *Ectoprocta* appears to be functional in *Cyphonautes* alone (i.e. the larva of *Membranipora*). It has, however, been shown to be present, more or less well developed, in *Tendra* (Repiachoff, 15), some *Cyclostomata* (Ostroumoff, 13), whilst I believe it to occur in *Flustrella*. Barrois (4) has moreover suggested that the mouth is really shown as the depression *ce* in Pl. VII, fig. 13 and elsewhere in his large memoir (1), so that there is a considerable amount of evidence in favour of the view that the *Ectoproct*-larvæ were formerly provided with a distinct alimentary canal. Even in those cases where a digestive tube with a complete ventral curvature does not exist, the hypoblast is formed in the embryo as in other *Polyzoa* with a better developed alimentary canal, but afterwards assumes the form of a mass of

cells filling up most of the interior of the embryo. This has been shown, for instance, by Barrois (4) and Ostroumoff (13) for *Cyclostomata*, by Vigelius (16) for *Bugula* and by Repiachoff (15) for *Bowerbankia*.

The discovery of a well developed (though probably not functional) alimentary canal in the larvæ of the *Ctenostomata* (*Alcyonidium*) and of the *Cyclostomata* (as shown by Ostroumoff) relieves us from the necessity of supposing that *Cyphonautes* is really an archaic larva:—an assumption which is very difficult to reconcile with current views as to the highly specialized character of the *Cheilostomata*.

Cyphonautes may perhaps be regarded as a much modified type of larva in which the alimentary canal has been preserved in a functional form (owing perhaps to a longer larval life than in other *Polyzoa*?), whilst the oral face has become transformed into an atrium in which are situated the pyriform organ and the internal sac.

It is at present hardly possible to affirm that the characters of the *Alcyonidium*-larva are retained throughout the group of the *Ctenostomata*, since the accounts given by Barrois (1, 3 and 4) and Repiachoff (15) of the larvæ of this division of the *Polyzoa* are by no means concordant.

Barrois (3) has stated that the *Ctenostomata* (in which group it may be assumed that he does not include *Alcyonidium*) are characterized by the absence of the internal sac. Repiachoff (15) has, however, given a description, with figures, of the development of *Bowerbankia* which may perhaps tend to show that this structure is not really absent in the larva of this genus. Repiachoff's description and figures are extremely difficult to understand thoroughly, but if we accept his statements, the larva of *Bowerbankia* is very different from that of other *Ctenostomata*. A comparison of Repiachoff's paper (and especially of the series of sections of the larva figured on Pl. IV) with my own preparations of *Alcyonidium* leads me to suspect that Repiachoff's identifications of the surfaces of his larvæ were not accurate.

A further investigation of the larva of *Bowerbankia* is needed to clear up its structure. I will at present merely point out that

a great part of the difficulty in the comparison between Repiachoff's larva and that of *Alcyonidium* would be removed if it could be shown (as I suspect will be the case)

(1) That Repiachoff's mantle-cavity (*c.t.* in the figures) is really the internal sac or sucker.

(2) That the 'dorsal ciliated furrow' of the *Bowerbankia* larva is the pyriform organ.

In conclusion I may allude to Repiachoff's statement (15) that the brown body of the recently fixed larva is ciliated. It is probably not very rash to assume that these cilia really belong to the external surface of the larva involuted to the interior during the process of fixation.

List of memoirs referred to:

1. Barrois, J.; Recherches sur l'Embryologie des Bryozoaires; Lille, 1877.

2. —— Mém. sur la Métamorphose des Bryozoaires; Ann. des Sci. Nat. (Zool.), 6e Sér., T. IX, 1879—1880, No. 7.

3. —— Embryogénie des Bryozoaires; Journ. de l'Anat. et de la Physiol., T. XVIII, 1882, p. 124.

4. —— Mém. sur la Métamorphose de quelques Bryozoaires; Ann. des Sci. Nat. (Zool.), 7e Sér., T. I, 1886, No. 1.

5. Harmer, S. F.; On the Structure and Development of Loxosoma; Quart. Journ. Micr. Sci., Vol. XXV, 1885, p. 261.

6. —— On the Life-history of Pedicellina; Quart. Journ. Micr. Sci., Vol. XXVII, 1887, p. 239.

7. Hassall, A. H.; Description of two new genera of Irish Zoophytes; Ann. and Mag. of Nat. Hist., Vol. VII, 1841, p. 484.

8. Hincks, T.; A History of the British Marine Polyzoa (two vols.); London, 1880.

9. Joliet, L.; Cont. à l'hist. nat. des Bryozoaires des Côtes de France; Arch. de Zool. Exp. et Gén., T. VI, 1877, p. 292.

10. Lankester, E. R.; Article 'Polyzoa'; Encycl. Britannica, 9th Ed., Vol. XIX, 1885, p. 440.

11. Nitsche, H.; Beiträge zur Kenntniss d. Bryozoen—I. Beobachtungen über die Entwicklungsges. ein. chilostomen Bryozoen; Zeits. f. wiss. Zool., Bd. XX, 1870, p. 1.

12. Ostroumoff, A.; Note sur la métamorph. du Cyphonautes; Zool. Anzeiger, VIII. Jahrg., 1885, p. 219.

13. —— Zur Entwicklungsges. d. cyclostomen Seebryozoen; Mitt. a. d. zool. Stat. zu Neapel; Bd. VII, 1887, p. 177.

14. Repiachoff, W.; Ueb. d. ersten embryonalen Entwicklungsvorgänge bei Tendra Zostericola; Zeits. f. wiss. Zool., Bd. XXX Suppl., 1878, p. 411.

15. —— On the Morphology of the Polyzoa (Russian); Proc. New Russian Soc. Naturalists, Vol. VI, Odessa, 1880.

16. Vigelius, W. J.; Zur Ontogenie d. marinen Bryozoen; Mitt. a. d. zool. Stat. zu Neapel, Bd. VI, 1886, p. 499.

EXPLANATION OF THE PLATES.

(Figs. 1—3 were drawn with $\frac{1}{12}$ oil immersion of Zeiss, 1 oc.—Fig. 4 was more highly magnified.)

General reference letters.

br. brain;
c.r. ciliated ring;
m. mouth;
m.c. mantle-cavity;
nv. nerve;
œs. œsophagus;
p.o. pyriform organ;
s. internal sac or sucker;
st. stomach.

In all the figures the yolk-spheres are lightly shaded.

PLATE I.

Fig. 1. Median longitudinal section of a young embryo.

Fig. 2. Median longitudinal section of an older embryo.

PLATE II.

Fig. 3. Median longitudinal section of an embryo almost ready to be hatched.

Fig. 4. Transverse section of an embryo of the age of fig. 3 (more highly magnified), passing through the region of the brain and pyriform organ.

The manuscript of the above paper was received by Prof. de Lacaze-Duthiers in the beginning of August, 1887. Since that time I have had an opportunity of becoming acquainted with two memoirs by Dr Ostroumoff on the Polyzoa of the Gulf of Sebastopol. I regret that it was not possible for me, during the correction of my proofs, to take into consideration the results arrived at by this observer.

ON THE EXISTENCE OF COMMUNICATIONS BETWEEN THE BODY-CAVITY AND THE VASCULAR SYSTEM

BY

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In the General Considerations which follow Mr Sedgwick's recent paper upon the development of Peripatus Capensis, he sums up the characteristics of the coelom in the following terms: (i) the coelom does not communicate with the vascular system; (ii) it communicates with the exterior through nephridial pores; (iii) its lining gives rise to the generative products; (iv) it developes either as one or more diverticula from the primitive enteron, or as a space or spaces in the unsegmented or segmented mesoblastic bands (in the latter case called mesoblastic somites). Later on he calls attention to the fact that "there are certain animals to which the above general considerations as to the distinctness of the coelom and the vascular system do not apply." The animals here referred to are the Hirudinea and the Nemertea. In a later paper Sedgwick suggests the possibility that the nephridial funnels of Leeches might possibly open into a closed vesicle which lies in, but does not open into the vascular system. That some such structure may have been overlooked is rendered more probable when one recalls the number of able observers who failed to observe similar structures in Peripatus, and the fact that so careful a worker as Oscar Schultze overlooked the comparatively large nephridial funnels, when working at the excretory system of Clepsine.

Last term I devoted some time to the examination of these points. The forms I investigated were Clepsine, and to some

extent Pontobdella amongst the Rhyncobdellidae, and amongst the Gnathobdellidae, Hirudo and Nephelis, and I may as well say at once that my researches on these forms confirm the results which Bourne published in the year 1884 in his exhaustive paper, "Contributions to the Anatomy of the Hirudinea[1]."

The points to which I particularly directed my observation fall under three heads.

Firstly: Do the internal funnels really open, or end blindly, and in what spaces do their internal ends lie? For instance, are there any such sacs as Sedgwick has described enclosing the funnels of the nephridia of Peripatus?

Secondly: the communication between the true blood spaces and the sinuses, the nature of the fluid found in these spaces, and the circulation of the blood.

Thirdly: the embryological origin of the sinuses. With regard to this last I have been unable to make any investigation, but a certain amount of information on this subject is found in the writings of Nusbaum, Whitmann, and others.

With regard firstly to the nephridial funnels of Clepsine, I can fully confirm Bourne's statements. The funnel is usually composed of two cells, but in some cases I have seen three nuclei indicating the presence of three cells in the funnel; these surround a lumen; on one side this lumen is continuous with the sinus, and on the other hand with a sac. The lumen of the funnel is lined with long cilia. Bourne's figure of this structure is rather diagrammatic; the lumen of the funnel is occluded; but he definitely states that it opens, and in some of my preparations the coagulated mass of fluid in the sinus is joined to a similar coagulum in the sac mentioned above, by a strand of coagulated matter which in all respects resembles blood. The sac is usually full of coagulated fluid with small corpuscles scattered in it. In one nephridium there were two funnels, each opening into the sac; and again, I once saw a bunch of three or four funnels connected with the single sac of a nephridium.

The internal end of the nephridium of Hirudo does not open,

[1] *Quarterly Journal of Microscopical Science*, Vol. xxiv. p. 419.

but is surmounted by a number of cells, each with a depression. The fact that it does not open is regarded by Bourne as due to degeneration. This swollen end lies in a space which contains red blood, and there is no sac full of coagulated blood and corpuscles as in Clepsine.

Nephelis, however, is provided with nephridial funnels which do open on the one hand into the space in which their internal ends are situated, and on the other into a sac similar to that found in Clepsine, which contains both coagulum and corpuscles.

With regard to the spaces in which the funnels lie, there seems to me to be no doubt that Bourne's description is correct. In Clepsine, the funnels lie in pairs, in the ventral sinus, with the ventral vessel and nerve cord between them. No trace of any special sac, such as is found in Peripatus, is present.

In Nephelis the funnels open into a special enlargement of the botryoidal tissue, but there is no reason to regard this as anything more than a development of the coelomic spaces, as Bourne has done.

Again, in Hirudo, where the funnels do not open, the blind internal end lies in a perinephrostomial sinus, which again possesses no characteristics which would justify the assumption that it is fundamentally different from other coelomic spaces.

Before passing on to consider the means of communication of the vascular and coelomic spaces, I wish to insert a few remarks upon the sacs which are present on the nephridia, which have internal open funnels, and in which numerous corpuscles from the blood are found. These corpuscles seem to be degenerating, and in some cases they appear rather more granular than the normal corpuscles in the blood.

It has occurred to me that we have to do here with a phenomenon similar to that which Durham[1] has described in Asterias rubens. The amoeboid corpuscles, after devouring some substance which it is to the advantage of the organism to excrete, instead of working their own way to the exterior, are taken up by the open

[1] H. E. Durham, "The Emigration of Amoeboid Corpuscles in the Starfish." *Proc. Roy. Soc.* Vol. 43, p. 327.

funnel of the nephridium, and in the sac they disintegrate and are eventually thrown out from the body. In Asteroideae, where there are no nephridia, the corpuscles work their way out through the body-wall.

We owe our knowledge of the paths by means of which the fluid passes from the blood vessels into the coelom chiefly to Lankester and Bourne. Besides the direct communications which exist in the Rhyncobdellidae, there is the communication by means of the botryoidal tissue which is seen at its best in the Gnathobdellidae. A fragment of the brown tissue of a Leech shews at once the connection of the lumen of the botryoidal tissue with that of the thin walled vessels. And my sections through Clepsine and Hirudo shew in numerous places the large openings by means of which the botryoidal tissue is put into communication with the sinuses, sometimes a continuous coagulum being found, lying half in one and half in the other system of spaces.

The same kind of blood is found in both the true vessels and the sinuses, except that, as Bourne points out, certain large corpuscles which occur in the sinuses of Clepsine and Pontobdella are not found in the blood vessels, being, as he suggests, too large to pass through the communicating channels.

The contraction of the dorsal vessel in its sinus can be seen without difficulty, and I have often watched the ventral vessel contract, sending the blood from before backward, whilst the current in the sinus surrounding the vessel flowed in the reverse direction. The fluid and corpuscles in both vessels and sinuses being apparently identical.

The foregoing facts fully corroborate Bourne's statements that the nephridia open into the sinuses, which in their turn are in communication with the blood vessels, and which contain the same fluid as the vascular system. With regard to the embryological nature of these spaces we are largely indebted to the researches of Nusbaum[1]. He describes in Clepsine the mesoblastic bands dividing into 33 somites. Each of these somites acquires a cavity which gradually increases in size. The walls of

[1] *Archives Slaves de Biologie*, Vol. 1, pp. 320 and 539.

this cavity on the upper side, towards the endoderm, become only one cell thick, they form the splanchnopleure. The opposite wall, the somatopleure, that next the ectoderm, is however several cells thick.

The anterior wall of each somite fuses with the posterior wall of the preceding somite, and thus septa, comparable to those of the higher worms, are formed, and persist for a short time in embryonic life. Soon, however, the somites fuse with one another, and their cavities become continuous. Then the walls of the two lateral cavities which are thus formed, and at first are only in the ventral face of the embryo, commence to grow round the endoderm. Part of the tissue forming the septa persists as the dorso-ventral muscles. The spaces on each side, growing dorsally and ventrally, fuse, and, by the arrangement of the dorso-ventral muscles two longitudinal septa are formed which divide the common space into a dorsal, ventral, and two lateral sinuses. These are the blood sinuses, which by the development of the connective tissue and muscles become relatively much smaller in the adult than in the embryo.

Nusbaum further describes and figures the development of the dorsal and ventral vessel, both of which apparently arise as a solid cord of cells, proliferated from the splanchnic layer of the mesoderm, in the middle dorsal and ventral line. They subsequently acquire a lumen, and, separating off, lie in their respective sinuses.

The same author, in describing the development of the nephridia, points out that in the young embryo they appear in every somite, even in those which form the posterior sucker, where they subsequently abort.

Thus with regard to the origin of the space and the opening into it of the nephridia, the sinuses of the Hirudinea are truly coelomic, the embryological researches of Nusbaum confirming in a most striking way the predictions of Bourne.

If we turn to the third characteristic of a coelom, that "its lining gives rise to the generative products," the evidence is not quite so satisfactory. The origin of the reproductive cells is probably an example of "precocious segregation." The sexual cells arise from the mesoblasts—the segment cells of Whitmann—which, arising posteriorly, multiply and pass forward till a heap of them

is formed laterally in each somite. One pair of these form the ovary and seven pairs become testes. According to Nusbaum the tunica of the generative glands is formed at the expense of the mesoderm. This doubtless buds off corpuscles, just as it does into the sinus, and thus forms the colourless corpuscles which Bourne found in the fluid surrounding the true ovary. Nusbaum traces the oviduct and vas deferens back to nephridia.

I have attempted so far to shew firstly that there is no doubt that the old statements with regard to the blood system of Leeches being in communication with the sinus system is true, and secondly that the sinus system is coelomic in nature. So that with regard to the group Hirudinea, the vascular system is undoubtedly in communication with the coelom.

Let us now turn to the Nemertines, the second group of animals mentioned by Sedgwick as forming an exception to the rule that the blood system is independent of the coelom.

The nephridial system of these animals is not so definite in its arrangement as amongst the Hirudinea. Oudemans[1] has examined it in a great number of forms, and I have to some extent been able to confirm his observations. In his summary at the end of his paper he states, "the nephridial system of the Nemertea consists of one or more canals, directly communicating, or not, with the vascular system, provided, or not, with cilia, and communicating with the exterior by means of excretory ducts."

But when we come to consider the nature of these spaces which contain blood, and in which the internal end of the nephridium is sometimes situated, we shall see that they differ considerably in their fundamental origin from the sinus system of the Hirudinea.

In his valuable work on the embryology of Lineus obscurus, Hubrecht[2] points out that the blood vascular system together with the proboscidian cavity represents the last remnants of the archicoel or segmentation cavity. Hubrecht has proposed the

[1] A. C. Oudemans, "The Circulatory and Nephridial Apparatus of the Nemertea." *Q. J. M. S.* 1885. Supplement.

[2] A. A. W. Hubrecht, "Contributions to the Embryology of Nemertea." *Quarterly Journal of Microscopical Science*, Vol. xxvi. p. 417.

name archi-coelom for this system of spaces, and in which, as is stated above, the inner ends of the nephridia sometimes lie.

I have already drawn attention[1] in a previous paper to the fact that the cavity of the heart in the embryo Lamprey is continuous with the segmentation cavity. In my account of the development of the heart the following passage occurs: "From the fact...that the mesoblast behind the heart has not split into somatic and splanchnic layers, and not united ventrally, it will be seen that the cavity of the heart communicates posteriorly with the space between the ventral yolk cells (hypoblast) and the epidermis. Such a space would be equivalent to the segmentation cavity." Such a space exists, and becomes for a time crowded with blood corpuscles budded off from the free edges of the mesoblast, which occupies its dorso-lateral angles. These subsequently become enclosed in a secondary cavity formed by the down-growth and fusion of the mesoblastic laminae, and so come to lie in the heart and subintestinal veins.

When I wrote the above I was not aware that Bütschli[2] had conjectured that the cavity of the vascular system of Vertebrates was derived from the segmentation cavity. What he conceived from theoretical grounds I was able to see in the developing Lamprey. I think we are therefore justified in applying to the vascular system of Vertebrates the term archi-coelom, which Hubrecht has suggested for the blood-containing spaces in the Nemertea.

The system of spaces then of Nemertea which contain blood, and in which the inner ends of the nephridia sometimes lie, are not coelomic in their nature, but archicoelomic; and as the cavity-sheath of the proboscis has a similar origin, we are driven to the conclusion that there is no coelom in these animals, and therefore there can be no communication between the coelom and the vascular systems in this group, such as has been demonstrated for the Hirudinea.

The Gephyrea form another group of animals in which, like

[1] "On some points in the Development of Petromyzon fluviatilis." *Q. J. M. S.* Vol. xxvii. p. 325.

[2] "Ueber eine Hypothese bezüglich der phylogenetischen Herleitung des Blutgefässapparates eines Theils der Metazoen." *Morph. Jahrbuch*, Vol. 8, 1883.

the Hirudinea, there is direct communication between the coelom and the blood vessels.

The body-cavity of Sipunculus is developed as a split in the mesoblastic bands; the cells lining it give rise to the generative products; and the nephridia open at their internal ends into it.

The blood vascular system arises late. Hatschek[1] describes its first origin during the metamorphosis of the larva, lying on the dorsal side of the alimentary canal. Although his description is not very detailed, there is nothing to shew that we have here to do with anything more than a normal blood vessel.

In the adult the main longitudinal vessel lies well surrounded by connective tissue, and between two of the longitudinal vessels; it contains usually only blood corpuscles, which are exactly like those found freely in the body-cavity; but in individuals which are sexually ripe, spermatozoa and ova are often found in it. The openings, by means of which the cavity of this vessel communicates with the coelom, can be seen if the vessel be dissected out and exposed under a microscope; and further, Vogt and Yung[2] state that it is easy to inject the former from the latter.

Another group which stands far apart from both the Hirudinea and the Gephyrea, and in which communications exist between the vascular system and the coelom, or at any rate with part of it, is the Echinodermata. Here, according to the observations of Hamann and Koehler, in Spatangids at least the blood system is in communication with the water vascular system, embryologically a part of the coelom and developed from an outgrowth of the body-cavity. And according to the French school of naturalists who have worked at this group, and amongst whom Perrier is the most prominent, this connection may be extended to the whole group of the Echinodermata.

Finally, in the class Vertebrata we again find the body-cavity, which is admittedly coelomic in nature, in communication with the vascular system, which is to some extent at any rate archicoelomic. The means of communication is through the lymphatic

[1] B. Hatschek, "Ueber Entwicklung von Sipunculus nudus." *Arbeiten aus dem Zoologischen Institut.* Wien, Bd. v. p. 33.

[2] Vogt and Yung, "Lehrbuch der praktischen vergleichenden Anatomie."

system. This opens on the one hand into the body-cavity by means of open stomata, and on the other by means of the thoracic duct into the venous system.

That fluids can pass from the body-cavity into the blood system by means of the lymphatic system has been shewn both by Recklingshausen and by Ludwig. The former found that milk put upon the peritoneal surface of the central tendon of the diaphragm—where numerous stomata exist—shewed little eddies caused by the milk globules passing through the stomata and entering the lymphatics. Ludwig's experiment is even more conclusive. He took a dead rabbit, and removed its viscera, and placed it so that the peritoneal surface of the diaphragm was exposed. He then poured into this a solution of Prussian blue, and, after imitating the respiratory movements for a few minutes, he obtained the lymphatics filled with a blue injection, shewing a beautiful plexus.

A more direct communication between the blood system and part of the body-cavity has been described in one Vertebrate. Weldon[1] has described and figured the structure of the head kidney in Bdellostoma Forsteri. He finds running through the substance of this organ a number of fine tubules, lined with columnar cells and anastomosing with one another. These tubules open on the one hand into the pericardium and on the other into a central duct. In this duct lies a clot which is exactly similar to the blood clots found in the surrounding blood vessels. Further, in some cases capillaries were seen to enter this duct. There seems to be no reason to doubt that in this animal we have a part of the vascular system in communication with a part of the body-cavity through the tubules of the head kidney.

That there is a very primitive connection between these systems, is further supported by the remarkable observations of Seeliger[2], and Van Beneden and Julin[3] in the development of the heart of Clavellina.

[1] "On the Head Kidney of Bdellostoma," by W. F. R. Weldon. *Q. J. M. S.* Vol. 24, 1884.

[2] "Die Entwicklungsgeschichte der Socialen Ascidien," Oswald Seeliger. *Jenaische Zeitsch. für Naturwissenschaft*, 1885.

[3] "Recherches sur la Morphologie des Tuniciers," Van Beneden and Julin. Gand, 1886.

These authors describe and figure in all stages the development of the heart and the pericardium of this Ascidian from an outgrowth of the ventral wall of that part of the endoderm which forms the pharynx, close to the end of the endostyle. This hollow diverticulum becomes separated from the endoderm and lies as a closed vesicle outside it. One half of the vesicle then invaginates, so that a two-walled vesicle results, there being a space left between the outer and inner wall. This space becomes the cavity of the pericardium, whose wall is formed of the outer layer of the double vesicle; this cavity is derived from the cavity of the endoderm.

The inner wall of the vesicle forms the wall of the heart, and the cavity of the heart is continuous with the primitive body-cavity. The longitudinal opening from the heart into the body-cavity persists for some time, until the free swimming larval stage; eventually it closes in the middle but still leaves an anterior and posterior opening through which the blood enters the heart from the body-cavity and leaves it again each time that organ contracts.

In Kleinenberg's[1] remarkable paper on the larva of Lopadorhyncus, he states that the segmentation cavity becomes the coelom in this and in many other Annelids. The coelom is therefore in these animals archi-coelic in nature, and we have seen that in some Vertebrates the vascular system is of this nature. In the Nemertea the spaces which may be perhaps considered to be both body-cavity and vascular cavity are also archi-coelic. This group of animals would therefore seem to have retained the most primitive of all cavities—the segmentation cavity—as the only system of spaces between the endoderm and ectoderm: whilst the primitive segmentation cavity has differentiated in the higher animals, on the one hand into body-cavity—Annelids, and on the other in the cavities of the vascular system—Vertebrates.

[1] "Die Entstehung des Annelids aus der Larve von Lopadorhyncus." Kleinenberg, *Zeit. f. wis. Zoologie*, Bd. 44, 1886.

On Some Points of the Anatomy of Polyxenus lagurus.

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With Plate III.

The following does not profess to be a complete account of the anatomy of this interesting little Myriapod. In working out the development of Julus terrestris, certain questions occurred which led me to investigate the adult anatomy of some other forms, amongst them of Polyxenus, and I considered that the following notes might be of interest to other observers. I found it very difficult to obtain material, and had it not been for the kindness of Dr. St. Remy, who was also working at Myriapods, and who took great trouble to procure a supply of Polyxenus for me, I must have delayed the publication of these notes for a considerable time. This form has been investigated by several naturalists, especially by Fabre and Bode (2, 1).[1] I have also availed myself of the excellent work of Latzel (4).

External Features.

In comparing the body of Polyxenus with that of Julus, the most striking peculiarity in Polyxenus is the composition of the individual segments. Each body-ring, as described by Bode, consists of a dorsal plate, two lateral plates, and two

[1] The figures refer to the list of literature at the end of the paper.

ventral plates. The anterior parts of the two ventral plates are fused so as to form a triangular point. A section through the fused part is shown in fig. 1. These plates are the "lames pedigères" of Brandt. In a former paper on Julus (5) I called attention to the fact that the differences between the body-form of the early stages and the body-form of the adult were essentially due to a diminution of the ventral region and an increase of the dorsal to such an extent that the dorsal plate came to form a complete ring round the body. I also pointed out that the larval condition showed a great resemblance to the earliest fossil forms of Myriapoda. Now Polyxenus, in its anatomy, resembles the larval rather than the adult Julus. If we compare a section through one of the segments of Polyxenus with a section through a larval Julus, such as is shown in fig. 34 of my former (5) paper; and again, with a section through a segment of a nearly adult Julus, such as is shown in fig. 2 of the same paper, the resemblance to the larval Julus and the difference from the adult shown in the well-developed sternal region, the widely separated bases of the legs, and the less developed dorsal region, is sufficiently striking to render it worth while to compare the features of its general anatomy with the results obtained by the investigation of the development of Julus.

Of the appendages, the pair that seems to differ most from those of other Chilognaths is that of the second post-oral segment, the deutomalæ; these have been described by Bode and Latzel (l. c.). The most noticeable feature about them is the possession of two palps on either side, the one short and broad, the other long and slender. The four-lobed plate of the adult Julus is of course without any vestige of similar structures, but the larval form possesses two short, broad projections on either side, which seem to me to be rudiments of structures similar to those of Polyxenus.

The sense-organs described by Bode, and supposed by him to be olfactory, may be mentioned here, as their microscopic structure has never been investigated. Each of these organs consists of a spine inserted into a structure formed by the

external cuticle and the hypodermic matrix. At the point of insertion of the spine the chitin and matrix are considerably thickened. At the external surface the chitin is raised up round the spine so as to form a rim or ridge (fig. 4) surrounding a semicircular cup of considerable depth. The hole for the spine to pass through is at the bottom of the cup, and on the internal surface the chitin round this hole projects internally so as to form a short wide tube corresponding to the semicircular depression on the external side (fig. 4, *t.*). The spine itself is long and rather stout, thicker in the middle than at either end. It is provided with a rim (fig. 4) which fits the perforation at the bottom of the semicircular depression, while the part below the rim projects internally within the tube and ends in a depression, into which a nerve-cell fits. The whole internal part of the organ (i. e. the tube and part of the spine) is embedded in a mass of hypodermic matrix cells, which serve for the renewal of the organ at the moults. On account of the manner in which this organ is adapted to convey movements to the sense-cell, and is rather fitted to convey actual pressure than delicate vibrations, I hold it to be a tactile organ rather than an olfactory one.

With regard to the external generative organs, they have already been described by several authors, but there is one point on which a little uncertainty exists. Fabre describes the male external generative organs as very long, and lying against the abdomen when not in use. Latzel says that they are similar to those of the female, with the exception that they have a round opening and not a slit-like one. I can confirm his account, having had the good fortune to obtain several males among the small number of Polyxenus at my disposal. Sections through the male and female external generative organs are shown in figs. 2 and 3. The dilation of the oviduct into which the external opening passes is shown more markedly than the corresponding dilation of the vas deferens; but I am inclined to believe this is due to differences in preserving. I have noticed that the small, very fine hairs present in both sexes round the external generative openings, are more

numerous in the male, but this may possibly be due to individual differences. I have not had a sufficient quantity of males to make certain.

The Malpighian Tubes.

Bode succeeded in dissecting out the Malpighian tubes, but their minute structure has never been described, and as they show a variation from the ordinary form of these organs which is not found in any other Myriapod, it is worth while to give a short account of them.

Each tube—there are a pair of them—leaves the junction of the rectum and mid-gut as a stout tube with a definite lumen. The lumen is surrounded by a ring of denser tissue which has a faintly striated appearance. Each tube passes backwards along the rectum to the terminal dilation of the latter where it becomes greatly thickened, and is doubled upon itself so as to form a great spherical knot, the greater part of which lies in the semicircular chitinous elevations which are placed at either side of the anus. From this coil each tube passes off greatly reduced in size so as to have the form of a thin tube (figs. 8, 9, 6, *r. malp. t.*) like any other Malpighian tube. These two thin returning portions pass forward and end blindly about the middle of the body. From the anterior end of the rectum, where the Malpighian tubes originate, the whole of these structures, together with the rectum, is enveloped in a membrane (figs 6, 8, 9) which passes backwards and becomes fused with the mass of cells forming the hypodermis. This membrane is perfectly definite on the external surface of the Malpighian tubes, but I have been quite unable to find any trace of it between the tubes and the rectum. I am convinced that it envelopes the tubes and the rectum together. Where the small returning portions of the Malpighian tubes pass beyond the origin of the tubes and the enveloping membrane, at the anterior end of the rectum, they pierce the membrane, and passing forward lie close to the mid-gut just like other Malpighian tubes.

The salivary glands, which are long and tubular, open on

the internal surface of the deutomalæ in the same position as those of Julus and other Chilognaths. I have not thought it necessary to give a figure.

The Nerve-cord.

The nerve-cord shows a greater resemblance to that of the larval Julus and also of Chilopods than does the nerve-cord of any other Chilognath with which I am acquainted. Between the ganglia the fibrous part of the ventral nervous system is divided into two distinct cords as shown in figs. 5, 6, and 12.

The Internal Generative Organs.

In both male and female the generative organ has the form of a long tube, which communicates with the exterior by two short oviducts or vasa deferentia. The female organ (fig. 6) consists of a long tube, formed of a single layer of cellular membrane, and containing the spongy connective tissue (or stroma) within which the ova are produced. Some of the cells of this tissue become ova, while others, indistinguishable at an early stage, form the follicles which surround the ova.

At its anterior end the ovary becomes constricted, as shown in fig. 5. Its walls increase in thickness, and are composed of two layers, an external and an internal, the latter consisting of larger cells. Just at the point of division into the two oviducts two large receptacula seminis communicate. They are composed of a single layer of cells (fig. 5, *rec. sem.*), and contain spermatozoa, as shown in the figure.

The male generative organ also consists of a tube, the testis, which divides anteriorly into two vasa deferentia. The walls of the testis are formed by a single layer of cells, and within it is a mass of spongy connective tissue from the cells of which the sperm-cells and the follicles arise. The spermatozoa originate by a sperm morula (fig. 7), and the morula is surrounded by a follicle which may perhaps serve to secrete the covering of the spermatophores which are formed inside the follicles. The spermatozoa are long and thread-like, resembling those of Lithobius and Scolopendra.

The Heart.

The heart has been described by Bode, who saw the dorsal vessel dividing into three branches in the head, and also found an artery in the middle of each segment. The dorsal vessel is suspended from the dorsal hypodermis by suspensory muscles, and muscle-fibres connecting it with the fat bodies are attached to its ventral surface. These muscles form a sort of interrupted pericardium like that in Julus.

In each segment of the body there are two pairs of ostia occupying the same position as those in Julus, but there is only one pair of arteries in the middle of each segment. The heart is composed of three coats, an intima or structureless internal lining, a muscular coat, and a cellular external covering. The layers are not so well marked as in Julus; perhaps this is owing to the small size of the animal. The muscular valvular apparatus of the ostia is the same as that found in Julus (5). The circulation is connected, as in Julus, with the spaces in the fat-bodies. These spaces are often crowded with blood-corpuscles. There is no definite blood-space round the nerve-cord as in Julus.

The Eyes.

The shape of the lens is peculiar, and more resembles that of Scutigera (see Grenacher's paper, 3) than that of any other Myriapod with which I am acquainted. Its external surface is highly convex, while the internal is flat. The cells of the hypodermis are continued round the circumference of the lens so as to form a kind of diaphragm. A section through the edge of the lens shows this (fig. 13, *h. c.*). The crystalline cones are arranged in groups, so that a transverse section through the retinal depression gives the appearance shown in fig. 14, *B.* I have been unable to find any intrusive connective-cells, but this may be due to want of material. The pigment is thickest at the base of the retina, and also at the commencement of the rods (fig. 13, *pgt.*, *inner pgt.*).

General Conclusions.

The principal interest of Polyxenus lies in the likeness of some of the features of its anatomy to the anatomy of the Chilopods. While it agrees with the Chilognatha in the position of its generative organs and the duplication of some of its segments (the first four segments are provided with only one pair of appendages, the next four have two pairs, and the last one pair—Latzel and Bode), and in the fact that it is a vegetable-feeding animal, in connection with which fact its salivary glands are long and tubular, like those of other Chilognaths; it nevertheless resembles the Chilopods in the form of its spermatozoa, which are long and filiform, and are contained in spermatophores; in the general structure of the segments, having the legs wide apart, with a ventral region between them; and in the differentiation of the ventral nerve-cord. The single artery given off in each segment seems at first sight to afford a resemblance to the Chilopod circulatory organ, but I believe this resemblance to be superficial. In its essential characters the heart resembles that of the Chilognaths, and remembering that the Chilognath heart is formed by the confluence of spaces in the tissues of the body, the formation of the arteries is not a deep-seated character.

Characters peculiar to itself are the peculiar form of the second pair of mouth appendages, and the absence of stink-glands and the substitution for them of numerous spines as a means of defence.

In a former paper (5) I advanced certain views about the phylogeny of Myriapods, and came to these conclusions:—First, that Myriapods were descended from some Peripatus-like ancestor; secondly, that the Chilopods and Chilognaths branched off from some common ancestor, not differing much from the fossil Archipolipoda. Now the characters in which Polyxenus resembles the Chilopods are characters common to the larval Julus, and to the Archipolipoda (5). With regard to the absence of stink-glands, and the substitution of spines arranged in tufts over the body, I found in Julus that the

stink-glands were formed comparatively late in the development as invaginations of the dorsal plate, and I came to the conclusion that they were not very deep-seated characters. If this is so it is not difficult to understand that they may never have been developed in Polyxenus, but that the spines may have been a sufficient protection. It is worth noting that the Archipolipoda had spines, and not stink-glands. From all these points in the anatomy of Polyxenus I am inclined to regard it, not as a recently formed link between the Chilopods and Chilognaths, but as an animal which has preserved certain traces in its anatomy of its descent from a common ancestor of the two classes, such ancestor being related to the Archipolipoda. I consider it as confirming my view that the Myriapoda are descended from a Peripatus-like form, and as opposing their descent from Thysanura. I am fully aware that insomuch as I investigated Polyxenus with a definite idea, I have probably taken a one-sided view of the points I worked at; but I hope that my work will induce others to investigate this animal more fully, and thus increase our knowledge of the various questions suggested by Myriapod anatomy and development.

My work was entirely carried on in the Cambridge Morphological Laboratory.

Literature.

1. J. Bode.—"Polyxenus lagurus," 'Zeitschr. für die gesammten Naturwissenschaften,' 1877.
2. Fabre.—"Anatomie des organes reproducteures des Myriapodes," 'Ann. des Sci. Nat.,' 4 sér., 1855.
3. H. Grenacher.—"Ueber die Augen einiger Myriapoden," 'Archiv für mik. Anat.,' 18.
4. Latzel.—'Die Myriapoden der oesterreichisch-ungarischen Monarchie,' Wien, 1880.
5. F. G. Heathcote.—"The Post-embryonic Development of Julus terrestris,' Phil. Trans. Roy. Soc.,' 1888.

DESCRIPTION OF PLATE III,

Illustrating Mr. F. G. Heathcote's paper "On Some Points of the Anatomy of Polyxenus lagurus."

FIG 1.—Part of a transverse section through the middle of the body, showing the ventral plate. The bases of the legs are separated and the ventral plate—that is, the fused anterior part of the two "lames pedigères" of Brandt—occupies the space between them.

FIG. 2.—Part of a transverse section through the body, showing the female external generative appendage. *dil. ovid.* Dilation of the oviduct. *ext. gen. org.* External generative organ.

FIG. 3.—Section through the male generative appendage. *dil. vas. def.* Dilation of the vas deferens.

FIG. 4.—Section through the sense organ. *ext. cut.* External cuticle. *hyp.* Hypodermis. *t.* Tube. *gan.* Ganglion-cell. *hyp. c. mass.* Hypodermic cell mass.

FIG. 5.—A transverse section through the fourth segment of a female, to show the ovary, receptacula seminis, and the general arrangement of the organs. The figure is semi-diagrammatic; the outline of the body, the gut, ovary, receptacula, and nerve-cord being from an actual section; while the heart, muscles, and fat-body are diagrammatic. *g. n. c.* The ganglionic part of the nerve-cord. *f. n. c.* The fibrous part. *rec. sem.* Receptaculum seminis. *spmzoa.* Spermatozoa in the receptacula. *ovidct.* Oviduct.

FIG. 6.—Part of a transverse section through the posterior part of the body of a female, to show the Malpighian tubes and the ovary. *g. n. c.* Ganglionic part of nerve-cord. *f. n. c.* Fibrous part. *fol. ov.* Follicle round ovum. *ov.* Ovum. *w. ov.* Wall of ovary. *r. Malp. t.* Returning part of the Malpighian tubes. *Malp. t.* Malpighian tubes.

FIG. 7.—Part of a section through the testis of a male, showing a follicle containing a sperm morula. *f.* Follicle. *sp. mor.* Sperm morula.

FIG. 8.—Part of a longitudinal section through the posterior end, to show the Malpighian tubes. *a. d.* Anal dilatation. *o. w.* Outer wall of the gut. *malp. t.* Malpighian tube. *l. malp. t.* Lumen of Malpighian tube. *memb.* Membrane.

FIG. 9.—Section through gut and Malpighian tubes. *malp. t.* Malpighian tube. *r. malp. t.* Reduplicated part of Malpighian tube. *memb.* Membrane.

FIG. 10.—Longitudinal section through a segment of the heart. *art.* Artery. *ost.* Osteum.

FIG. 11.—Transverse section through heart. *ext. cut.* External cuticle. *ext. w. ht.* External wall of heart. *int.* Internal lining of heart. *m. w. ht.* Muscular wall of heart. *musc.* Muscle-fibres from the heart to the fat-bodies, forming a sort of pericardium. *susp. musc.* Suspensory muscle of the heart.

FIG. 12.—Section through the nerve-cord. *gnc.* Ganglionic part. *fnc.* Fibrous part.

FIG. 13.—Section through region of eye, showing two eye-spots and the lens of another. *r. c.* Retinal cells. *inner pgt.* Pigment round the base of the crystalline cones. *l.* Lens. *h. c.* Cells of the hypodermis. *pgt.* Pigment around the base of the retinal cells.

FIG. 14.—Section through the region of the eyes, showing one spot cut horizontally and one longitudinally. *A.* An eye-spot cut longitudinally. *B.* An eye-spot cut transversely. *l.* Lens. *pgt.* Pigment. *c.* Crystalline cones.

Notes on the Anatomy of Dinophilus.

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With Plates IV and V.

The anatomy of *Dinophilus*, a genus established by Oscar Schmidt in 1848, has formed the subject of several memoirs, amongst which attention must be specially called to the recent papers of Korschelt (6), Repiachoff (12), and Weldon (13). A complete account of the synonymy of the genus was given by v. Graff* in 1882, whilst Korschelt (7) has, within the last year or two, published a review of the facts known with regard to the anatomy of the various species of *Dinophilus*. Full references to the literature of the subject will be found in v. Graff's monograph (loc. cit.) as well as in the memoirs of Weldon (13) and Korschelt (6 and 7). In view of the recent appearance of the above-mentioned papers, it is unnecessary for me either to give a complete list of references or to attempt any historical account of our knowledge of the genus.

The animal which forms the subject of the present paper was found at Plymouth†, and has been described as a new species, under the name *Dinophilus tæniatus*, at a meeting of the Cambridge Philosophical Society.‡

D. tæniatus was found, in very great numbers, in rock-pools far above low-water mark, during the latter end of March and the first half of April. It was unfortunately necessary to interrupt the observations on April 18th, a day or two before which time it was noticed that the eggs which were being produced by the females were rapidly developing. On returning to Plymouth on June 26th no trace of the animal was discovered. Other observers, as Hallez (4) and Weldon (13) have recorded the fact that the species of *Dinophilus* which they have respectively described are only to be found during the spring.

* v. Graff, L., Monographie der Turbellarien. I. Rhabdocœlida. Leipzig, 1882. p. 1.

† The study of the anatomy of *Dinophilus* was greatly facilitated by the excellence of the arrangements of the Laboratory of the Marine Biological Association, to the Director of which, Mr. G. C. Bourne, I desire to express my best thanks for the courtesy with which I have been treated during my visits to Plymouth.

‡ Proc. Camb. Philosoph. Soc., vol. vi, 1889.

It will not be superfluous to call attention to the fact that the bright orange colour which is so conspicuous a feature of *D. tæniatus* (as of certain other species of *Dinophilus*) cannot easily be regarded as a protective colouration. The rock-pools inhabited by this species of *Dinophilus* contain numerous bright green Algæ, and there is not the slightest difficulty in detecting with the naked eye individuals of *D. tæniatus*, whether crawling on this green background or on the mud or rocks which occur at the bottom of the tide-pool.

With regard to the habits of the animal, it may be noted that, so far as I am aware, it never performs those gyrations round a centre formed by the attachment of the tail to a foreign body, which have been described as of frequent occurrence in *D. metameroides*, for instance (4). The animal crawls (no doubt by means of its cilia) with considerable rapidity, but it is able to swim freely in the water; the latter method of progression appears to be specially characteristic of young individuals.

Specific Characters.—*Dinophilus tæniatus* is characterised as follows: Head with two circlets of præoral cilia. Body composed of five segments and a tail. Segments sharply marked off from one another in young individuals, each encircled by two rings of cilia, incomplete ventrally, where they are interrupted by the uniform ciliation of the ventral surface. Anus placed dorsally to the base of the conical unsegmented tail, surrounded by a ring of cilia, incomplete ventrally. Skin containing large numbers of transparent glandular bodies. Sexes not dimorphic. Maximum length, in either sex, about 2 mm. Colour bright orange, usually brighter in the male than in the female. Testes in the male extending nearly the whole length of the body, on the ventral and lateral sides of the alimentary canal; spermatozoa very long and undulating. Vesicula seminalis formed by the modification of the fifth nephridum on each side, opening into a median copulatory organ, whose external aperture is ventral and slightly posterior to the anus. Ovaries in the female four-lobed. Nephridia ten in number (five pairs), the fifth pair modified as a vesicula seminalis in the male. Ventral nervous system segmented.

As characters recognisable in living specimens, and which are sufficient to distinguish this species from all others at present known may be mentioned the following:

(1) The existence of five body-segments (in addition to the tail), each encircled dorsally and laterally by *two* rings of cilia; the segmentation being sharply marked in immature individuals.

(2) The four-lobed condition of the ovaries in the female.

(3) The existence, in the male, of a median penis and of lateral

vesiculæ seminales (in which respect, however, *D. vorticoides* may possibly be found to agree with *D. tæniatus*).

The characters above given appear to be amply sufficient to justify the formation of a new species. The species which most resembles *D. tæniatus* is probably *D. gigas*, Weldon, which, however, differs from it in such important features as the number of the segments, the arrangement of the ciliated rings, the general character of the reproductive organs, and more particularly the absence of a copulatory organ in the male sex.

External Features.—The form of the body is shown in Pl. IV, fig. 1, which represents a rather young individual (the distinctness of the cilia having been somewhat exaggerated). In an old animal, distended with ripe generative products, the external segmentation is not nearly so conspicuous as in the specimen figured. The arrangement of the cilia is often difficult to make out in living specimens, but may be very easily observed after treatment with hot corrosive sublimate, and before the extraction of the orange pigment by means of alcohol. In specimens thus treated, the cilia appear as white bands running over an orange background; when seen from the dorsal surface, the two rings of each segment together give rise to the impression that the middle region of the segment is encircled by a broad band; this appearance has suggested the specific name *tæniatus*.

The ciliation of the head is best studied in a sublimate specimen, seen from the anterior pole (fig. 8). The general surface of the head is not ciliated, the cilia occurring, on the contrary, as two definite præoral rings, between which are situated the eyes, near the dorsal surface. The anterior ring is more or less triangular, the apex of the triangle being directed dorsally.

In looking at the animal from above, it is seen that the posterior cephalic ring passes dorsally across the equator of each of the eyes (fig. 1). This ring, unlike all the other ciliated rings of the animal, is composed of several circlets of cilia. Of these, the first consists of long cilia directed forwards, and the third or last of somewhat shorter, backwardly-directed cilia. Between the two circlets occurs an intermediate series of very minute cilia (figs. 1, 15). It follows from this description that in structure, as in position, the second cephalic ring resembles the præoral ciliated band of a Trochosphere larva. No ciliated pits were observed. The head bears long, stiff sense-hairs arranged in two groups, situated within the area circumscribed by the anterior ciliated ring (fig. 1). Similar sense-hairs occur on various parts of the body and tail.

The study of longitudinal sections, in which, however, the cilia were not very well preserved, appeared to show that the second præoral

ring becomes much broader in approaching the ventral surface, and that it becomes indistinguishable from an investment of cilia which clothes the ventral surface of the head and which passes continuously into the ciliated lining of the œsophagus (cf. fig. 3). The examination of the ciliation of the ventral surface of the head is always difficult in fresh specimens, but at the time when these were accessible to me, I believed that I could convince myself that the anterior circlet of the second præoral ring passed completely round the head, as shown in fig. 15. The most satisfactory way, it appears to me, of reconciling the apparent discrepancy between fig. 3 and fig. 15, is to assume that, whilst the anterior circlet of the second præoral ring does really pass continuously round the ventral surface of the head, the middle and posterior circlets become, ventrally, an extensive ciliated area which is continuous with the ciliated lining of the œsophagus.

The arrangement of the five pairs of ciliated rings which occur on the body and of the perianal ring is sufficiently explained by fig. 1. All these rings are interrupted by the cilia which cover, in a uniform sheet, the entire ventral surface of the body and of the tail.

Alimentary Canal.—The mouth occurs on the ventral surface, at the limit between the head and the first segment of the body. The aperture of the œsophagus is guarded by two lip-like structures, an outer and an inner. Of these, the former constitutes the outer wall of a triangular space (fig. 15) which includes in front the aperture into the œsophagus, and behind the end of the tongue-like structure formed by the muscular appendage of the œsophagus. The arrangement of this organ is well seen in the longitudinal section figured (fig. 3), where it will be noticed that the end of the muscular appendage (which is covered by a modified, probably hardened epidermis) projects into the space enclosed by the outer lip. A similar arrangement is figured by Repiachoff (No. 12, pl. iv, fig. 1) in *D. gyrociliatus*, whilst the disposition of the organ appears, from Weldon's description (13), to be somewhat different in *D. gigas*.

In front of the tongue-like structure is seen the aperture into the œsophagus (fig. 15). This aperture is subtriangular, and is bounded by the two richly ciliated inner lips.

The course of the alimentary canal is shown in fig. 3. The œsophagus ascends obliquely towards the dorsal surface, the lateral walls of its first part being thickened (*v.* fig. 10), and passing continuously into the inner lips. The posterior section of the œsophagus lies very near the dorsal skin, and is lined by cells which have a more glandular appearance, and which bear longer cilia than those which line the anterior two thirds of the œsophagus. The posterior division corresponds to the proventriculus ("Vormagen") described by Korschelt in *D. apatris*.

As in other species of *Dinophilus*, salivary glands open into the anterior division of the œsophagus.

The stomach (which, during life, is of a rich orange colour) is ciliated throughout: it ends cæcally on the dorsal side of the commencement of the intestine, as in *D. gigas*.

The intestine, like the rest of the alimentary canal, is ciliated. It opens into the stomach by a narrow aperture situated on the ventral side of the latter.

As will be seen by reference to fig. 1, the œsophagus and its muscular appendage belong to the first segment of the body, the stomach occupying the second, third, and fourth segments, whilst the intestine is found in the fifth and posterior part of the fourth segment.

Nervous System.—Although Korschelt (6) and Repiachoff (12) succeeded in finding the brain of *D. gyrociliatus*, our knowledge of the nervous system of *Dinophilus* is in the main due to Weldon (13), who has not only described the brain, but has shown that this structure is connected with ventral cords, whose arrangement resembles that found in *Protodrilus* (*v.* Hatschek, No. 5).

The nervous system of *D. tæniatus* exhibits a feature which has not hitherto been described in any species of *Dinophilus*. The ventral cords are distinctly segmented, the number of ganglionic enlargements—five—corresponding with that of the segments of the body.

The ventral cords (figs. 3, 10 and 11) are situated outside the basement-membrane of the skin, and lie, widely separated from one another, immediately on the median side of the longitudinal muscles (as in *D. gigas*). The cords seem to be provided with an external investment of ganglion-cells along their whole length. The ganglionic swellings (fig. 3) appear to be shifted backwards, relatively to the segment to which they respectively belong, so that the middle of the segment on the dorsal side (as indicated by the ciliated rings) is in front of the corresponding ganglion.

In transverse section (fig. 10) it may be seen that each pair of ganglia is connected by a transverse commissure. I could not satisfy myself of the existence of ganglion-cells in connection with this commissure, although, as the whole ventral nervous system lies in the ectoderm, it is possible that some of the nuclei which are adjacent to the commissures may really belong to ganglion-cells, and not to the epithelial portion of the skin. No transverse commissures were discovered other than those which pass between the ganglia.

The brain is very large, and fills up nearly the whole of the præoral lobe (figs. 3, 9). It consists internally of fibres, and externally of numerous ganglion-cells arranged in groups. The structure of the brain is very complicated; its surface appears lobulated, owing to

the arrangement of the ganglion-cells. A similar arrangement is figured by Repiachoff (12, pl. ii, fig. 10).

The brain gives off a pair of strong œsophageal commissures (fig. 9), which pass round the sides of the mouth to become connected with the ventral cords, as has been described by Weldon in *D. gigas*. The brain itself is, for the most part, separated from the skin by the basement-membrane of the latter. The œsophageal commissures at first lie inside the basement-membrane, but perforate the latter shortly before they become continuous with the ventral cords.

On the ventral side, in front and on the median side of the origin of the œsophageal commissures, the brain becomes continuous with the ectoderm at two points, one on each side of the middle line (cf. fig. 6). It is probable that the tactile organs of the head itself receive their nerve-supply from this region of the brain, which, however, sends off at the same point an œsophageal nerve (figs. 6, 9, and 10) which may be traced, on each side of the œsophagus, as far as the end of the latter; these nerves were not observed to occur in the proventriculus. The œsophageal nerve supplies the wall of the œsophagus itself, and gives off a branch which can be traced as far as the surface of the muscular appendage.

The eyes, which are of a bright red colour, lie on the dorsal surface of the brain, immediately below the basement-membrane of the skin (fig. 9). Each consists of a double pigmented sac, filled with a clear substance, which no doubt functions as a lens. In surface view (fig. 1) the cavity of the eye is not seen, but it is shown in the horizontal-section, fig. 7. Remembering that the plane of the section, fig. 9, is at right angles to that of the section, fig. 7, the difference between the two eyes in the former is readily accounted for by the obliquity of the section.

The ventral part of the head is provided with a pair of small sacs, each of which has an extremely fine lumen opening to the exterior at one side of the anterior portion of the mouth (fig. 9). These bodies are presumably sense-organs, since they are supplied by the above-mentioned œsophageal nerves. Similar organs are described by Repiachoff (12, pl. iv, figs. 1, 3, *y*) in *D. gyrociliatus*, in which species it must be noticed that they occur in addition to lateral, cephalic, ciliated pits.

Body-cavity.—The body-cavity is represented partly by irregular spaces in the loose connective tissue, as described by Weldon in *D. gigas*, and by Repiachoff in *D. gyrociliatus*, partly by more definite spaces, which seem to be specially connected with the internal ends of the nephridia. In males which are sexually mature, by far the greater part of the space between the alimentary canal and the skin is taken up by the very largely developed generative organs (*v.*

fig. 13). The further relations of the body-cavity may be conveniently considered in connection with the excretory and reproductive systems.

Nephridia.—Like *D. gyrociliatus*, as figured by Ed. Meyer (11, and as described, on Meyer's authority, in Lang's Polycladen, p. 678), *D. tæniatus* possesses five pairs of nephridia, whose arrangement is in some respects different from that of the same organs in *D. gyrociliatus*. It may be at once noted that the occurrence, in two species so distinct as *D. gyrociliatus* and *D. tæniatus*, of five pairs of nephridia, raises the question whether the body may not possibly consist of five metameres throughout the genus *Dinophilus*, in spite of variations in the number of the ciliated rings. Thus, according to Korschelt (6), Repiachoff (12)* and Meyer (11), *D. gyrociliatus* is characterised by the possession of seven post-oral ciliated rings (one of which is perianal), in spite of which fact there only five pairs of nephridia. It may, however, be noted that Korschelt figures (pl. xxii, fig. 43) a recently hatched (female) individual, in which the body consists of six segments, sharply marked off from one another, in addition to the tail.

In the female *D. tæniatus* the five pairs of nephridia are all alike, whilst in the male the fifth pair is modified as a part of the generative apparatus. The fifth nephridia of the female occur in the fifth segment of the body, on the ventral side of the intestine (behind the cæcal end of the stomach). The fourth nephridium has exactly the same position with regard to the stomach as the fourth nephridium of the male; it lies behind the posterior ovarian lobe. The third nephridium is situated between the two lobes of the ovary, whilst the second and first nephridia are in the same position as in the male sex.

The following, more detailed description refers entirely to the male, in which the nephridia can be more easily investigated than in the female. The general arrangement of the system may be understood from fig. 15, which illustrates the anatomy of a male *D. tæniatus* as seen from the ventral surface under a compressorium. The figure of course represents the combined results of a long series of observations, but it must be premised that the opacity of the animal was sufficient to prevent any complete elucidation of the structure of the nephridia.

The first four pairs of nephridia may be considered together. Each nephridium opens to the exterior on the ventral side of the body, and probably not far from the longitudinal nerve-cords. The observation of the exact point where the nephridium pierces the skin

* Repiachoff is strongly of opinion that there is no specific difference between Korschelt's *D. apatris* and the earlier described *D. gyrociliatus*.

was extremely difficult, but it may be taken as probable that the external aperture, in each case, is at a level between the two rings of cilia possessed by the segment to which a given nephridium belongs. The inner end of the first nephridium is very slightly behind the principal (second) præoral ring of cilia; this nephridium opens to the exterior on the first body-segment, and may be regarded as the equivalent of the head-kidney of a Trochosphere larva. The second nephridium commences at the anterior end of the stomach, runs at first dorsal to the testis, then bending round to open to the exterior on the ventral surface of the second segment. The third nephridium lies at the level of the middle segment, and, like the second, has its excretory portion situated on the dorsal surface of the testis, its duct curving round to open ventrally on the third segment. The fourth nephridium lies, in the fourth segment, on the ventral surface of the stomach, its internal end occurring close to the aperture from the stomach into the intestine. Its duct, unlike the ducts of the second and third nephridia, runs entirely ventral to the testis.

The internal end of each of the above nephridia lies in a perfectly definite space, which contains an orange fluid and which is probably merely a specialised portion of the general body-cavity. It is almost certainly the case that the spaces which surround the internal ends of the nephridia are continuous with one another, as shown on the right side of fig. 15. In the case of the first three nephridia, the space in question lies on either side of the alimentary canal, and in living specimens was usually most readily distinguishable in the region of the third nephridium, as a distinct cavity, apparently without proper walls, between the stomach and the membrane of the testis. In transverse sections it could usually be seen that this part of the body-cavity extended to the ventral side of the stomach (*v.* fig. 13), whilst in the region of the fourth nephridia, the median portion of the cavity was, in most specimens, observed to pass down ventrally as far as the skin, thus dividing the testis, in this region, into two symmetrical, right and left lobes. In the median space thus formed are situated the internal ends of the fourth nephridia.

The remainder of the general body-cavity consists of a meshwork of spaces, filling up the intervals between the various organs and the skin. These spaces are, like those described by Weldon in *D. gigas*, devoid of an epithelial lining. Many of the cells which bound these lacunæ are large, branching connective-tissue cells, which contain an orange pigment. The pigmented cells are usually more numerous in the male than in the female, their pigment in the female being often markedly paler in colour than in the male, whilst (in the female) their tint tends to be yellow rather than orange. The difference in the colouration of the two sexes, above alluded to

in the description of the specific characters, is dependent on the condition of the connective-tissue cells.

Each nephridium (of the first four pairs) consists of three portions: (i) the ciliated appendage; (ii) the excretory portion; (iii) the duct. The entire nephridium is almost certainly composed of a small number of perforated cells, although no nuclei were discovered: it forms a moderately short tube, without convolutions, the curvature of the tube, as actually observed, doubtless depending to some extent on the position of the animal in the compressorium. Thus the differences between the nephridia of the two sides in fig. 15* probably imply nothing more than that the direction of the compression was not the same in all the observations made.

The excretory portion of the nephridium is of a distinct greenish-yellow or orange colour, the walls of this portion of the tube containing numerous colourless vacuoles, and granules of various sizes. One or two of the granules are very frequently large and deep orange in colour. The excretory portion is pear-shaped, the narrow end shading off insensibly, by gradual loss of the vacuoles and granules, into the duct. The first nephridia seem to be usually provided with two swollen portions, whose walls contain excretory granules and vacuoles, instead of with one only, as in the case of the remaining excretory organs. The nephridium is often suspended in a cord of the above-mentioned pigmented connective-tissue cells.

The internal end of the nephridium is composed of a triangular, ciliated appendage, the apex of which is inserted into the excretory portion of the tube. This insertion, in the case of the second, third, and fourth nephridia, takes place at some little distance from the proximal end of the excretory portion. The appendage is ciliated, the cilia together giving the appearance of a pointed flame-like structure which projects obliquely into the excretory portion of the organ. In certain conditions of the nephridium the ciliated appendage has exactly the appearance of a flame-cell, although as the animal dies and the cilia become more sluggish in their movements, the flame-like appearance is lost. I am inclined to believe, as the result of a long series of observations, that the appendage is provided with a number of cilia, which, working together, produce the optical illusion of a vibratile flame. This is almost certainly true of the portion of the tube described above as the duct, this region being undoubtedly lined by cilia, which, under certain conditions, give rise to a very flame-like effect.

In spite of having devoted a large amount of time to the observation of the ciliated appendages, I am unable to say whether or not

* The form of each nephridium representing the result of one or more actual observations, made at different times.

these structures open into the portion of the body-cavity which undoubtedly surrounds them. In some cases the appendage appeared distinctly bifid (fig. 15), whilst in others it had a fimbriated appearance, and seemed to be composed of a large number of minute, elongated, pear-shaped bodies, each attached by its narrow end to the point where the appendage as a whole passed into the excretory portion of the tube. These minute bodies vibrated individually (*i. e.* not in connection with their neighbours) in the body-cavity space in which they were situated. These observations do not appear to favour the view that the ciliated appendage contains a single vibratile flame, nor indeed to render it easy to suppose that the appendage opens into the body-cavity.

At the same time, it must be noted that the ciliated appendages of the first nephridia are somewhat larger than those of the other nephridia, and that several observations were made which seemed to show that the appendage did really open into the body-cavity. In one of these cases I believed that I could see the individual cilia of the appendage projecting into the body-cavity. It is not impossible that the anterior nephridia have attained a somewhat higher degree of differentiation than the remainder.

The proximal end of the excretory portion, into which the cilia of the appendage project, as above described, does not seem to be ciliated, whilst the lumen of this region of the nephridium appears to be often in the condition of a series of isolated vacuoles rather than of a single passage continuous with the cavity of the rest of the organ. Cilia make their appearance towards the end of the pigmented portion, and can be followed uninterruptedly, from that point, as far as the external aperture. The "duct" has extremely delicate, colourless walls, and, as just stated, is richly ciliated internally.

Generative Organs.—A. *Male.*—The testes consist at first (as is shown by the examination of young individuals) of minute, paired, linear cords of cells (fig. 11), lying on the ventral side of the stomach in the general connective-tissue of the body.* It appeared probable that the testicular cells were simply differentiated connective-tissue cells. Owing to an injury to the tail end of the individual from which fig. 11 was drawn, it could not be ascertained whether or not a penis was already developed.

At a slightly later stage the cords of cells which constitute the young testes are found to have become slightly expanded in a lateral

* It is not impossible that this and the next stage described may really be young conditions of the *female* generative organs, and that, for instance, the structure described as the penis may be the unpaired oviduct. I believe, however, that I am right in identifying the animals in question as young males.

direction, so as to form a pair of narrow, horizontally placed plates of cells, still separate from one another. The penis is already developed as a hollow mass of cells attached in its definitive position by a narrow stalk to the ventral ectoderm of the body. There is no connection between the testes and penis, nor could any vesiculæ seminales be identified with certainty in the sections on which the observation of this stage was made. As development proceeds, the lateral extension of the testes goes on increasing, and the two originally separate rudiments fuse from place to place across the middle line. The testis now consists of a solid plate, composed of a few layers of cells, extending along the ventral side of the stomach, and still showing obvious traces of its double origin. The testis next extends laterally round the stomach, still composed of a solid mass of cells. In the final condition, some of these sperm mother-cells are found in groups in various parts of the testis, whilst ripe and half-ripe spermatozoa are found moving about freely in the indefinite cavity which is by this time excavated in the interior of the organ. The testis is separated from the body-cavity by a distinct membrane.

Although, in the adult condition, the testis is constantly continuous across the middle line in its anterior and posterior regions, it is usually divided into two lateral halves, in the region of the aperture from the stomach into the intestine, by a median extension of the body-cavity, which, as already explained, contains the internal ends of the fourth nephridia. The testis, in its most fully developed form, extends from the region of the muscular appendage of the œsophagus nearly as far as the anus, as shown in fig. 15.

Unripe spermatozoa are found, attached together in sperm-morulæ, in the cavity of the testis. The fully developed spermatozoon (fig. 4) is an extremely long, actively moving, undulating fibre. It hence closely resembles in form the spermatozoon of *D. vorticoides* as described by van Beneden (1) and Mereschkowsky (10), excepting that Mereschkowsky describes and figures a swollen head in the spermatozoon of *D. vorticoides*. I believe that no such structure occurs in *D. tæniatus*, although at the time when fresh material was accessible to me I was not familiar with Mereschkowsky's paper.

Although ripe spermatozoa may be found in any part of the adult testis, they are always present at its posterior end, if they have anywhere reached their mature condition. As has been already explained, the testes are fused together across the middle line in the region of the fifth body-segment, and the ripe spermatozoa which accumulate in this part of the organ are taken into the interior of a pair of vesiculæ seminales (*v.* fig. 15). In their most fully developed condition these structures are much larger than in the figure

just alluded to (cf. fig. 3), and occupy a large proportion of the cavity of the fifth segment.

The connection between the testis and the vesiculæ seminales is by no means easy to discover in sections, but can be best made out by careful compression of the living animal. Under these conditions, it may be observed that the anterior end of the vesicula seminalis is quite closed, and that the communication with the testis is effected by the agency of a ciliated funnel, which passes forwards from the posterior end of the vesicula, and somewhat from its ventral surface, to open into the posterior median region of the testis (fig. 15). This region is reduced to a narrow space between the two vesiculæ seminales (and therefore ventral to the intestine) during the condition of full distension of these structures by spermatozoa.

The funnel and the adjoining part of the inner wall of the vesicula are ciliated, but I believe that cilia do not occur in all parts of the latter. The vesiculæ seminales never contain unripe spermatozoa, although mature, actively moving spermatozoa are to be found in the cavity of very young and small vesiculæ, even when no such spermatozoa could be seen in the testis itself. This implies that the spermatozoa tend to make their way to the posterior part of the testis as soon as they become ripe.

It is perhaps worth while to mention that the above account of the communication between the testis and the vesicula seminalis has been confirmed, in its general features, by the study of sections.

The fully developed vesiculæ seminales are regularly ovoid in form, with their principal axes parallel to the main axis of the body of the animal. The posterior pole of each vesicula passes into a very obvious duct, which opens laterally into the sheath of the copulatory organ.

The generative pore is a median structure, situated on the ventral side of the base of the tail, a little posterior to the level of the anus (figs. 3, 15). The pore opens into a vestibule, into which projects the extremity of the penis. This organ is embedded anteriorly in a solid glandular mass of cells, and consists of two parts. The first of these is composed of very distinct cells, of a glandular appearance, and staining very deeply with carmine or hæmatoxylin. These cells radiate in a single layer from the internal cavity of the organ. The second part of the penis projects into the generative vestibule, and consists of a series of narrow, spike-like rods (in which nuclei could be distinguished), which, lying side by side, form a truncated cone, open at its extremity, and continuous with the cavity of the penis.

A copulatory organ of the same general character as that above described is well known to occur in the dwarf males of *D. gyrociliatus* (Korschelt, Repiachoff, &c.), whilst from a figure (plate viii, fig. 7)

given by M'Intosh (9) of *D. vorticoides* it appears probable that the entire male generative apparatus of this latter species closely resembles that of *D. tæniatus*.

So far as I am aware, copulation has not hitherto been actually proved to take place in any species of *Dinophilus*.* The proof that such a process takes place in *D. tæniatus* is very readily obtained by merely placing a considerable number of individuals of both sexes in a small quantity of sea-water, as in a watch-glass. Under these circumstances, it is noticed, even a very short time after the animals have been placed together, that here and there a male is attached, by means of its penis, to the body of a female. In these cases, the terminal, conical portion of the penis is protruded through the generative pore, and is passed into the skin of the female; spermatozoa are then seen to have passed from the vesiculæ seminales, through the skin of the female, and to be accumulating themselves into a mass immediately beneath the perforation made by the penis.

There seems to be no localisation of the spot at which spermatozoa can be introduced into the female. The penis can obviously be inserted into the skin at any point, as is shown by the fact that, in the cases actually observed, the point selected was sometimes in the region of the neck, in other cases far back in the body of the female, and in other cases near the middle of the body.

The act of copulation has no relation to the maturity of the ova of the female, nor is it prevented by the fact that the female has already received an ample supply of spermatozoa by a preceding operation. It was extremely difficult to discover any female, in which ovaries were recognisably developed, which did not contain large numbers of spermatozoa in its body-cavity. These were observed in almost any part of the body of the animal, their position being probably partly dependent on the manner in which fertilization had been previously effected. The spermatozoa show, however, a great tendency to accumulate into a large compact mass, situated in a space on the ventral side of the stomach (*v.* fig. 14, and description of the female generative organs). In some cases it was observed that the female was receiving spermatozoa simultaneously from two males; in others that while, for instance, fertilization was being effected near the posterior end of the body, a great mass of spermatozoa (obviously obtained on a previous occasion) was visible at the anterior end of the body. In many cases the females were enormously distended with spermatozoa, which could hardly have been all received at one time.

The common occurrence of great numbers of spermatozoa in the body of the supposed female might suggest that *D. tæniatus* was hermaphrodite. Such a supposition is rendered sufficiently improbable

* Korschelt (6) has probably seen something of this process in *D. gyrociliatus*.

by the following considerations: (i) That no other species of *Dinophilus* is known to be hermaphrodite; (ii) that the process of fertilization was frequently observed in *D. tæniatus;* (iii) that the spermatozoa so constantly seen in the female of the same species were, without exception, ripe and actively moving, no trace of sperm-morulæ or unripe spermatozoa being discernible. Such stages in the development of the spermatozoa were never missed in any adult male individual.

It will be noticed that the above-described process of copulation in *D. tæniatus* exactly resembles the processes which have been described by Lang (8, p. 231) in certain *Polyclada* (*Anonymus*, &c.).

The morphology of the vesiculæ seminales is one of the most interesting features of *D. tæniatus*, since there is reason to believe that these structures are the modified fifth nephridia of the male. The reasons for this conclusion are two:

(i) Five pairs of ordinary nephridia occur in the female *D. tæniatus* (as in the female *D. gyrociliatus*), whilst the most careful examination, often repeated, of the males of the same animal failed to show any trace, in that sex, of the existence of a fifth pair of undifferentiated nephridia.

(ii) The consideration of young stages of the vesiculæ seminales.

Fig. 5 represents the earliest of these stages which was observed. The vesiculæ seminales were in their definitive position in the fifth body-segment, and their identification as vesiculæ was rendered sufficiently certain by the fact that they contained ripe spermatozoa. The vesiculæ were arranged in an obliquely transverse position, their outer portions ending blindly at a level between the two ciliated rings of the fifth segment, their inner ends opening into the cavity of the testis. A part of the vesicula immediately succeeding the internal aperture was lined with long cilia; the next part of the tube contained a small mass of spermatozoa. The penis was well developed, and obscure indications of a duct leading from the vesicula to the penis were observed; the existence of this duct was not, however, completely proved. The resemblance of the young vesicula seminalis to an ordinary nephridium was manifested, not only in its shape and position, but still more conspicuously by the fact that its walls contained an orange pigment, exactly resembling that so commonly found in the walls of the excretory tubes.

Stages intermediate between that represented in fig. 5 and the mature form of the vesicula seminalis were frequently observed. The final form is acquired by the gradual distension of the originally subcylindrical tube by spermatozoa, this distension being accompanied by an alteration in the direction of its axis, the result of which processes is that the end which, in the young vesicula, is

external, is situated, in the adult condition, in front, the whole organ having now acquired an antero-posterior direction. The funnel, during the above changes, will naturally come to be situated near the posterior end of the organ.

There seems, therefore, fair reason to assume that the young vesicula seminalis shown in fig. 5 is morphologically the fifth nephridium; it must be especially noted that the funnel of the vesicula is in a position corresponding with that of the ciliated appendage of an ordinary nephridium, and that the original external aperture of the modified nephridium was probably (in the phylogenetic history of the organ) at the opposite end of the tube, which ultimately becomes the blind anterior end of the vesicula. The relations of the outer end of the young vesicula to the ciliated rings of the fifth segment further support this conclusion. The connection of the vesicula seminalis with the penis would, in this case, have to be regarded as having been acquired secondarily. Should the above account of the vesiculæ seminales of *D. tæniatus* be confirmed, the structure and mode of origin of these organs might be held to have an important bearing on the question of the phylogeny of the differentiated Chætopod nephridium. The structure of the first four nephridia in the male *D. tæniatus*, or of all five nephridia in the female, is obviously comparable with that of the head-kidney of a Chætopod larva. In this connection the figures given by Ed. Meyer (11) of the larval excretory organs of *Nereis* (Taf. xxvii, figs. 2, 3) and of *Polymnia* (Taf. xxvii, fig. 11) may be especially alluded to. The possibility of the conversion of the internal end of a head-kidney-like nephridium into a ciliated funnel, and of the entire nephridium into a vesicula seminalis, is a fact (if it be a fact) of some morphological interest.

Whilst the excretory nephridia of the male *D. tæniatus* open into a space which has been described above as a part of the body-cavity, the vesiculæ seminales open into the cavity of the testis. In certain other Archiannelids (*Protodrilus, Polygordius*), the space which is partially lined by generative cells is certainly part of the body-cavity. From the analogy of these forms, it may perhaps be concluded that, in *Dinophilus*, the hardly differentiated space which occurs in the interior of the ripe testis is also a part of the body-cavity. In this case we could assume that whilst the excretory nephridia open into the general body-cavity, the vesiculæ seminales of *D. tæniatus* have acquired an opening into a special generative division of the cavity. Attention may be called to the similarity between the young generative organs shown in fig. 11 and the mesoblastic bands of a Chætopod larva, and also to the similarity between the subsequent history of the testis of *D. tæniatus* and of the body-cavity of the developing Chætopod. Although I make

this suggestion with all reserve, it is perhaps possible* that in the connective-tissue lacunæ of the body of *Dinophilus* we have the representative of the so-called "primary body-cavity," whilst in the fully developed male (fig. 13) the "secondary body-cavity" is represented by the cavity of the testis, with which the funnels of the vesiculæ seminales are connected.

B. *Female.*—The generative organs in the female *D. tæniatus* differ considerably from those of other known species of the genus, in the fact that the ovaries are four-lobed. The general arrangement of the ovaries will be understood by referring to fig. 2, where it will be seen that the ovaries, like the testes, are paired bodies, but that each half is subdivided into two lobes. Each lobe consists partly of small primordial ova and (in a moderately mature condition) partly of larger eggs which have already acquired the orange colour which characterises the ripe eggs. The ovaries are covered by a cellular investment, which is readily seen in fresh specimens to be continuous from lobe to lobe on each side of the body. The ovaries, as in *D. gigas*, are found on the ventral side of the stomach. No ducts could be discovered in the living animal. Spermatozoa, received during the process of copulation, occurred in almost every individual in which the ovaries were at this stage or more highly developed. In specimens in which the ova had become still further developed, the eggs were no longer confined to the four ovaries. As many as fourteen large spherical eggs of a distinct orange colour may, in such cases, occur on the ventral side of the stomach or intestine, and the two ovarian lobes of each side are then usually pushed apart from one another by the occurrence of ripe eggs between them.

Fig. 14 represents a transverse section through the region between the anterior and posterior ovaries of a female with numerous and fully developed ova. On the ventral side of the stomach is a large space, containing a great mass of ripe spermatozoa, which appears to have no proper wall on its dorsal side at least, being in this region merely roofed in by the stomach. Laterally its walls are formed by the cellular investment of the ovaries, this investment passing across the middle line of the body on the ventral side of the space. In a section which passed through one of the ovaries on each side, the ovarian lobes would simply take the place of the ripe eggs shown in fig. 14. The cellular investment of the ovaries already noticed in fig. 2 would be seen to surround each lobe completely, and to be further continuous across the middle line on the ventral side of the interovarian space, exactly as in fig. 14.

Fig. 12 represents a longitudinal section through the two ovaries

* As has previously been suggested, for other animals, by the Hertwigs.

of the same side at a much earlier stage of development, at a period, indeed, when the entire ovary is composed of a mass of small, uniform, primordial ova. The relations of the investment of the ovaries are further explained by this figure, in which it is seen that the space between the anterior and posterior lobes is, as in the later stage, devoid of any epithelium on its dorsal side. Ventrally, the space is floored by a single layer of cells, separated from the skin by loose connective tissue; the space itself contains (as was occasionally observed in older stages) a few free cells of unknown function.

In the absence of any developmental evidence it is not easy to say what is the nature of the interovarian cavity. From the analogy of the male, as well as from a consideration of the general arrangement of the ovaries, it would appear that the ovaries are primitively paired bodies, and not merely lateral thickenings of a median cavity. The interovarian cavity would thus be a specialised portion of the general body-cavity, which conclusion would be supported by the absence of any proper wall, the space being bounded partly by the investment of the ovaries and partly by the wall of the stomach. The conclusion is further strengthened by distinct evidence obtained from sections, that the internal ends of the fourth nephridia project into the space.

In most females observed in section there was found to be a mass of spermatozoa at the sides of the stomach and dorsal to the ovaries, these masses of spermatozoa usually passing continuously into the large central mass which is nearly always present in the interovarian cavity. The spaces in which these lateral masses of spermatozoa lie appear to be parts of the general body-cavity, which is hence continuous with the interovarian cavity at those points where the spermatozoa enter the latter. This continuity does not necessarily prove that the ventral space is really part of the body-cavity, as, from the method in which the spermatozoa are introduced into the female, they must probably often have to make their way through various obstructions in order to reach the ventral space.

The layer of cells connecting the two ovaries (figs. 12 and 14) across the middle ventral line of the body may thus be provisionally interpreted as resulting from the median fusion of two originally separate organs, and this process probably takes place at an early stage of development, as in the case of the testes of the male.

The interovarian cavity extends along the middle line of the body throughout the whole of the region of the stomach, and therefore occurs, not only between the ovaries themselves, but also behind and in front of the ovaries, which are lateral thickenings of the walls of the cavity, projecting into it. In consequence of this pro-

jection, the posterior part of the cavity in fig. 12 is separated (in the particular section in question) from that part which occurs between the anterior and posterior lobes; the posterior part of the cavity is of course continuous with the anterior part. It will be noticed from fig. 12 that the posterior part of the interovarian cavity has an epithelial wall on its dorsal side as well as on its ventral side, and the same is true of the anterior end of the cavity (not involved by the section shown in fig. 12). The complete conversion of the interovarian cavity into a tube which runs backwards below the intestine takes place at the level of the posterior ovarian lobes, and appears to be due to the fusion across the middle line of the investments of the ovaries of opposite sides. The tube thus formed runs backwards, becoming much smaller as it approaches the end of the body. In one specimen examined, the tube was distinguishable almost as far back as the anus, although very minute in the hinder part of its course.

In fig. 14, the eggs which are cut by the section are still outside the interovarian cavity. Most of the large eggs in this individual possessed two nuclei, as shown in one of those figured. They were further provided with a somewhat shrivelled membrane, which is probably the vitelline membrane. In the fresh condition, the only case noticed in which the vitelline membrane was acquired before the eggs reached the exterior was in a dead female, most of the tissues of which were beginning to break up into fragments.

In other sections of the series from which fig. 14 is taken, eggs are found in the interovarian space. The posterior, tubular continuation of this space may probably be regarded as an oviduct, although the process of egg-laying was not directly observed. It does not appear to me probable that the eggs are liberated by the death of the female, as Weldon (13) supposes to be the case in *D. gigas*.

In *D. vorticoides* (van Beneden, No. 1) and in the species described by Korschelt (6) as *D. apatris* (probably identical with *D. gyrociliatus*), the eggs are known to pass to the exterior by means of a minute pore situated on the ventral side of the animal, at the base of the tail. This pore is said not to be recognisable except when the eggs are being laid; the eggs completely lose their shape in passing through the aperture, but regain their spherical form on arriving in the water.

In *Protodrilus*, an animal to which *Dinophilus* is probably allied, the eggs are said by Uljanin and Repiachoff (*v.* Repiachoff, No. 12, p. 29) to escape from the body in the same way as in the above-mentioned species of *Dinophilus*. According to the observations of Uljanin, quoted and confirmed by Repiachoff, the ripe eggs of *Protodrilus* move about freely in the meshes of the network of connective tissue

which fills the general body-cavity, passing from segment to segment through apertures which remain between the interlacing muscle-fibres constituting the dissepiments, and finally escape from the body on the ventral side of the last segment.

The above description shows that in *Protodrilus* the eggs fall into the general body-cavity, whilst the same is true of *D. gyrociliatus*, where the body-cavity opens to the exterior by means of a ventral pore situated near the base of the tail. The fact that in *D. tæniatus* the interovarian cavity has been above shown to be continued ventrally almost as far as the anus, taken in conjunction with the admitted difficulty of discovering the actual generative pore except when eggs are being laid, is distinctly in favour of the view that the eggs of *D. tæniatus* are laid in the same manner as that which has been already described in other species of *Dinophilus*. The analogy of *D. gyrociliatus*, in which the eggs undoubtedly fall into the general body-cavity, further suggests that the interovarian cavity, into which the ova fall in *D. tæniatus*, and which is continuous with a passage which leads towards the exterior, is similarly a part of the general body-cavity.

On the Affinities of Dinophilus.—It has been repeatedly pointed out, by Metschnikoff, Lang, Repiachoff, and Korschelt, that *Dinophilus* has affinities with the Annelids, and more particularly with the Archiannelids. Weldon (13) expresses himself even more definitely in favour of the Archiannelid relationships of this form, supporting his conclusions by referring to the muscular œsophageal organ, to the ciliated ventral surface, associated with lateral nerve-cords, and to the character of the excretory organs, as described by Meyer.

The similarities between *Dinophilus* and the admitted Archiannelids are so numerous and so striking that it can hardly be doubted that the above conclusion is amply justified by the facts. It may, however, be worth while to call attention to the special resemblances shown by *D. tæniatus* to admitted Archiannelids, and to one or two considerations which are suggested by the study of this animal.

1. *External ciliation.*—The existence of two rings of cilia on each segment, a feature which appears to be so characteristic of *D. tæniatus*, is common to this species and to *Protodrilus Leuckartii* (Hatschek, No. 5). In the latter animal each segment is provided with two rings, interrupted, as in *Dinophilus*, by the uniform cilia which cover the ventral surface (ventral groove in *Protodrilus*). Two præoral rings of cilia exist in *Protodrilus*, which, however, differs from *Dinophilus* in possessing an elongated "postoral region of the head" (containing the muscular appendage of the œsophagus, and hence probably identical with the first body-segment of *Dinophilus*) which bears five rings of cilia.

2. *Nervous system.*—In *Protodrilus*, as in *Dinophilus*, ventral nerve-cords run along the sides of the ciliated ventral region of the body. In both cases, these cords are connected with the brain by œsophageal commissures running round the sides of the mouth. Further, the œsophageal commissures in *Protodrilus* acquire a relation to the longitudinal muscles which is precisely similar to that which obtains, not only in the same region, but throughout the body, in *Dinophilus*. *Protodrilus* is well known to possess an almost continuous layer of longitudinal muscles, which are separated by small interspaces into two ventral and two dorsal groups. In the region of the head (*v.* Hatschek) the four groups of muscles become widely separated; by referring to Hatschek's fig. 14 (Taf. ii), representing a section passing through the region of the mouth, it will be seen that the ventral longitudinal muscles, in their relative size and in their relations to the œsophageal commissures, are exactly similar to the longitudinal muscles of *Dinophilus*. Still further forwards in *Protodrilus*, the dorsal muscles (which do not seem to be represented in *Dinophilus*) disappear altogether.

The ventral nervous system of *Protodrilus* is not known to be segmented, and Hatschek describes only one transverse commissure between the two cords, occurring at the junction of the "head" and body.

The researches of Foettinger (2) have shown that *Histriobdella* is to be regarded as an Archiannelid. Foettinger re-names this animal *Histriodrilus*, in order to mark its removal from the group of the Leeches to that of the Archiannelids.

In one respect, the nervous system of *Histriodrilus* shows a closer resemblance to that of *Dinophilus tæniatus* than is manifested by that of any other Archiannelid. The ventral nervous system has been shown by Foettinger to be definitely segmented, in correspondence with the external segmentation indicated by metameric constrictions of the skin. *Histriodrilus* possesses about eight ventral ganglia, which, however, differ from those of *Dinophilus* in being continuous across the middle ventral line. In the intersegmental regions alone, the ventral nervous system consists of separated ventro-lateral cords. Paired œsophageal nerves, similar to those of *Dinophilus*, are described and figured by Foettinger (pl. xxv, figs. 10, 11).

3. *Excretory and generative organs.*—The nephridia of *D. tæniatus* closely resemble those of *Protodrilus*, as described by Hatschek. According to this observer, each nephridium of *Protodrilus* commences with a small funnel, opening into the body-cavity, and bearing internally a single, very long cilium. The difficulty of the investigation of nephridia of this type makes it possible that the difference between the funnel in *Protodrilus* and the ciliated appendage in

Dinophilus is really less considerable than would appear from a comparison of Hatschek's figures with my own.

In many of its features *Polygordius* differs from *Dinophilus* far more than does *Protodrilus*. This is sufficiently obvious by such characters of *Polygordius* as the fusion of the ventral nerve-cords, the absence of a muscular œsophageal appendage, the form of the nephridia, the greater development of the longitudinal muscles, &c. (cf. Fraipont, No. 3). All these facts justify us in concluding that *Polygordius* is less closely related to *Dinophilus* than is *Protodrilus*.

Histriodrilus (*Histriobdella*), on the contrary, is probably more closely related to *Dinophilus* than is *Protodrilus*. The similarity in the nervous systems of the two genera has been already alluded to, and the same general resemblances characterise the excretory and generative systems.

The arrangement of the excretory system in *Histriodrilus* is said to differ in the two sexes. The nephridia are somewhat S-shaped, intracellular tubes (unfortunately not figured by Foettinger in much detail); it is stated that five (or perhaps six) pairs are found in the male, and four pairs in the female; their relations to the segments are shown by means of woodcuts on p. 469 of Foettinger's Memoir. The second nephridium was observed on two occasions to end internally in a ciliated ampulla.

In the existence of structures connected with the generative apparatus, and which may possibly be regarded as modified nephridia, *Histriodrilus* again shows evidences of affinity to *Dinophilus*.

In the female *Histriodrilus* there are two ovaries, which are more or less fused posteriorly (as in *D. gigas*). These ovaries are situated, as in *Dinophilus*, on the ventral side of the alimentary canal. The ripe ova fall into the body-cavity, whence they are taken up by the ciliated funnels of a pair of tubes which open to the exterior laterally. These funnels (woodcut, p. 481 of Foettinger's paper) are large, and open into the body-cavity on the ventral side of the ovaries. The tubes into which the funnels lead possess a dilatation, containing spermatozoa which have been presumably derived from a male individual. The resemblance of these structures to the vesiculæ seminales of the male *D. tæniatus* (in which evidence has been brought forward above to show that the vesicula is a modified nephridium) suggests that they too are possibly modified nephridia.

The male generative organs of *Histriodrilus* appear to be very complicated, and their structure and functions were not thoroughly understood by Foettinger. The testes are placed on the ventral side of the alimentary canal, and are more or less paired in front, whilst they are fused posteriorly. At the posterior end of the generative segment are a pair of vesicles containing spermatozoa (Foettinger,

pl. xxix, fig. 3), and obviously comparable with the vesiculæ seminales of *Dinophilus*. As in the latter animal, the vesicles open by ducts into a median organ, supposed by Foettinger to be copulatory, and of very complicated structure. No communication between the vesicles and the body-cavity or testis is described. Anteriorly the generative segment has a pair of lateral eversible penes. The existence of three separate copulatory organs in *Histriodrilus* recalls the condition met with in some Polyclads (*Anonymus, Thysanozoon*), where more than a single penis is found.

The above facts, together with other well-known and striking resemblances between *Dinophilus* on the one hand and *Protodrilus, Polygordius,* or *Histriodrilus* on the other, make it in the highest degree probable that *Dinophilus* is a true Archiannelid, as has been insisted on by so many of the more recent writers on the subject. In the number of segments, in the segmentation of the ventral nervous system, and in the arrangement of the muscular system, of the nephridia, and of the generative organs, *Dinophilus* more nearly approaches *Histriodrilus* than any of the remaining Archiannelids. On the other hand, in the character of the muscular appendage of the œsophagus, in the wide separation of the ventral nerve-cords, and in the method adopted by the female for laying its eggs, *Dinophilus* most closely resembles *Protodrilus*. Although *Dinophilus* seems so clearly an Archiannelid, it is nevertheless possible to hold with Korschelt, Weldon, and others that it gives evidence of having been derived from Platyhelminth-like ancestors.

Weldon (13) has called special attention to the significance of the muscular œsophageal appendage as a representative of the pharynx of a Planarian. The median position of the generative pore, and the method of fertilization adopted by the male *Dinophilus tæniatus*, further support the view of the Platyhelminth origin of the Archiannelids. The median penis of *D. tæniatus* and *D. gyrociliatus* is strictly comparable with the same structure in a Planarian, although it is probably a highly significant fact (if this is really the case) that this organ has entered into relations with a pair of modified nephridia which receive the spermatozoa from the testes.

Korschelt (6) and others have drawn attention to the remarkable fact that, whilst the female of one species of *Dinophilus* differs comparatively little from that of any other species, there are very great differences between the males of the various species. In *D. gyrociliatus* (including *D. apatris*) (and possibly in *D. metameroides*, in which the male is not known) there is very striking sexual dimorphism, the female being many times larger than the male. In *D. vorticoides, D. gigas,* and *D. tæniatus,* on the contrary, the males do not differ appreciably in size from the females. Whilst in *D. gigas*

the male is said to have neither penis nor vesiculæ seminales, these structures are found in *D. tæniatus*, which is probably closely allied to *D. gigas*.

I have no observations which explain the disappearance of *D. tæniatus* during the summer. It is, however, important to notice that the eggs develop immediately after being laid. Small individuals were of common occurrence during the early part of April, although I did not succeed in finding the segmenting eggs till April 16th ; the termination of my visit to Plymouth occurring a day or two after that date, I have no observations worth recording on the development. The eggs may be easily obtained by looking through mud drawn by means of a siphon from the bottom of a rock-pool which is inhabited by *D. tæniatus*. The general course of the development is apparently similar to that which has been described by Korschelt in *D. gyrociliatus* (*D. apatris*) ; the embryo, as in this species, acquiring most of its adult characters while still enclosed in its vitelline membrane. The absence of any metamorphosis in *Dinophilus* appears to me a noteworthy fact. It is perhaps a legitimate inference, from the facts known with regard to *Dinophilus*, that a Trochosphere stage is not to be expected in the ontogeny of this animal, since in the persistence of the præoral ring of cilia, and probably of the head-kidneys, and in the general characters of the alimentary canal, the adult *Dinophilus* may be considered to remain in a condition which is practically that of a Trochosphere.

Postscript.—I owe to the kindness of Dr. Norman the opportunity of referring to the description which has been given by G. N. R. Levinsen of *Dinophilus caudatus*, published in a paper which had previously been inaccessible to me (*Bidrag til Kundskab om Grönlands Turbellarienfauna*, Vidensk. Meddel. fra den naturh. Foren. i Kjöbenhavn, 1879—1880).

D. caudatus is identified by Levinsen with the *Planaria caudata* of Fabricius (Fauna Groenlandica, 1780) and of O. F. Müller (Zool. Danica), and, in the words of Fabricius, " Habitat stupenda multitudine in confervis, et ulvis littoralibus, sæpe illas tegens."

It resembles the species above described as *D. tæniatus* in the division of the body into segments by deep constrictions of the skin, in the form of the testes, and in the existence of a penis and of vesiculæ seminales, but is stated to be so well known that detailed description is unnecessary ; it is, moreover, unfortunate that Levinsen has published no figure of the species described by him.

It appears to me quite possible that " *D. tæniatus* " is identical with *D. caudatus*, but as the evidence on this point is quite inconclusive, I do not propose to withdraw, for the present at least, the

specific name, which has already been published in the Proceedings of the Cambridge Philosophical Society (vol. vi). According to Levinsen, *D. caudatus* is the species which has been described by other writers as *D. vorticoides;* its colour is stated to be red, whilst no mention is made of the existence of four-lobed ovaries or of segmental ciliated rings.

REFERENCES.

1. VAN BENEDEN, P. J.—*Notice sur un nouveau Némertien de la côte d'Ostende.* Bull. de l'Acad. Royale de Belgique, Tome xviii, 1re Partie, 1851, p. 15 [*Dinophilus vorticoides*].
2. FOETTINGER, A.—*Recherches sur l'organisation de Histriobdella homari, P. J. van Beneden, rapportée aux Archiannélides.* Archives de Biologie, Tome v, 1884, p. 435.
3. FRAIPONT, J.—*Le Genre Polygordius.* Fauna und Flora des Golfes von Neapel, xiv Monographie, 1887.
4. HALLEZ, P.—*Contributions à l'Histoire Naturelle des Turbellariés.* Lille, 1879, p. 155 [*Dinophilus metameroides*].
5. HATSCHEK, B.—*Protodrilus Leuckartii. Eine neue Gattung der Archianneliden.* Arbeiten a. d. Zool. Inst. d. Universität Wien, Tom. iii, 1880, p. 79.
6. KORSCHELT, E.—*Über Bau und Entwicklung des Dinophilus apatris.* Zeits. f. wiss. Zool., Bd. xxxvii, 1882, p. 315 (and p. 702).
7. KORSCHELT, E.—*Die Gattung Dinophilus u. der bei ihr auftretende Geschlechtsdimorphismus.* [Spengel's] Zoologische Jahrbücher, Zeits. f. Syst., Geog., u. Biol. der Thiere, Bd. ii, 1887, p. 955.
8. LANG, A.—*Die Polycladen.* Fauna und Flora des Golfes von Neapel, xi Monographie, 1884, p. 678, &c. [*Dinophilus gyrociliatus*].
9. M'INTOSH, W. C.—*The Marine Invertebrates and Fishes of St. Andrews.* Edinburgh and London, 1875, p. 108, and pl. viii, figs. 7—10 [*Dinophilus vorticoides*].
10. MERESCHKOWSKY, C.—*Ueber einige Turbellarien des Weissen Meeres.* Arch. f. Naturg., xlv Jahrg., i Bd., 1879, p. 51 [*Dinophilus vorticoides*].
11. MEYER, ED.—*Studien über den Körperbau der Anneliden.* Mitt. a. d. Zool. Stat. zu Neapel, Bd. vii, 1886–87, p. 592 [Taf. xxvii, figs. 9, 10, *Dinophilus gyrociliatus*].
12. REPIACHOFF, W.—*On the Anatomy and Developmental History of Dinophilus gyrociliatus*, O. Schmidt. Odessa, 1886 [in Russian].
13. WELDON, W. F. R.—*On Dinophilus gigas.* Quart. Journ. Mic. Sci., vol. xxvii, 1887, p. 109, and Studies-Morph. Lab. Univ. Cambridge, vol. ii, 1886, p. 258.

DESCRIPTION OF PLATES IV AND V.

Illustrating Mr. S. F. Harmer's paper, "Notes on the Anatomy of Dinophilus."

N.B.—All the figures refer to Dinophilus tæniatus.

FIG. 1.—Dorsal view of a young individual; the mouth, which is ventral, is represented as being visible through the semitransparent tissues of the head.

FIG. 2.—Ventral view of an adult female, somewhat compressed.

FIG. 3.—Longitudinal section of an adult male (combined from several sections). Most of the organs are shown as they appear in a median section; *i. e.* the brain, alimentary canal, testis, penis, and generative pore. The eye, ventral ganglia (the distinctness of

which is slightly exaggerated), and vesicula seminalis, being laterally placed, would not appear in a strictly median section. The two ciliated rings of each of the five segments of the body are indicated by one of the brackets to which the numbers 1, 2, 3, 4, 5 refer.

FIG. 4.—Spermatozoon.

FIG. 5.—Ventral view of part of the posterior end of a young male, as seen in a compressorium. The vesicula seminalis is still very young and nephridium-like, opening at its internal end into the cavity of the testis. The existence of the structure marked "duct ?" was not established with certainty.

FIG. 6.—Longitudinal section of head, almost median, showing one of the œsophageal nerves.

FIG. 7.—Horizontal section of eye.

FIG. 8.—View, seen from the front, of the surface of the head of an individual killed with hot corrosive sublimate.

FIG. 9.—Transverse section through the head, passing through the origin of one of the œsophageal commissures.

FIG. 10.—Transverse section through the region of the first postoral pair of ganglia.

FIG. 11.—Transverse section through the middle region of the body of a young individual (probably a male).

FIG. 12.—Longitudinal vertical section, not median, passing through the two ovaries of one side of the body, of a young female.

FIG. 13.—Transverse section through the middle region of the body of an adult male.

FIG. 14.—Transverse section through the region of the interval between the anterior and posterior ovaries of an adult female.

FIG. 15.—Ventral view of an adult male, as seen under strong compression in a compressorium. The figure represents the results of a long series of observations. The vesiculæ seminales have been drawn at a rather young stage of development; at their period of maximum development they would appear very much swollen, and would extend forwards as far as the posterior end of the stomach. The double ciliated rings of the five segments are indicated, as in fig. 3, by the numbers 1, 2, 3, 4, 5. The testis is not shown on the left side of the figure.

The Spinning Apparatus of Geometric Spiders.

By

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With Plate VI.

The familiar circular snare constructed by the "geometric" spiders has always been an object of interest to naturalists, but it is remarkable how little has been known until lately of the highly complicated organs which compose the spinning apparatus of these animals.

Thanks mainly to the labours of Blackwell,[1] Emerton,[2] Bertkau,[3] and lastly Apstein, a tolerably complete knowledge has now been obtained of the structure and general arrangement of these organs.

Apstein's excellent paper,[4] recently published, contributes much that is new and valuable, and fairly represents our present knowledge of the subject. Recent researches, however, have led me to dissent from some of that author's conclusions as regards the functions of the various spinning glands, conclusions based upon evidence for the most part too indirect to be entirely satisfactory.

Before discussing this matter, some description of the

[1] "On the Mammalæ of Spiders in Spinning," 'Trans. Linnean Soc. London,' 1839, vol. xviii, pt. ii.

[2] 'The Structure and Habits of Spiders,' Boston, Cassino & Co., 1883.

[3] "Cribellum und Calamistrum," 'Archiv für Naturgeschichte,' 1882, p. 316.

[4] "Bau und Function der Spinnendrusen der Araneida," 'Archiv für Naturgeschichte,' 1889, p. 29.

morphology of the organs in question will be necessary. The large garden spider, Epeira diademata, is taken as the most convenient type of the family, but the following remarks apply in the main to all its orb-weaving congeners.

External Spinning Organs.

These occupy a small round area on the under surface of the abdomen towards the posterior end, where, when at rest, they present a bluntly conical protuberance (figs. 1 and 2, *sp.*). If this area be examined under a low power, it is seen to be occupied mainly by four conical spinnerets, their bases forming a quadrilateral, and their apices meeting in the centre of the area (fig. 8). The narrow space which intervenes between the bases of the anterior (or inferior) spinnerets (*a*) is filled by a small tongue-like process (*t*). The wider gap separating the posterior (or superior) spinnerets (*p*) is occupied by a terminal projection of the abdomen (*z*) containing the anus. Each of these spinnerets is two-jointed, and furnished at its extremity with a multitude of hair-like tubes containing the ducts of the spinning glands.

They are possessed of a wonderful mobility, and can be widely separated, or energetically rubbed upon each other with a rotary motion at the will of the animal. Their separation discloses a third and smaller pair of spinnerets consisting of one joint only, and having their apices directed backwards and inwards, so as to lie immediately beneath the apices of the posterior spinnerets (fig. 10, *i*).

These again present a large number of glandular orifices. They will be referred to hereafter as the intermediate spinnerets. Thus we have, in all, three pairs of spinnerets capable of a great variety of movement, and bearing at their extremities, as will be presently seen, about 600 spinning tubes.

Internal Spinning Organs.

Apstein has shown that there are, in this group of spiders, five distinct kinds of glands, to which he assigns the names Ampullaceal, Aggregate, Tubuliform, Piriform, and

Acinate. The first three kinds are few in number and of large size, extending throughout the greater part of the abdomen. The piriform and acinate glands are minute and numerous, and are closely grouped together immediately above the spinnerets.

Their exact arrangement is important and may be summarised as follows:

There are two pairs of Ampullaceal glands (fig. 3) debouching on the anterior and intermediate spinnerets respectively on the inner side.

There are three pairs of Aggregate glands, their three outlets on each side being situate upon the inner surface of the posterior spinneret.

There are three pairs of Tubuliform glands, two opening on the inner side of the posterior spinnerets, and one upon the outer surface of the intermediate spinnerets.

The above glands are comparatively large, and their ducts terminate in distinct tubular prominences.

There are about 200 Piriform glands, all connected with the anterior spinnerets, where their ducts terminate in hair-like tubes.

Finally, there are about 400 Aciniform glands, each posterior and each intermediate spinneret bearing the hair-like terminations of about a hundred ducts.

Or thus, tabulating for one side only:

Glands.	Ant. Spinneret.	Intermediate.	Posterior.
Ampullaceal . .	1 on inner side	1 on inner side	...
Aggregate . .	...	...	3 on inner side.
Tubuliform . .	...	1 on outer side	2 on inner side.
Piriform . . ,	About 100	...	...
Aciniform . .	...	About 100	About 100.

The question naturally arises as to the different functions

performed by glands apparently so distinct. Apstein attempts its solution by reasoning which is mainly indirect and, in my opinion, misleading. It occurred to me that the problem might be attacked in a more direct manner, and with this view the experiments to be now described were performed.

A spider of this group usually trails a line from its spinnerets while walking. With a little dexterity it can be quickly seized, and imprisoned in such a manner that the spinnerets from which the line is proceeding can be microscopically examined.

This may be best effected by means of a piece of wood about the size and shape of a microscope slide, with a narrow band of cloth attached by its end to one extremity. The cloth band is then held in front of the crawling animal, which may, with a little practice, be thus trapped between the cloth and the wood, so that the band passes beneath the cephalothorax, leaving the abdomen free for examination with the lately emitted line still attached.

The fourth pair of legs must be kept from interfering with the experiment by pins suitably adjusted. The spinnerets will now be in their quiescent position, and the precise origin of the threads therefore invisible. If, however, it be gently drawn forwards, i. e. towards the animal's head, certain facts with regard to it become at once clear. As, however, the phenomena differ at different times, we must take the various cases in succession.

In the simplest case (fig. 9) one of the anterior spinnerets will be pulled forward with the thread, which will be easily seen to consist of a single line emanating from one large tube.

More frequently (fig. 10) the line will be double issuing from similarly situated tubes on the inner sides of the two anterior spinnerets. This is probably the most usual case, and I have drawn out from a spider many yards of such a double line of silk, its origin being all the time plainly visible.

It is important to note that there is no adherence between the two lines, which remain perfectly distinct throughout their whole parallel course.

The spider will probably tire of having its silk thus drawn out—a process which it can only influence indirectly. Were its hind legs free it would seize the thread and break it. It sometimes contrives to do this by a rapid movement of its spinnerets, but occasionally it decides to strengthen the thread instead. The spinnerets are accordingly actively rubbed together, and a little flocculent mass of silk appears upon the line, which is thereafter seen to consist of four strands, two of finer calibre having made their appearance between the former lines (fig. 11). To see their origin the anterior spinnerets must be kept forward by a gentle strain on the thread, and the posterior spinnerets thrust aside with a needle. The new lines may then be traced to the intermediate spinnerets, and proceed from large spinning tubes on the inner side. Again, the four lines remain distinct and non-adherent.

Should the spider still resolve on strengthening the line a further rubbing together of the spinnerets occurs, and presently a large number of strands are seen to proceed from the numerous hair-like tubes on the anterior spinnerets (fig. 12). The four previous lines are still distinguishable by their greater thickness.

If after drawing out several inches of this compound line it be slightly slacked, a puff of air separates the strands, showing that, though contiguous, they are not adherent.

Lastly, upon rare occasions, the whole battery of tubes seems to be brought into play, the posterior spinnerets contributing their quota to the strengthening of the line. Thus the "trailing line," as I have called it, will be found at any moment to be constituted as indicated in one of the cases above described.

It appears, therefore, that such a line usually consists of either two or four non-adherent threads emanating from what Apstein has shown to be the origin of the Ampullaceal glands, and that it may on occasion be strengthened by contributions from the Piriform and Acinate glands opening upon the anterior and posterior spinnerets respectively.

It was next attempted to apply the same direct method to

the observation of the animal when employed naturally in its various spinning operations. Here the difficulties experienced were considerable, but some results were obtained by the aid of a simple contrivance, consisting of a pair of compasses with the points fixed some two inches apart, and between them a narrow strip of cloth stretched.

A flat piece of wood was held behind the spider while at work, and between this and the strip of cloth the creature was suddenly trapped, the points of the compasses, which projected the eighth of an inch beyond the cloth, being buried in the wood on either side.

Flies were now placed in the various webs, and the spiders seized in the act of binding them up in the usual manner. The fly is held and rotated by means of the jaws, palps, and anterior legs, while the fourth pair of legs draw up from the spinners the bands of silk which are to enclose it. These silken bands were found to be constituted as shown in figs. 12 or 13. There seems no doubt, therefore, that the Aciniform and Piriform glands are mainly used in performing this operation.

The structure of the geometric snare was next investigated.

This is a familiar object, and may be said to consist of—

(1) a sort of frame or scaffolding, to which are attached the distal ends of

(2) the radial lines;

(3) the spiral line, extending from the periphery to near the centre.

(1) The thread of the framework was generally found to be composed as exhibited in fig. 11. When necessary the spider strengthened the line by repeating the journey, and laying it down a second time.

(2) The same line, or that of fig. 10, was also employed in constructing the radii of the snare.

Thus the framework and radii of the geometric web are supplied by the Ampullaceal glands.

(3) The spiral line requires a more detailed description.

A low power shows it to consist of bead-like viscid globules

strung upon a thread with remarkable regularity, as shown in fig. 14 *d*.

It was until a few years ago supposed that these globules were separately deposited by the spider, whereas a uniform coating of viscid matter is given to the thread in the first instance, and its subsequent subdivision into globules is an entirely physical phenomenon. Boys[1] well describes the spider's action as follows:

"The spider draws these webs slowly, and at the same time pours upon them a liquid, and, still further to obtain the effect of launching a liquid cylinder into space, he pulls it out like the string of a bow, and lets it go with a jerk."

That this separation into globules is really a secondary phenomenon I have shown by taking upon a slide a portion of such a spiral immediately upon its completion. It readily stains with hæmatoxylin, and on microscopic examination shows the various stages indicated in fig. 14.

We have thus separately to consider the ground-line (Grundfaden, Apstein) and the viscid matter with which it is enveloped.

Apstein imagines the ground-line to be furnished by the Aciniform glands, and to be many-stranded.

I have not yet succeeded in tracing it with certainty to its origin, but have established the following facts with regard to it:

In the first place, it is not many-stranded, but double only.

When engaged upon this line the creature is so absorbed as to allow of pretty close examination with a hand-lens. I have at such times noticed that the posterior spinnerets are partly open, and that the line is, at first, distinctly double, fusing, by virtue of its viscid envelope, where grasped by the leg which draws it forth. Moreover, on staining and teasing the spiral line, the ground thread readily shows its double nature (fig. 15), but no amount of teasing breaks it up into further strands, as would surely be the case if such existed, for their separate

[1] "Quartz Fibres," by C. V. Boys, F.R.S., 'Nature,' July 11, 1889.

existence as threads implies a degree of dryness inconsistent with complete fusion.

As far as I have been able to trace these lines they have appeared to emanate from the intermediate spinnerets. They are much more elastic, however, than the radial lines, and can therefore hardly proceed from the Ampullaceal orifices.

The only other paired orifices on the intermediate spinnerets are those of the Tubuliform glands. Now, an important function of these glands is undoubtedly, as Apstein remarks, the spinning of the egg cocoon, for they are always distended with yellow fluid in the female just before the deposition of ova, and comparatively inconspicuous after, while the cocoon consists of yellow silk.

If, however, they also furnish the ground-threads, this would help to explain their presence in the male spider, which has not hitherto been very easy to understand.

The objections to this view are, first, that cocoon silk is not especially elastic, and secondly, that I have not been able to find threads in the cocoon of the precise diameter of the ground-threads.

In spiders of the species under consideration the following thread-diameters were found to be fairly uniform:

Cocoon line	·006 mm.
Anterior Ampullaceal	·003 „
Ground-line of spiral	·0025 „
Intermediate Ampullaceal	·0016 „

The imperfect view I obtained of the origin of the ground-thread led me to think that though it proceeded from the intermediate organs, it had some subsequent relation to the posterior spinnerets.

It is possible, therefore, that Apstein is correct in supposing that the Aggregate glands, which debouch on the inner side of the posterior spinnerets, deposit the viscid matter above described.

The arguments hitherto adduced in support of this view are, first, the convenient arrangement of the Aggregate orifices for such a purpose, and secondly, the presence of these glands in

such spiders—and such only—on whose threads the viscid matter has been observed. On dissecting out the various glands from a spider, isolating them on slides, and crushing them, I found that the contents of the Aggregate glands retained their viscidity the longest. Evidence was also sought from histological changes in the glands themselves before and after web-spinning, and though a much larger series of observations would be necessary to afford trustworthy results, alterations similar to those known to occur in active serous glands seemed to be taking place (figs. 19 and 20).

This would show that the Aggregate glands are used in spinning the web, in which case they must furnish the viscid matter, all the other structures being accounted for.

The unsafe nature of such indirect evidence is, however, freely admitted, but it may be pointed out that the certainty which now exists with regard to some of the glands gives greater probability of the true function being allotted to the remainder.

One other web structure remains to be briefly discussed. Foundation lines are attached to surrounding objects, and ordinary non-viscid lines are glued to one another by little patches of silk which we may call attachment discs (Haftscheibe, Apstein). The spider rubs its anterior spinnerets against a surface, emitting silk from the Piriform glands, and upon walking away a line is drawn out from the spinnerets.

I have been best able to study these structures in a small bottle in which a spider was obliging enough to deposit its eggs, fixing the cocoon in its place by a multitude of cross threads fixed to the sides of the bottle at their ends, and to one another where they intercrossed. Their appearance is given in figs. 16—18. It was this structure which led to the belief in the highly compound nature of the spider's line.

Summary.

1. Facts newly established.—A spider's line does not consist of many strands fused or woven together, but ordinarily of two or four distinct threads.

The framework and the radii of circular snares are supplied by the Ampullaceal glands.

The Acinate and Piriform glands are those mainly employed in binding up captured prey.

The "trailing line" consists primarily of Ampullaceal threads, sometimes strengthened by contributions from the Acinate and Piriform glands.

The ground-line of the spiral is double only, and the two strands are bound together merely by the viscid matter which envelops them.

2. Corroborative of Apstein.—The "attachment discs" are furnished by the Piriform glands.

The Tubuliform glands supply the silk for the egg-cocoon.

The viscid matter of the spiral is probably the product of the Aggregate glands.

Finally, the origin of the spiral ground-line is uncertain, but it may proceed from the Tubuliform orifices on the intermediate spinnerets.

EXPLANATION OF PLATE VI,

Illustrating Mr. Cecil Warburton's paper on "The Spinning Apparatus of Geometric Spiders."

FIG. 1.—Profile of Epeira diadematа, sp. spinnerets.

FIG. 2.—Ventral aspect of the same species.

FIG. 3.—Ampullaceal gland.

FIG. 4.—Aggregate gland.

FIG. 5.—Tubuliform gland.

FIG. 6.—Piriform gland.

FIG. 7.—Acinate gland.

FIG. 8.—External spinning organs at rest. *a*. Anterior, *p*. Posterior spinnerets. *t*. Anterior tongue-like fold. *z*. Terminal fold of abdomen.

FIGS. 9—13 show the composition of the "trailing-line" under various circumstances. *i*. Intermediate spinnerets.

FIG. 14.—Stages in the formation of the viscid globules. *d*. Shows the final arrangement.

FIG. 15.—Teased spiral line, showing that the "ground-line" is double.

FIG. 16.—"Attachment disc" (Haftscheibe, Apstein).

FIG. 17.—The same, more in profile.

FIG. 18.—Attachment disc, gluing together irregular strands which held an egg-cocoon in position.

FIG. 19.—Section (somewhat diagrammatic) of aggregate gland at rest.

FIG. 20.—Ditto of aggregate gland when the spider had just constructed its web. (The right half only of Figs. 19 and 20 is shaded.)

ON PHYMOSOMA VARIANS.

BY

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With Plates, VII.—X.

THE material which forms the basis of the following paper was collected and preserved by Mr W. F. R. Weldon, of St John's College, Cambridge, during a visit to the Bahamas. On his return to England Mr Weldon commenced to work at Phymosoma, and made many microscopic sections and drawings. When, however, he received the appointment which he now holds at Plymouth he handed the whole material, together with his drawings, to me, with a request that I would complete the work thus interrupted. This statement will serve to show how much I am indebted to Mr Weldon, both for material and for many of the drawings; but I have further to express my indebtedness to him for many suggestions and much help in completing the work he was unfortunately obliged to lay aside.

The observations here recorded were made on a species of Phymosoma (Ph. varians, Selenka) collected in the Bahama Islands.

This species was sufficiently common in the island of New Providence; but it occurred still more abundantly in the lagoon of the Bemini atoll. The specimens were obtained by breaking up soft masses of coral rock with a hammer. Pieces

of rock which were completely covered at low water contained many more specimens than those which were left dry by the tide.

The species seems to be capable of much variation; and the descriptions hitherto published are incomplete in one or two important points. A detailed account of the external characters may therefore be not altogether useless.

External Characters and Ectoderm.

The length of fully extended specimens averages 50 mm., varying, however, from about 40 mm. to 55 mm. The greatest diameter of the trunk is from 4 mm. to 5 mm.; that of the introvert about 2 mm. The introvert is at least equal in length to the rest of the body.

The head (figs. 1 and 5) bears a crown of about eighteen tentacles, arranged in the form of a horseshoe, with the open ends directed backwards; the whole structure lying far back on the dorsal region of the head (fig. 1). The ends of the tentacular horseshoe are connected with the lower lip; which is a thick vascular crescent enclosing considerably more than three-fourths of the circumference of the head (figs. 2 and 6). The mouth is a narrow crescentiform slit, extending between the dorsal margin of the lower lip and the convex surface of the crown of tentacles. These relations of tentacular crown, mouth, and lower lip are shown in the diagram (figs. 1 and 32). It will be seen that in this species the condition of the head presents a marked resemblance to that which obtains in Phoronis.

The tentacles themselves are short and simple, the surface directed towards the outer (convex) side of the lophophor being grooved, and the groove is ciliated; the opposite surface is covered with a deep brown pigmented epithelium (fig. 5).

The space included within the concavity of the lophophor (the representative of the præoral lobe) is covered with a wrinkled, pigmented skin. In its centre lies a deep depression, similar to that of Sipunculus, at the base of which lies the

brain; while a sense-pit opens on to it on each side[1] (figs. 1 and 7).

The introvert is dividable into several regions. Immediately behind the head follows a narrow, perfectly smooth region, extending for about 2 mm. At the posterior edge of this region is attached a small but very extensile collar, its anterior margin being free (figs. 1 and 4). Behind the attachment of the collar the introvert swells slightly, and there follows a region about 6 mm. in length, which bears about twenty rows of hooks. Then follows a region of variable length, bearing papillæ; and lastly a second region of hooks, which in our specimens bore from forty to between fifty and sixty rings. Among the hooks of the posterior region are many papillæ; and these in passing backwards get more and more conspicuous, at the expense of the rings of hooks. These papillæ also exhibit traces of a tendency to form rings round the base of the proboscis. The characters of the hooks have been well described by Selenka and by Keferstein[2]: it will be sufficient here to refer to the description given by these authors, and to the drawing (fig. 21).

The papillæ on the introvert have the form shown in fig. 15; they are hemispherical or hemielliptical, being often higher than broad, each having a central opening surrounded by three or four plates of chitin, which often fuse into a single piece; and surrounding this central piece are numerous small rounded plates covering at least the upper half of each papilla.

The papillæ on the trunk (figs. 11, 14, and 16) have a somewhat different appearance, being larger and flatter, and having no marked central plate. They are also surrounded by a much pigmented ring. These trunk papillæ agree with the description given by Selenka, who, however, seems to have overlooked the difference between the papillæ in the two regions of the body. The papillæ are large and conspicuous at the two extremities of the trunk, where they are present on all sides;

[1] Cf. Spengel, "Die Sipunculiden," 'Reisen im Archipel der Philippinen,' Bd. iv. 1883.

[2] Selenka, loc. cit., Keferstein, 'Zeit. für Wiss. Zool.' Bd. xv. 1865.

in the middle of the body they are, however, almost entirely confined to the dorsal surface. These papillæ are shown in fig. 11.

The colour varies in different specimens. The ground colour is always yellowish-brown, with a peculiar iridescence, noticed by other observers: on this are patches of a black or deep brown pigment, which are generally so arranged as to form a few irregular rings in the middle of the introvert and smaller patches on the anterior dorsal part of the trunk. Individuals are, however, found in which the pigment is only very slightly developed; while in others the whole dorsal surface of the body is thickly mottled with dark patches.

The body wall is everywhere covered by an ectodermal epithelium, one cell thick. The characters of the cells presenting marked differences in different regions.

The ectoderm covering the lower lip and the outer grooved surface of the tentacles is columnar and covered with short thickly set cilia (figs. 4 and 8).

The præoral lobe, together with the inner surface of the tentacles, is covered by a layer of cubical cells, the outer half of each cell in this region being loaded with granules of a dark brown pigment (figs. 4, 7, and 8). These cells are not ciliated.

The epithelium covering the collar is formed of short cubical cells, which appear to become more flattened when this organ is extended (fig. 4).

On the remainder of the introvert the ectoderm secretes, except in the region of the hooks and papillæ, a clear homogeneous cuticle 0·02 mm. thick.

Each hook is secreted by a raised papilla, which projects into the cavity of the hook. The cells covering the papilla being large and cubical, provided with conspicuous spherical nuclei (fig. 21).

Behind each hook is a small organ, apparently sensory, which will be described below.

The ectoderm of the trunk consists of lamellar, dome-shaped cells, secreting a thick cuticle almost 0·1 mm. in thickness (fig. 13). The outer surface of this cuticle is rough and

granular; and it absorbs staining fluids with a certain readiness, while the main body remains in all the preparations quite unstained. The cuticular substance appears in the greater part of the body to be arranged in wavy columns, running more or less regularly at right angles to the surface of the body, and resting each on a single ectoderm cell (fig. 10). Each column exhibits a further tendency to a laminated structure, the layers composing it lying concentrically to the body of the animal.

A result of the peculiar shape of the ectoderm cells in the trunk-region is the formation beneath them of a series of small cavities, containing a coagulum. By a kind of lifting up of several cells from the adjacent muscles, these cavities communicate with one another and so attain a considerable size (fig. 10). They communicate with the cavities, to be presently described, which lie between the two layers of the papillæ (fig. 16).

The function of these channels is in all probability connected with the circulation of the nutrient fluids; but I have not succeeded in tracing a connection between these and any other of the cavities of the body. The analogy between these spaces and the dermal spaces of Sipunculus need hardly be pointed out. A surface view of the skin shows that the cuticle is broken up into a series of fusiform areas (fig. 11). These areas roughly correspond with the skin-papillæ, the lines limiting them being formed by thickened portions of cuticle. When the animal is in an expanded condition the areas become thicker and shorter.

The papillæ of the introvert and trunk are entirely ectodermal. Their external appearance has already been described; the arrangement seen in section is shown in figs. 14 and 16.

The cuticle seems, in the region round the base of each papilla, to contain irregular spaces, as if its inner and outer surfaces had been pulled apart, an appearance which may, of course, be due to the action of the knife used in cutting sections. On the papilla itself, the plates seen in surface views

are visible as local thickenings of the cuticle, and are often loaded with a bright yellow-brown pigment.

The body of the papilla has the form of a double cup, as if it had been formed by the invagination of a spherical outgrowth of the general ectoderm. The outer layer of the cup is composed of flattened cells, which are continuous with those of the general ectoderm at the base of the papilla, and with those of the inner cup at its apex. The inner layer of the cup consists of large cells, loaded with granules of a bright yellow substance, so that the remains of their protoplasm are seen as slender strings of stained material, separating masses of the yellow formed material. This inner cup contains a small cavity, which communicates with the exterior by the pore at the apex of the papillæ. Between the two cups is a cavity, continuous with the subepidermal system of spaces above mentioned.

In the absence of a detailed knowledge of the habits of the living Phymosoma it would be rash to assign any function to these very curious organs, but it seems not improbable that the secretion they produce may assist in softening the coral rock in which the animals form long tubular passages.

General Anatomy.

The arrangement of the internal organs is shown in fig. 3 which represents a Phymosoma cut open longitudinally and the body wall turned back to expose the viscera. The introvert is invaginated to almost its full extent, the true anterior end of the body being at the point where the sense-pits lie.

The longitudinal and circular muscles of the skin have been omitted for the sake of clearness; a detailed description of them is given below.

The retractors of the introvert are four in number. They fuse round the first half of the œsophagus forming a muscular tube, and then separate into a dorsal and a ventral pair. The former are much the shorter pair; between them lies the dorsal blood-vessel, whilst the ventral pair have at their base the generative ridge and between them the nerve-cord. The

spindle muscle supporting the alimentary canal is shown running up the axis of the intestinal coil. The œsophagus is anteriorly surrounded by the retractor muscles, but the posterior half is free and ends in the coiled intestine. The number of coils varies, usually there are about fifteen. The intestine forms a thicker tube than the œsophagus, it ends in the rectum which passes straight to the anus in the dorsal middle line.

The only part of the vascular system visible is the crumpled dorsal vessel.

The brain is indicated through the walls of the introvert, and close behind it, at the sides, two black spots, the sense-pits, are visible; the ventral nerve-cord is seen running down the body.

The nephridia or brown tubes are conspicuous objects, varying very much in size and shape in different individuals. Their external opening is at the anterior end and a little in front of the level of the anus. The opening is followed by a short neck which opens into the swollen portion or bladder which passes into the true secreting portion. The anterior half of the nephridia is attached to the body wall by muscle-fibres, the posterior is free (fig. 18).

The generative ridge runs across the body at the base of the ventral retractors (fig. 22). It is sometimes V-shaped, the ridges slanting backward in the middle ventral line.

The Muscular System.

The muscular system is composed throughout of fusiform fibres with simple pointed ends. Each fibre consists of an outer contractile and an inner granular portion, the outer portion being longitudinally striated. The elongated oval nucleus lies entirely within the inner layer, the nucleus and the contractile layer being easily stained, while the inner substance does not absorb staining fluids (figs. 13 and 21).

The fibres of the retractor muscles are much larger than those of the body wall, their diameter being at least twice as great.

The fibres of the general body wall are arranged in an external circular and an internal longitudinal layer, separated by an exceedingly delicate layer of oblique fibres. This latter can only be seen in surface views, as, owing to its extreme thinness, it is difficult to detect in sections.

The circular muscles commence behind the collar fold, where they form a series of rings round the introvert, one lying beneath each ring of hooks (fig. 1). Posteriorly to the hook-bearing region the circular fibres form a continuous sheath, which extends to the posterior end of the animal (fig. 22).

The longitudinal fibres form a complete sheath round the introvert, commencing anteriorly just behind the attachment of the collar. At the posterior extremity of the introvert these fibres separate into longitudinal bundles, generally about twenty-two in number, which run parallel with one another down the trunk. In passing backward these bundles gradually fuse with one another, and so become fewer and larger, till near the "tail" they form a series of projecting ridges, giving to a section of the body-cavity in this region a characteristic star-shaped appearance (fig. 13). At the posterior extremity of the body the bundles finally unite. The longitudinal bands occasionally give off side branches, which pass into the adjacent bands (fig. 22).

The retractor muscles of the proboscis arise by a common origin from a kind of dissepiment, stretching across the body at the level of the origin of the mantle fold, and just behind the skeletal tissue of the collar (fig. 9). Almost immediately after their origin they split into two bands, which pass backwards, one on each side of the œsophagus, for about half its length. Each lateral band then again divides into two branches, a shorter dorsal and a longer ventral branch, which run to the body wall, where they fuse with the adjacent bands of longitudinal fibres. The ventral bands, being longer than the dorsal, are attached to the body wall behind these, lying one on each side of the nerve-cord, and being connected by the generative ridge. The posterior ends of the retractor muscles are fan-

shaped and split up into bundles of fibres, which pass into the adjacent longitudinal bundles.

A special muscle accompanies the nervous system on each side (fig. 29), and is described in connection with the nerve-cord. Its purpose is probably to regulate the movements of this important organ during the eversion or retraction of the introvert.

The spindle-muscle and the intrinsic muscles of the alimentary canal are described with the digestive organs, and the intrinsic muscles of nephridia with the account of these organs.

Except along the generative ridge, the body wall is lined by a layer of flat epithelial cells, which is never ciliated, in this respect differing from that of Sipunculus.

The Skeletal Tissue.

A curious form of tissue is found in the collar and the tentacular crown of Phymosoma. As it seems to subserve the purpose of supporting and stiffening the collar and tentacles, and as a support for the insertion of the retractor muscles, I propose to call it the skeletal tissue.

The cells composing this tissue are large rounded cells, which lie close to one another, but are not so crowded as to become hexagonal. The cell nucleus is large, and both it and the protoplasm of the cell stain deeply. Running across the cell, usually in a radial direction, are a small number of wavy lines.

This tissue forms a ring lying in the substance of the collar, which it seems to stiffen. The horseshoe-shaped blood-space lies internal to this tissue, which is thicker at some parts, and thus serves to break up the blood-space as indicated in figs. 4 and 6. It also sends extensions into the tentacles, a group of these skeletal cells being formed on both sides of the tentacular nerve in each section of the tentacle (fig. 17).

From the position of this skeletal ring in the collar it will be readily understood that it is just in front of the invaginable introvert, and consequently it affords a valuable hold for the

insertion of the retractor muscles which are attached to this part of the body.

The Alimentary Canal.

The digestive tube may be divided into three parts: (1) the œsophagus, which extends from the mouth to the beginning of the coiled intestine; (2) the intestine which forms a close, fairly regular coil with from ten to sixteen turns; in its coiled state it is almost 10 mm. long; (3) the rectum, which is a straight tube passing from the anterior end of the coil to the anus.

In spirit specimens the whole of the alimentary canal is white in colour, and is usually full of fine sand. A spindle-muscle serves to support and keep in position the coiled intestine and rectum. This muscle arises from the extreme posterior end of the body wall, and passes forward along the axis of the coiled intestine and then parallel with the rectum, to be inserted into the body wall a little in front of the anus (fig. 3). It gives off during its course numerous fibres, which are inserted into the walls of the intestine and rectum. In addition to the spindle-muscle the intestine is held in position by a thin muscle, which arises from the ventral surface of the body and is inserted into the anterior end of the coil.

The position of the mouth has been described above. It is a crescentiform slit, lying between the lip and the convex side of the tentacular crown (fig. 6). It is lined with a continuation of the columnar ciliated cells which cover the inside of the lip and the ciliated grooves of the tentacles. The walls of the œsophagus are produced inwards into a series of from six to eight ridges, which reduce the lumen of the œsophagus to a star-shaped tube. The grooves between these ridges are continuous with the grooves on the outside of the tentacles (fig. 9). The whole is beset with short thick-set cilia. Surrounding the œsophagus are a few muscle-fibres arranged circularly. For about half its length this first part of the alimentary canal lies between the retractor muscles, which in this region of the body have been reduced to two bundles of

fibres by the fusion of the anterior and posterior muscles of the left and right side respectively. These lateral bundles have fused with the œsophagus, a small amount of gelatinous connective tissue containing branched cells being found between them and the circular muscles of the œsophagus. The dorsal blood-vessel lies between the lateral muscles in a groove, closely applied to the dorsal side of the œsophagus and extending back almost to the beginning of the intestinal coil.

Owing to the presence of very fine sand in the intestine and the delicacy of the tube which make it impossible to satisfactorily wash the sand out, I had considerable difficulty in studying the histology of this part. The intestine is lined throughout by a layer of columnar epithelial cells, one cell thick. The nuclei of these cells are situated near the base. Outside this layer is a thin membrane in which muscle-fibres are sparsely scattered. I do not think the intestine is uniformly ciliated, but patches of cilia occur here and there. The arrangement of these ciliated patches I failed to make out. There is no groove with long cilia running the whole length of the animal, such as has been described by Keferstein in Sipunculus.

The lumen of the rectum is almost occluded by the presence of numerous folds projecting into it. These folds are covered with a number of columnar cells some of which are ciliated, but the majority are crowded with large vacuoles containing minute granules; these are devoid of cilia. The rectum has no cæca opening into it, such as are found in Sipunculus.

The external cuticle is folded into the anus for a little way, and the circular muscle-fibres of the body wall are thickened around the anus in this region, forming a very efficient sphincter. A number of radially arranged fibres also pass out all round the anus; these fibres are derived from the longitudinal muscles. Their action is obviously antagonistic to that of the sphincter.

The Vascular System.

There are two varieties of blood-corpuscle found in Phymosoma. The larger kind exist in great numbers in the body-cavity, together with the ripe generative products (fig. 30). They are oval, about ·02 mm. long and two-thirds as broad; their protoplasm is very clear and transparent, but the nucleus stains well and they have a very definite outline. The cœlomic fluid, in which these corpuscles float, bathes all the internal organs of the animal, and when the contraction of the posterior circular muscles forces the fluid forward it would serve to evert the introvert, which is withdrawn again by the retractor muscles.

The second variety of blood-corpuscle is much smaller than the first, being about half as long and as broad; the protoplasm is not so transparent and stains more readily. These corpuscles are contained in a close space which is usually called the vascular system. This space may best be described as consisting of three parts, all communicating with one another. The first of these is a horseshoe-shaped space (figs. 2 and 7) at the base of the tentacles. From this space there runs up into each tentacle a series of three vessels which anastomose freely with each other and communicate at the tip. As a rule sections of the tentacles show one vessel near the inner pigmented surface of the tentacle, just external to the tentacular nerve and two near the outer surface, one each side of the ciliated groove (fig. 17). The free ends of this horseshoe-shaped space at the base of the tentacles, near the dorsal middle line, are continuous with the ends of another horseshoe-shaped space which lies in the collar. This forms the second of the above-mentioned spaces. As the diagram (fig. 2) shows, it is very irregular in form, breaking up and anastomosing into a number of spaces. This communicates only with the inner smaller horseshoe, between the two is the crescentiform space in which the mouth opens. The third space—usually termed the dorsal blood-vessel—is a very extensile sac running along the dorsal middle line of the œsophagus between the

right and left retractor muscles (figs. 2, 3, and 9). It usually extends about $\frac{1}{2}$ cm. behind the head, and it ends blindly behind. Anteriorly it opens in the middle ventral line into the smaller or tentacular horseshoe, and at the point of junction is a large sinus which surrounds about three quarters of the brain—in fact, all those parts which are not in contact with the epidermis (figs. 2, 4, and 8). The nervous matter is thus in close contact with the blood, being separated only by a thin layer of connective tissue, and the endothelium of the blood-space (fig. 27).

The walls of this third part or dorsal vessel are muscular, and in some specimens are much contracted and crumpled. This vessel appears to serve as a reservoir for the corpusculated fluid, and when it contracts and the fluid is forced forward, it would serve to evert the lip and extend the tentacles. The whole of this space is lined by flat epithelium. I have never seen cilia on the walls, and it is entirely closed.

The Nephridia.

The nephridia or the renal organs are in the form of a single pair of "brown tubes," as in other Sipunculidæ. They lie on either side of the middle ventral line at some little distance from the nerve-cord. Their anterior extremities, near which are the external openings, being a little anterior to the level of the anus (fig. 3).

Each nephridium is about 1 cm. long, the length in preserved specimens varying according to the space of contraction of its muscular coat; by means of this muscular layer the whole organ has the power of shortening and dilating, and also of throwing itself into a number of curious curves.

At the anterior extremity is a dilated bladder, the diameter of which is from four to five times that of the posterior cellular portion of the organ. The internal opening is situated at the anterior extremity of the bladder and is provided dorsally with a prominent ciliated lip[1] (fig. 18). The external orifice is just

[1] The existence of this opening is doubted by Selenka, 'Die Sipunculiden,' but it is sufficiently obvious in all the specimens. It was demonstrated in another species of Phymosoma by Dr Spengel.

behind the internal, and opens also into the bladder. The opening to the exterior is surrounded by a thickened ring of connective tissue with muscle-fibres intermingling, the latter forming a sphincter. The walls of the passage are folded and lined with cubical epithelial cells. The communication between the internal opening and the bladder is effected by means of a short passage, the epithelium of which is ciliated. The walls of the bladder itself are formed of a single layer of cubical cells, a middle coat of irregularly arranged muscle-fibres, and an external investment of peritoneum. The relations of the bladder and its openings will be evident from the diagram, fig. 18. The walls of the bladder are very elastic, they contain many muscular fibres, and are lined with cubical epithelial cells.

The tubular portion of the kidney is a backward prolongation of the bladder, and is attached from the anterior half of its course to the body wall by a mesentery, its posterior half being free. The tube possesses anteriorly a simple lumen, which is broken up posteriorly by a number of septa, producing an appearance which reminds one of that presented by the interior of a frog's lung, the transition between the two regions is very gradual.

The epithelium lining the tubular portion of the kidney is generally one cell thick; it is produced internally into a series of long papillæ, which are separated from one another by a series of depressions (see figs. 19 and 20).

The cells forming the papillæ are extremely long, and are loaded with fine, yellowish granules. In specimens killed during the functional activity of the organ these papilla-cells are furnished at their inner extremities with a series of large thin-walled vesicles, which appear to be thrown off from time to time into the lumen of the kidney (fig. 20).

The granules, with which the kidney-cells are loaded, appear to decrease in number as the vesicles are approached; and it seems possible that the excretory products of the nephridial cells are stored up in the vesicles before being thrown, together with the vesicles themselves, into the nephridial tube. The

whole process is very similar to what takes place in a mammary gland during the excretion of milk. Théel mentions that the excretory organs of Phascolion emitted yellow vesicles which resembled drops of oil when the living animal was disturbed[1].

Between the papillæ lie a series of hemispherical depressions lined by a flattened epithelium, the cells of which are usually loaded at their base with the yellow granules above mentioned. These cells seem to develop into the high columnar cells described above.

The muscle-fibres form an irregular network outside the nephridial cells, lying chiefly at the bases of the papillæ. The hemispherical depressions seem to pass through the meshes of the muscular coat, and to lie in direct contact with the peritoneal investment of the organ (figs. 19 and 20), forming a series of projections visible on the external surface.

The peritoneal epithelium which surrounds the kidney is distinguishable from the nephridial cells by the greater ease with which it absorbs staining fluids, and by the absence of secretion granules. In the region of the hemispherical depressions the peritoneal cells frequently form thick masses several cells deep.

It is difficult to avoid the conclusion that the excretion products are passed through the peritoneal cells to the cells of the hemispherical cups, and thence to the cells of the papillæ, the internal opening of the nephridium having relation chiefly to its function as a generative duct.

The relative amount of the secreting epithelium to the cubical epithelium lining the bladder varies greatly; in one specimen even the area between the external opening and inner end of the internal opening was lined with the former cells, thus reducing the bladder to a very small structure.

The lumen of the nephridium contains nothing but the vesicles above described, together with ripe ova or spermatozoa. It is remarkable that the cœlomic corpuscles appear never to pass through the internal opening of the organ.

[1] Théel, "Recherches sur le Phascolion strombi," 'Kongl. Svenska Vetenskaps-Akademiens Handlingar,' Bandet 14, No. 2.

The Nervous System and Sense-Organs.

The brain is a bilobed organ, continuous by its anterior face with the ectoderm of the invaginated præoral lobe, and surrounded elsewhere by a process of the lophophoral blood-vessel, from which it is separated, not only by the endothelium of the vessel, but also by a connective-tissue capsule (see figs. 2, 4, 8, and 27). The groove between the two lobes is deepest and widest on the anterior surface, where the substance of the brain is continuous with that of the præoral ectoderm.

In the brain, as in the ventral nerve-cord, the ganglion-cells are aggregated in the side nearest the skin; they are on the dorsal side of the animal in the brain, on the ventral in the nervous system.

As the figs. 24, 25, and 26 show, there is a cap of ganglion-cells covering the anterior, dorsal, and posterior surfaces of the brain. The ventral surface is not invaded by the ganglion-cells; but here the fibrous tissue, which makes up the rest of the brain, comes in contact with the thin connective capsule. It is this region of the brain which projects into the blood-sinus.

The majority of the ganglion-cells are small, with deeply stained nuclei, occupying about one half of the cell; they are either unipolar or bipolar. At the postero-dorsal angle of the brain, however, a certain number of giant ganglion-cells are found (fig. 27). These cells have a diameter of ·02 mm., at least four times that of the smaller cells; their nuclei are relatively smaller, and they are unipolar. I was unable to trace what becomes of the fibres given off from these giant-cells. No such giant-cells occur in any other part of the nervous system.

A pair of sense-organs, usually described as eyes, lie embedded in the substance of the brain.

Each of these sense-organs has the form of a long tube bent upon itself, so that one limb is nearly at right angles to the other. The outer limb, the lumen of which is narrow, opens on to the surface of the præoral lobe (figs. 1 and 25), the opening

lies at the dorsal lateral angle of the brain, just dorsal to where the circumœsophageal nerve-commissure leaves the brain; the lumen of the inner limb dilates into a vesicular swelling in the substance of the brain (fig. 23); the whole tube has, therefore, nearly the shape of a retort, and lies entirely in the lateral part of the brain. The wall of the tube is everywhere formed by a layer of clear, nucleated cells. In the outer limb these cells form a fairly regular columnar epithelium one cell thick, which becomes less regular as the inner limb is approached. The cells bounding the inner limb are arranged irregularly, and they appear to send out processes from their peripheral extremities, which may be supposed to communicate with the processes of adjacent nerve-cells. The cells of the inner limb also secrete a deep black pigment, which lies in that portion of each cell which is turned towards the lumen of the tube. A clear coagulum sometimes lies in the cavity of this sense-pit. These organs are visible as two black spots at the level of the brain in the dissected animal (fig. 3).

No trace exists in this genus of the curious finger-like processes which project from the brain of Sipunculus into the body-cavity.

Three pairs of nerves are given off from the brain: (1) dorsally, a small pair supplying the skin of the præoral lobe—these lie nearest to the middle line (fig. 26); (2) ventrally, a nerve on each side, going to the corresponding area of the lophophor, and supplying a branch to each tentacle (fig. 24); (3) and posteriorly on each side arises a nerve which passes round the œsophagus, and joins its fellow of the opposite side to form the ventral cord (fig. 24). The lophophoral nerve arises between the point of origin of the nerve of the præoral lobe and the exit of the circumœsophageal commissures.

The ventral cord itself shows no trace either of a division into two halves, or of a segregation of its nerve-cells into ganglia. It runs along the ventral surface of the body as a perfectly uniform filament, terminating posteriorly without any ganglionic swelling such as that found in Sipunculus.

The fibres are on the dorsal, the cells on the ventral side of the cord.

Along each side of the nerve-cord runs a longitudinal band of muscle-fibres, the cord and its pair of muscles being together enclosed in a special peritoneal sheath. The space between the sheath and the cord is filled with a peculiar connective tissue (fig. 29), which has been regarded by some observers as clotted blood, the cord being said to lie in a blood-vessel. My preparations afford no evidence in support of this view; and I am strongly of opinion that the substance lying between the nerve-cord and its peritoneal investment is, as above stated, connective tissue.

By contraction of the muscles within the peritoneal sheath the nerve-cord may become crumpled, so that while the sheath is perfectly straight the cord within it presents the appearance shown in fig. 28.

The nerve-sheath is attached to the ventral body wall by a series of mesenteric cords, each of which contains, not only a prolongation of peritoneal epithelium, but also a central axis of connective tissue (figs. 28 and 29).

The peripheral nerves form, as in Sipunculus, a series of rings encircling the body, and lying between the circular and the longitudinal muscles. In the region of the introvert a nerve-ring lies beneath each ring of hooks, at the base of the circular muscle which supports them (figs. 1 and 2).

Each nerve-ring is connected with the ventral cord by a single short nerve, which runs from one to the other in the middle ventral line.

The lophophoral nerve runs along the base of the tentacles, one on each side of the lophophore. Each gives off a series of small nerves, one of which passes up the axis of each tentacle, lying immediately beneath the ciliated groove (figs. 2, 5, and 17).

In addition to the sense-pits on the brain there are a number of ectodermal structures on the introvert, which are probably sensory in function, and may well be described here. These bodies are arranged in circles parallel to the rows of hooks

running round the introvert (fig. 21). One of these organs is shown in fig. 12; the ectoderm-cells have multiplied and increased in size, forming a small heap; some of these cells have then formed stiff processes, which project beyond the level of the skin. These processes are gathered up into a small brush by a chitinous ring which surrounds the base.

The hooks (fig. 21) are very closely packed in a series of ridges formed by the circular muscle-fibres of the introvert. The point is directed backward, while the row of sense-organs lies immediately behind them, embedded in the muscular cushion.

The Generative Organs.

Phymosoma varians is dicecious; in no case are ova and spermatozoa found in the body of the same individual.

The ovaries are formed by a fold of the peritoneal epithelium, elsewhere flat, which occurs at the base of the insertion of the long ventral pair of retractor muscles. This genital ridge extends beyond the inner edge of the muscle attachment across the ventral middle line lying between the nerve-cord and the skin; it does not extend beyond the outer or dorsal end of the muscle. The ridge is not quite continuous, but it is interrupted from time to time; its free border is also irregular, and this gives it a puckered or frilled appearance (fig. 22).

In transverse section—parallel to the long axis of the Phymosoma—the ovary is seen to be much thicker at its free border than at its base; the latter indeed is formed of but two layers of cells, thus giving the appearance of a simple fold of endothelium. These layers, however, thicken towards the free edge. Nearly all the cells have become ova, and are held together by a very scanty matrix. The organ is solid, and the ova dehisce from it into the body-cavity.

In the ovary the ova increase in size towards the thickened free edge, where the oldest are. Those found free in the body-cavity also differ somewhat in size, and undoubtedly grow whilst suspended in the perivisceral fluid; but there is a very

marked difference in size between the largest ovarian ovum and the smallest floating one—a difference I am quite unable to account for.

The floating ova are oval in shape, the largest about 1 mm. long, with a thick zona radiata, in which the radial markings can only be detected with very high powers (fig. 30). This membrane stains deeply except its outermost layer, which does not absorb any staining fluid. The protoplasm is very granular, and stains well. The nucleus is very large, and sometimes reaches almost from one side of the cell to the other; it does not stain at all. No micropyle was to be seen.

The testis occupies in the male a position similar to that of the ovary in the female. The mother-cells of the spermatozoa separate from the testis before or whilst dividing. Whilst floating in the perivisceral fluid the nuclei of these cells commenced to divide, and the whole floats about as a multinucleated mass of protoplasm. The stages which most commonly occurred were those with eight or sixteen nuclei (fig. 8). The males were much rarer than the females, and none of them contained ripe spermatozoa.

Summary.

The following is a brief summary of the more important points described in detail in the body of the paper.

(1) The head of Phymosoma is surrounded by a stiffened vascular horseshoe-shaped lip, the dorsal ends of which are continuous with the ends of a hippocrepian lophophor. The lophophor bears a crown of about eighteen tentacles—the number is always even. In the hollow of the lophophor lies the brain, which is continuous with the ectoderm of the præoral lobe. The inner surface of the tentacles and the ectoderm above the brain is crowded with dark brown pigment-granules, and the ectoderm of the præoral lobe is curiously wrinkled. Between the hippocrepian lophophor and the vascular lip is the crescentiform opening of the mouth.

(2) At some little distance behind the lip is a thin but very

extensile collar, which may be so extended as to entirely cover the head.

(3) The ectoderm consists of a single layer of cells. This secretes outside a cuticle of varying thickness. The ectodermal cells are vaulted, so that spaces are left in which a nutrient fluid might circulate between the circular muscles and the ectoderm. The ectoderm of the lower lip and of the outside of the tentacles is ciliated.

(4) The skin-glands are of two kinds; each is formed by the modification of ectoderm-cells, which results in the pushing in of certain of the cells to form a double cup. The inner layer of cells thus produced develops a number of granules, which are extruded through a median aperture. In one kind of skin-gland, those of the introvert, this aperture is surrounded by a chitinous ring, which is absent on those of the trunk.

(5) Rows of hooks set very closely together are found in the introvert; these are each secreted by a small multicellular papilla.

(6) A skeletal tissue is present in the lip and tentacles. This seems to stiffen these structures, and to form a firm hold for the attachment of the retractor muscles of the introvert.

(7) The nephridia or brown tubes consist of two parts, the bladder and the secreting part. The former opens both to the exterior and to the body-cavity, the latter opening being shaped like a flattened funnel and ciliated. The secreting part opens only into the bladder. Its walls are lined with a columnar epithelium, the cells composing which are crowded with granules. From time to time a vesicle or bubble crowded with these granules is formed at the free end of the cell, and ultimately breaks off into the lumen of the nephridium, and so passes out of the body. The only other structures found in the cavity of these organs besides these vesicles, were the ripening generative cells.

(8) The vascular system consists of a horseshoe-shaped plexus in the lower lip, a similar plexus in the lophophor which gives off branches into each tentacle, and a reservoir

lying dorsal to the œsophagus. This communicates with the lophophoral sinus in the dorsal middle line. Just at this point is a blood-sinus which surrounds all those parts of the brain which are not continuous with the ectoderm. This system of blood-vessels is closed. It contains numerous small oval corpuscles. In addition to these the cœlomic fluid contains a number of much larger corpuscles, as well as ova and sperm morulæ. The cœlom is lined by a flat epithelium which is not ciliated.

(9) The brain is a bilobed mass, partly connected with the ectoderm of the præoral lobe and partly surrounded by a blood-sinus. The relative position of the ganglion-cells and fibrous tissue is described above. There are a number of giant ganglion-cells arranged in the lateral and posterior parts of the brain.

(10) The brain gives off three pairs of nerves: (1) the first pair pass to supply the pigmented tissue of the præoral lobe; (2) the second pair run along the base of the lophophor, and send a branch into each tentacle; (3) the third pair pass round the œsophagus, and unite to form the ventral nerve-cord. This is supported by a strand of muscle in each side, and by numerous connective-tissue strands which pass to the body wall. It has no trace of a double structure, and no segmentally arranged nerve-ganglia. It gives off from time to time a median nerve, which soon splits, and each half runs round the body, these fuse together again in the dorsal middle line, thus forming a nerve-ring.

(11) The sense-organs consist of two pigmented pits in the brain, and of certain structures in the introvert. The former pits open on to the præoral lobe, and then pass into the brain at each side. Each pit is bent on itself, and expands slightly at its inner end. The cells lining the pit are crowded with black pigment. The sense-organs on the introvert lie in rows close behind the rows of hooks. Each consists of a number of ectodermal cells produced outwards into a stiff process. These processes are gathered up into a little brush by a chitinous ring which surrounds their base.

(12) The animals are diœcious. The generative organs are in the form of ridges at the base of the ventral retractors. The flat cœlomic epithelium is here modified to give rise to ova in the females and the sperm morulæ in the males.

Conclusions.

I do not propose to consider at any length the theoretical conclusions which might be drawn from the facts above indicated until I have worked out in detail other forms of the Gephyrea, which I hope to do in the immediate future. I should, however, like to say something in favour of maintaining the genus Phoronis in its old position—that is, as a form closely allied to the more normal Gephyrea inermia.

This relationship is most easily seen by comparing a view of the head of Phymosoma as seen from above with a view of Phoronis (figs. 31 and 32). In both genera the mouth is surrounded by a pair of vascular horseshoe-shaped ridges, one of which is dorsal and the other ventral: the sole point of difference lies in the fact that while in the one case the tentacles of the lophophor extend along both the ventral and the dorsal horseshoe, they are in the other case confined to the dorsal limb.

Again, the præoral lobe of Phoronis bears two large sensory pits, one on each side of the middle line; these are obviously comparable to the similar pits which open into the area in the concavity of the Gephyrean lophophor which I have spoken of as the præoral lobe. Further, the nervous system of Phymosoma, like that of Phoronis, is permanently connected with the epidermis.

I do not enlarge upon the resemblances in the position of the anus, and the lengthening of the ventral surface at the expense of the dorsal, or on the presence of two nephridia, as these points have been already emphasized by Lankester. But I would direct attention to two structures hitherto, I believe, undescribed in the Gephyrea, which in my opinion have homologues in Phoronis.

The first of these is the skeletal tissue; this, as the descrip-

tion above shows, agrees in position and function with the mesoblastic skeletal tissue which supports the tentacles of Phoronis as described by Caldwell. The second structure I wish to refer to is the thin membranous fold which I have above termed the collar. This seems to me to correspond very closely with the calyx or web which surrounds the base of the head in Phoronis.

The absence in the unarmed Gephyrea of mesenteric partitions in the post-oral body-cavity, similar to those which exist in Phoronis, may be accounted for by the twisting of the intestinal loop in the more normal genera. The radial muscles which extend from the visceral loop to the body wall are, in all probability, the remains of an ancestrally continuous mesentery.

It will be remembered that in Phoronis the body-cavity is divided into an anterior and a posterior division by a transverse septum passing from the body wall to the œsophagus, at the level of the nerve-ring. The former division includes the cavity of the præoral lobe and tentacles, the latter the rest of the body-cavity. I am disposed to think that a similar disposition of parts obtains in Phymosoma. The organ which is usually regarded as forming the blood-vessels in the Gephyrea occupies precisely the same position as the anterior body-cavity in Phoronis; it has, however, acquired a reservoir—the dorsal vessel—into which the fluid may pass when the head is retracted. As this involution is impossible in Phoronis no such reservoir has been developed. If this homology holds, there is nothing in the Gephyrea homologous with the true blood system of Phoronis. In connection with this it is perhaps worth noticing that the so-called vascular system in the Gephyrea gives off no vessels or capillaries, but simply consists of a number of intercommunicating spaces.

DESCRIPTION OF PLATES VII, VIII, IX, and X,[1]

Illustrating Mr Arthur E. Shipley's paper "On Phymosoma varians."

PLATE VII.

FIG. 1.—A semi-diagrammatic view of the anterior end of Phymosoma varians. The introvert is everted and the tentacular crown expanded. The collar is not extended and lies at the base of the head. Only two rows of hooks are shown.

FIG. 2.—A semi-diagrammatic view of the closed vascular system and nervous system, showing their relation to the alimentary canal. The vascular system shows the three parts, the lophophoral, the lower lip, and the dorsal blood-vessel. The latter communicates with the lophophoral in the middle line, and just at this point the sinus round the brain is given off. The brain is relatively too small. The three main nerves are shown, and the circular nerves which run in the skin. The œsophagus is cut off abruptly in front in order to display the vascular ring.

FIG. 3.—View of a Ph. varians which has been opened along the median dorsal line. The introvert is retracted, the true anterior end of the body being where the eye-spots lie. Here and there patches of skin are seen which bear papillæ.

PLATE VIII.

FIG. 4.—A median longitudinal section through the head. The introvert is retracted, and the collar expanded until it encloses the whole head. The section is not quite in the middle line, or the lip on the dorsal surface would not be shown, cf. Fig. 6. The brain is cut through that part which is continuous with the ectoderm.

FIG. 5.—A transverse section through the tentacles: the introvert is retracted. The tentacles show the ciliated groove on the outer surface, the pigmented epithelium in the inner, and the vascular spaces and tentacular nerves.

FIG. 6.—A transverse section through the base of the lophophor and lower lip, just where the two fuse dorsally: the introvert is retracted. The skeletal tissue is shown in the lip, which is ciliated all round.

FIG. 7.—An oblique transverse section through the base of the lophophor, showing the blood-space; and in the centre some of the wrinkled pigmented tissue of the præoral lobe. The introvert is everted.

[1] I am indebted to Mr Weldon for the following figures:—Nos. 1, 7, 10, 12, 14, 15, 16, 20, 21, 23, and 27.

FIG. 8.—A transverse section through the head in the region of the brain. The introvert is everted. This specimen had its body wall pushed upwards inside the lower lip in the ventral side into a kind of hernia, this accounts for the swelling containing blood-corpuscles and sperm-morulæ. The brain is shown in its sinus, also the depressions in the tissue of præoral lobe leading to the sensory pits.

FIG. 9.—A transverse section through the œsophagus. The dorsal and ventral retractor of each side have fused into a common lateral muscle, which almost fills up the body-cavity. The lumen of the œsophagus is occluded by ciliated ridges.

FIG. 10.—A section through the ectoderm and cuticle. Below the ectoderm some fibres of the circular muscle may be seen. The ectoderm is vaulted leaving spaces which sometimes contain a coagulable fluid. The cuticle is traversed by numerous perpendicular lines, and the outer part only stains.

FIG. 11.—A surface view of the skin, showing the longitudinal and circular muscle-fibres, the skin papillæ, and the ridges formed by thickenings of the cuticle.

FIG. 12.—A section of one of the sense organs on the introvert, at the base of the ring of hooks.

FIG. 13.—A transverse section through the posterior end of the animal. The longitudinal muscles have fused together and reduced the lumen of the body-cavity to a star-shaped mass. The skin papillæ are very numerous in this region, and the cuticle unusually thick.

PLATE IX.

FIG. 14.—Section taken through one of the skin papillæ of the trunk. It shows the opening to the exterior, and the small cavity in the cup composed of enormous cells crowded with spherules.

FIG. 15.—Surface view of the papillæ and hooks in the introvert. The chitinous plates round the orifice of these papillæ are shown.

FIG. 16.—An oblique section through a trunk papilla. This section shows the space between the two layers of the cup in communication with the sub-ectodermal spaces of the skin.

FIG. 17.—Transverse section of a tentacle. At the base of the ciliated groove the tentacular nerve lies. Three blood-spaces are seen, and between them certain skeletal cells. The inner epithelium is crowded with pigment grains.

FIG. 18.—A diagram showing the anatomy of the nephridium. The posterior blind diverticulum is the secreting part, the anterior thin-walled part is the bladder. The arrangement of the internal and external openings may also be seen.

FIG. 19.—An oblique section through the secreting part of the nephridium, under a low power. This shows the peritoneal epithelium, then a

dark layer of muscle-fibres and internally the secreting epithelium. The breaking up of the lumen into numerous side chambers is also shown in this figure.

FIG. 20.—A portion of the same under a high power. The secreting epithelium is seen crowded with granules; at their free edges these cells form vesicles, which break off and fall into the lumen.

FIG. 21.—A section through parts of several of the hooks on the introvert. The multicellular papillæ which secrete the hooks are shown. One of these sense organs at the base of the hooks is also shown cut tangentially.

FIG. 22.—A view of the base of the two ventral retractor muscles, showing the generative organ. The ventral nerve-cord lies between the muscles and dorsal to the generative ridge. The circular and longitudinal muscles are also shown, and the outline of the papillæ.

PLATE X.

FIG. 23.—A section through the antero-dorsal corner of the brain, to show the blind end of the sense-pit. The cells lining the inner end of the pit are crowded with pigment. A few cells of the ectoderm of the præoral lobe are seen, and part of the blood sinus in which the brain lies.

FIG. 24.—An oblique section through the lateral part of the brain, showing the origin of the circumœsophageal commissure and of the lophophoral nerve. This figure and the three succeeding ones show the arrangement of the ganglion-cells, the giant cells, and nerve-fibres.

FIG. 25.—A section through the brain, transverse to its long axis, and nearer to the middle line than the preceding figure. It shows the fusion of the brain with the ectoderm of the præoral lobe, and the commencement of the præoral lobe nerve.

FIG. 26.—A section in a place parallel to the preceding, but still nearer to the median line, it shows the origin of the præoral lobe nerve.

FIG. 27.—A horizontal section through the posterior part of the brain at right angles to the preceding. This shows the histology of the giant-cells and their relative size.

FIG. 28.—A longitudinal median section of the ventral nerve-cord, showing the arrangement of the ganglion-cells and fibres, and the mesenteries which attach the cord to the ventral body wall.

FIG. 29.—A transverse section of the nerve-cord, showing a mesentery from the ventral body wall, the arrangement of ganglion-cells and nerve-fibres, the connective-tissue sheath, and the lateral muscles which run along each side of the nerve-cord.

FIG. 30.—An ovum and some of the cœlomic corpuscles. The ovum shows the granular protoplasm, the large nucleus, and the zona radiata.

FIG. 31.—A diagrammatic view of the head of Phoronis, seen from in front.

FIG. 32.—A similar view of Phymosoma.

ON THE PERCEPTIONS AND MODES OF FEEDING OF FISHES.

BY

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In the course of observations made at Plymouth and elsewhere it appeared that the majority of Fishes are diurnal in their habits and seek their food by sight, but that a minority are almost entirely nocturnal and hunt by scent. To the latter class belong *Protopterus*, Skates and Rays, the Rough Dogfish, Sterlet, Eel, Conger, Rocklings, Loaches, Soles, &c. These creatures remain buried or hidden by day but career about at night in search of food, returning to their own places at dawn. If while they are thus lying hid, food or even the juice of food-substances is put into the water, they come out after an interval and search vaguely, without regard to the direction whence the scent proceeds. Some of the animals (Rocklings, Sterlet) have special tactile organs in the shape of barbels or filamentous fins with which they investigate their neighbourhood, while others (Conger and Eels) feel about with their noses. None of the fishes which hunt by scent seem able to recognise food by the sense of sight, even though it be hanging freely before their eyes.

The mode of feeding of the Sole is peculiar. When searching for food its skin is more or less covered with sand, which renders it inconspicuous when moving on the bottom. This sand adheres to mucus which is probably exuded when the smell of food is perceived. The Sole seeks its food exclusively on the bottom, creeping about and feeling for it with the lower side of its face. If a worm is lowered by a thread until it actually touches the

upper side of the head of a Sole, the animal is still unable to find it but continues to feel for it on the sand. There is however no reason to suppose that the sight of these fishes is deficient. A Rockling at Plymouth had already learnt to come out to be fed if any one came near the tank, though it still did not recognise a worm swimming in the water. Particulars were given of the various irideal mechanisms which occur among fishes.

This investigation was undertaken at the instance of the Marine Biological Association as a preliminary step towards improving the supply of bait. The experience gained suggests that a bait for the south coast, where Conger and Skate are chiefly caught, could be made by extracting the flavour of Squid or Pilchard and compounding it with a suitable ground-substance. Though few practical experiments were made, it was found that an ethereal extract of *Nereis* or Herring, for example, greatly attracted some of these fishes.

ON THE ORIGIN OF THE EMBRYOS IN THE OVICELLS OF CYCLOSTOMATOUS POLYZOA.

BY

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THE species investigated belonged to the genus *Crisia*, in which, as in other forms of *Cyclostomata*, the mature ovicells contain a large number of embryos. These embryos are imbedded in the meshes of a nucleated protoplasmic reticulum, which also contains a mass of indifferent cells, produced into finger-shaped processes, the free ends of which are from time to time constricted off as embryos. The embryos have, at this stage, a structure identical with that of the youngest embryos described by previous authors. After developing various organs, they escape as free larvæ through the tubular aperture of the ovicell. The budding organ from which the embryos are formed makes its appearance at an early stage in the development of the ovicell. Evidence was brought forward to show that it must be regarded as an embryo, produced from an ovum. The supposed ovum is found in very young ovicells, imbedded in a compact follicle, and appears to give rise, by a remarkable process of development, to the budding organ above described. The embryos are thus produced by the repeated fission of a primary embryo developed in the ordinary way from an egg.

ON A NEW SPECIES OF PHYMOSOMA.

BY

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DURING a visit to the Bahama Islands, Mr Weldon was fortunate enough to find three specimens of a large brown *Phymosoma*, whilst investigating the Fauna of the Bimini lagoon. He came to the conclusion that these specimens belonged to no described species of *Phymosoma*, and was good enough to hand them over to me for description. I propose to call this species *Phymosoma Weldonii*.

The length of the three specimens varied between 3·5 cm. and 3 cm.; their bodies are plump and slightly curved. The ground colour of the preserved specimens is light yellow, but this is modified over the surface of the body by dark brown papillæ. In all three specimens the introvert is retracted, and in this condition is about 1 cm. long. The papillæ are of two kinds, flat, brown, rectangular, low elevations on the skin of the trunk, and conical, elevated protuberances of a light colour on the introvert.

No hooks or traces of hooks were found on the introvert.

At the base of the introvert, just behind the head, is a well-developed collar, such as I have described in detail in *Phymosoma varians*.

The mouth is surrounded by a vascular lip, which at the dorsal middle line is continuous with the base of the lophophor. The latter is in the shape of a double horseshoe, and is composed of from 70 to 80 tentacles.

There is nothing to call for remark in the arrangement of the internal organs, with the exception of the fact that there are only two retractor muscles. Such an arrangement is only met with elsewhere in *Ph. Rüppellii* from the Red Sea. The absence of hooks and of any traces of them is striking, but it occurs in five other species out of a total of 28 described.

Habitat; the Bahama Islands, Bimini lagoon.

LAND-PLANARIANS AT CAMBRIDGE.

BY

S. F. HARMER, M.A.

A LAND-PLANARIAN (*Rhynchodesmus terrestris* O. F. Müller) was first described as a native of England by Rev. L. Jenyns (*Observations in Natural History*, London 1846), who discovered it in abundance in the woods of Bottisham Hall, near Cambridge. In the present instance, a search (made by kind permission of R. B. Jenyns, Esq.) in the same locality resulted in the discovery of a few specimens; and it was ascertained subsequently that *R. terrestris* is by no means uncommon in Cambridge (King's College, Botanic Gardens). It may readily be found by examining the damp lower surface of logs of wood which have been lying for some time on the ground. Since the first discovery of the animal in England, it seems to have been very seldom found: but from its wide distribution in Europe generally and in England, and from the fact that it is not very likely to be found unless it is specially looked for, it is probable that this animal is much commoner than is usually supposed. Several egg-capsules of *R. terrestris* were discovered on May 15, on examining fragments of rotten wood among which some specimens of the animal had been kept for a week.

NOTES ON A COLLECTION OF SPIDERS, WITH A LIST OF SPECIES TAKEN IN THE NEIGHBOURHOOD OF CAMBRIDGE.

BY

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ALL attempts to preserve spiders in the dry state have hitherto proved ineffectual.

When put up in alcohol, the specimens must either be mounted in some way, and certain specific characteristics concealed, or allowed to lie loosely in tubes, and to present a distorted and unsightly appearance.

For the purposes of exhibition, the former alternative seems preferable, especially if care be taken to minimise as far as possible its disadvantages.

A simple but effective method of mounting specimens is here described, as likely to prove useful to collectors in this and other groups, where no satisfactory dry method of preservation is available.

A specimen tube is filled about one-third full of plaster of Paris powder. Water is added, and the tube corked and shaken, and then laid lengthwise upon a horizontal surface. When the plaster is set, the block is slipped out, smoothed if necessary, and the specimen mounted upon its flat surface with strong gum or "liquid glue"—a substance not dissolved by alcohol.

When replaced, the block of course fits its mould, and cannot crush the specimen, as the width of its flat surface is nearly the diameter of the tube. It moreover affords a white back-ground which is not liable to much discolouration. It is often convenient to mount male and female of a species in the same tube.

The tubes are then labelled and exposed on tiers of shelves, inclined at a small angle to the perpendicular.

Thus arranged, the specimens bear some resemblance to the living species they typify, and present as sightly an appearance as the difficulties of the case will admit.

List of Spiders taken in the neighbourhood of Cambridge.

DYSDERIDÆ.

DYSDERA
Cambridgii, Thor.,—occasional, on Castle Hill, Gogmagog hills, etc.

HARPACTES
Hombergii, Scop., not rare, at the bottom of Clare wall, and in the court of Christ's College.

OONOPS
pulcher, Temp., rare, on Gogmagog hills.

DRASSIDÆ.

MICARIA
pulicaria, Sund., frequent, on Castle Hill, Gogmagog hills, etc.

PROSTHESIMA
Petiverii, Scop., rare, Fleam Dyke.
nigrita, Fabr., rare, Fleam Dyke.

DRASSUS
lapidicolens, Walck., common.
pubescens, Thor., very rare.

CLUBIONA
pallidula, Clk., frequent, in ivy leaves.
terrestris, Westr., occasional.
lutescens, Westr., in the fens.
holosericea, De Geer, occasional, in curled leaves.
brevipes, Bl., rare.
comta, C. L. Koch, occasional, in trees.
subtilis, L. Koch, rare, Wicken Fen.

AGRŒCA
brunnea, Bl., frequent, in grass.

HECAERGE
maculata, Bl., occasional.

DICTYNIDÆ.

DICTYNA
arundinacea, Linn., frequent, on shrubs.
uncinata, Westr., occasional.

AMAUROBIUS
fenestralis, Stroem, rare, in dry grass, vegetable débris, etc.
similis, Bl., frequent, in out-houses.
ferox, Walck., frequent.

AGELENIDÆ.

TEGENARIA
Guyonii, Guérin, not rare, in buildings.
Derhamii, Scop., common, in buildings.
campestris, C. L. Koch, frequent, under ledges of walls.

AGELENA
labyrinthica, Clk., common, on banks.

HAHNIA
elegans, Bl., occasional in Wicken Fen.

TEXTRIX
denticulata, Oliv., rare, enclosure of University Bathing Sheds.

THERIDIIDÆ.

THERIDION
formosum, Clk., rare, Botanical Gardens.
tepidariorum, C. L. Koch, in hot-houses.
pictum, Hahn., frequent, on holly bushes.
sisyphium, Clk., very common, on holly, etc.
denticulatum, Walck., occasional, on shrubs, etc.
varians, Hahn., common, in boathouses, etc.
pulchellum, Walck., rare, on trees.
bimaculatum, Linn., frequent, in grass.
pallens, Bl., not rare, on trees, shrubs, etc.

NESTICUS
cellulanus, Clk., occasional in damp places, e.g. tanks in Christ's College gardens.

PHYLLONETHIS
lineata, Clk., very common; everywhere.

STEATODA
bipunctata, Linn., not rare, in out-houses.

NERIENE
longipalpis, Sund., common, on railings, etc.
dentipalpis, Wid., occasional.
rufipes, Sund., taken at the University Bathing Sheds.
rubens, Bl., frequent, in grass.
isabellina, C. L. Koch, rare.
fusca, Bl., occasional.
livida, Bl., occasional.

WALCKENÄERA
Hardii, Bl., very rare; one example taken in the "Backs."
antica, Wid., rare, Wicken Fen.

PACHYGNATHA
Clerckii, Sund., frequent, in damp grass.
Degeerii, Sund., frequent, in grass.

LINYPHIA
nebulosa, Sund., in Christ's College garden.
zebrina, Menge, occasional.
leprosa, Ohl., frequent.
tenebricola, Wid., common, in grass.
socialis, Sund., frequent, on trees.
dorsalis, Wid., occasional, in plantations.
bicolor, Bl., frequent, in grass.
bucculenta, Clk., common on Castle Hill, etc.
montana, Clk., frequent, on Clare wall.
triangularis, Clk., common, on bushes.

EPEIRIDÆ.

META
segmentata, Clk., everywhere.

TETRAGNATHA
extensa, Linn., frequent, on Clare wall, etc.

CYCLOSA
conica, Pall., rare, in wood on the Gogmagog hills.

ZILLA
x-notata, Clk., everywhere.
atrica, C. L. Koch, frequent.

EPEIRA
cucurbitina, Clk., frequent, on trees, bushes, etc.

diadematа, Bl., common.
scalaris, Walck., rare, in woods.
arbustorum, C. L. Koch, rare, in woods.
cornuta, Clk., frequent, in nettles, etc.
patagiata, Clk., rare, in woods.
sclopetaria, Clk., not rare, on Clare College wall.
umbratica, Clk., not rare, at University Bathing Sheds, etc.

THOMISIDÆ.

Xysticus

cristatus, Clk., common.
viaticus, C. L. Koch, occasional, on Castle Hill.
pini, Hahn., rare.
lanio, C. L. Koch, frequent in wood on the Gogmagogs.
ulmi, Hahn., rare.
erraticus, Bl., rare.

Oxyptila

atomaria, Panz., Wicken Fen.

Philodromus

aureolus, Clk., common, in fir trees, etc.

Thanatus

hirsutus, Camb. (or striatus, C. L. Koch), frequent in Wicken Fen.

Tibellus

oblongus, Walck., common in grass, Castle Hill, etc.

LYCOSIDÆ.

Ocyale

mirabilis, Clk., occasional, Fleam Dyke, etc.

Pirata

piraticus, Clk., common, near water.

Trochosa

ruricola, De Geer, frequent.
terricola, Thor., occasional.

Tarentula

pulverentula, Clk., common.
audrenivora, Walck., frequent.

Lycosa

amentata, Clk., very common.
lugubris, Walck., very common but local.
Farrenii, Cambr., rare, in Wicken Fen.
pullata, Clk., frequent.
riparia, C. L. Koch, occasional.
nigriceps, Thor., common.
monticola, C. L. Koch, occasional.

SALTICIDÆ.

Epiblemum

scenicum, Clk., frequent, on sunny walls.

Heliophanus

cupreus, Walck., rare.

Euophrys

frontalis, Walck., frequent in grass, Castle Hill, etc.

Attus

pubescens, Fabr., rare, on walls.

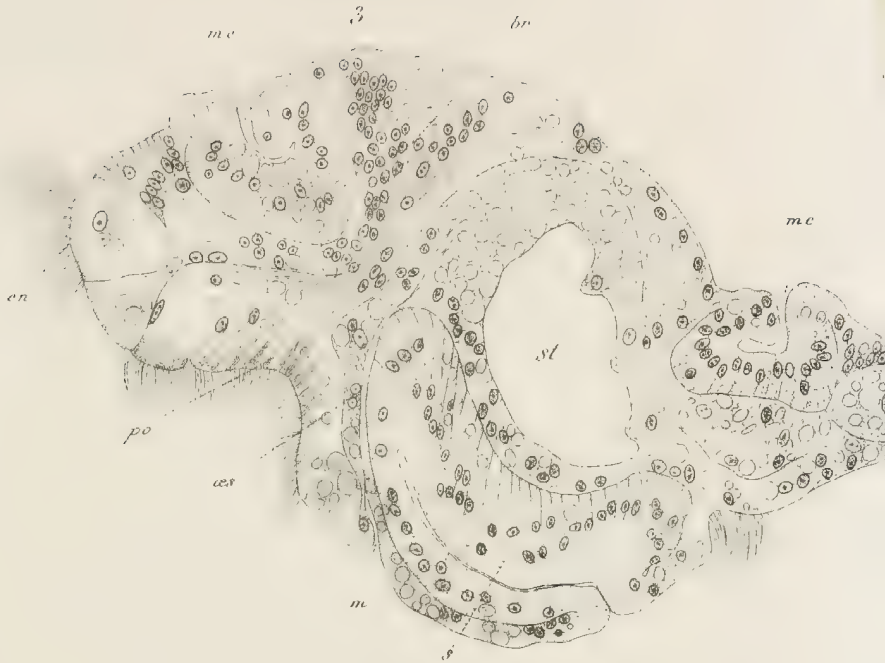
1

2

ormer del.

ALCYONIDIUM POLYOUM

Dufour sc.



S F Harmer del.

ALCYONIDIUM POLYOUM

Fig. 1.
Muscle.
muscles
ventral plate.
leg
leg

Fig. 2.
ext gen.
leg

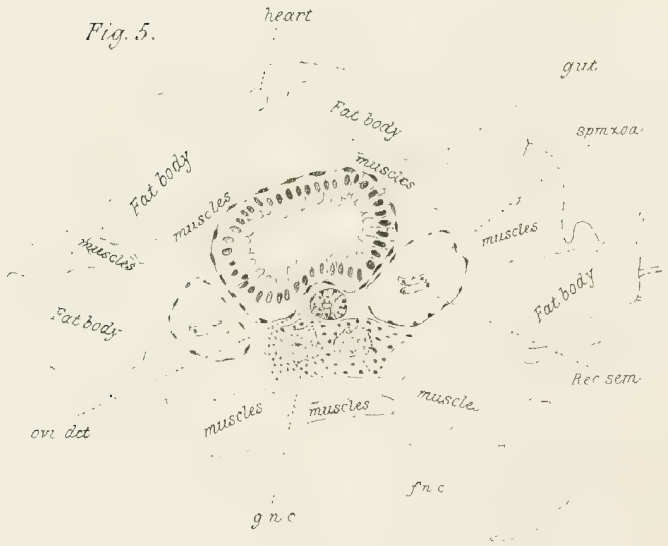


Fig. 5.
heart
gut.
Fat body
spmxoa.
Fat body
muscles
muscles
muscles
muscles
muscles
Fat body
Fat body
Rec sem.
muscles
muscles
muscle
ovi dct
fn c
g n c

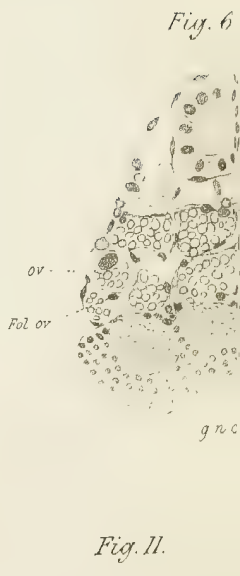


Fig. 6
ov
Fol ov
g n c

Fig. 9.
memb.
R m t
gut.
malp t

Fig. 10.
ost
Art.
ost

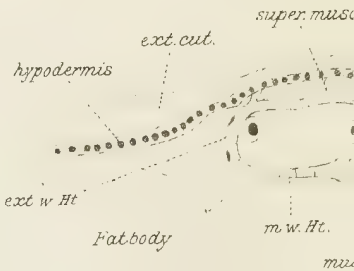


Fig. 11.
super. muscle
ext. cut.
hypodermis
ext w Ht
Fat body
m w. Ht.

Fig. 3.

Fig. 4.

Fig. 8.

Fig. 7.

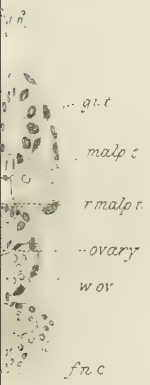


Fig. 12.

Fig. 13.

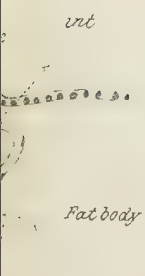


Fig. 14.

F. Huth, Lith. Edin.

Fig. 1.

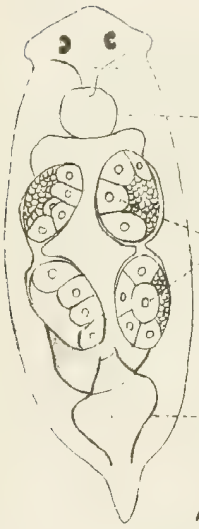
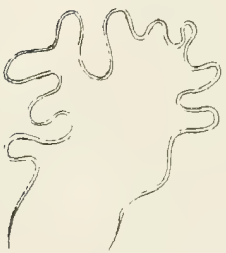


Fig. 2



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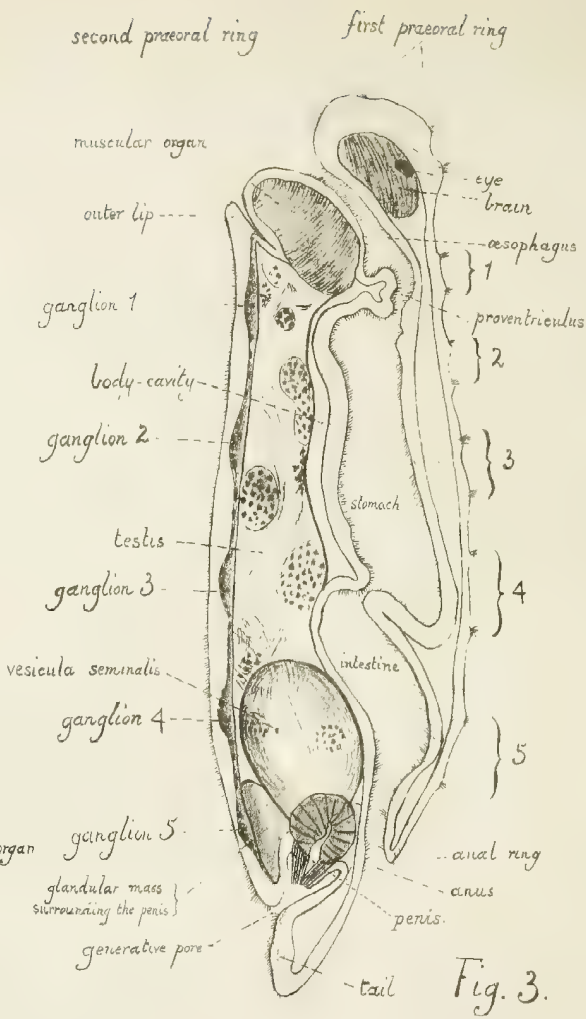

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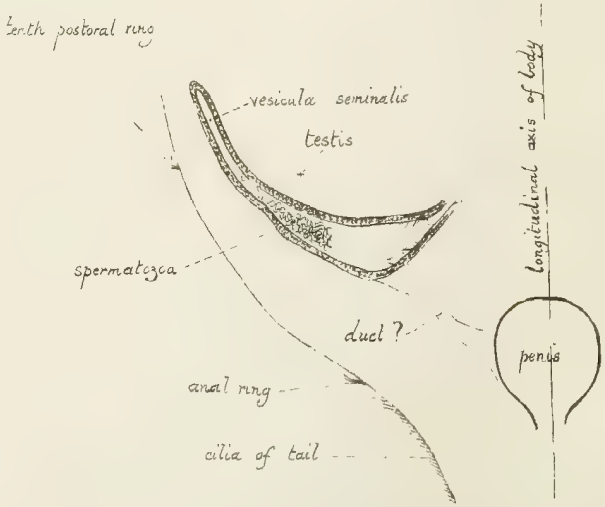

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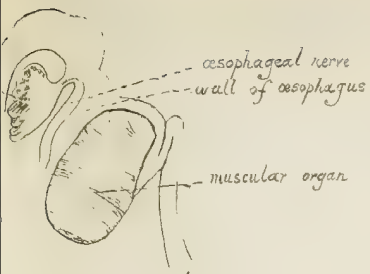


Fig. 6.

3

Fig. 7.

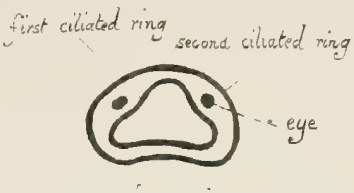
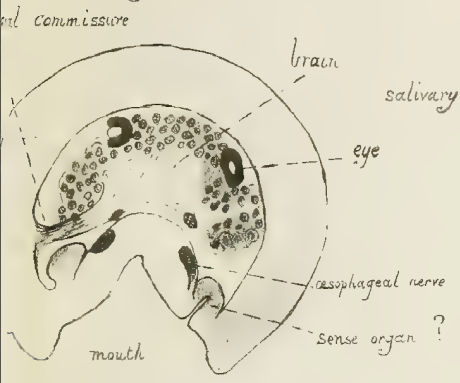


Fig. 8.



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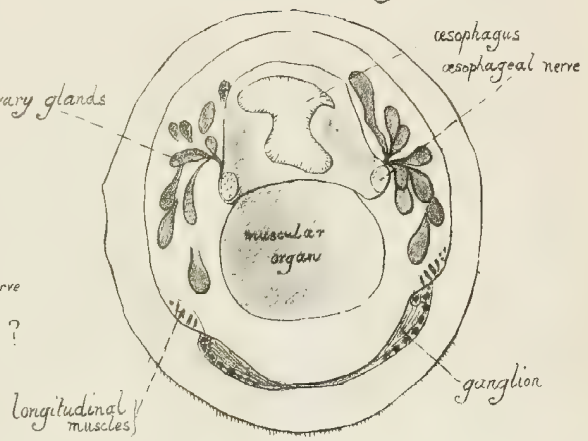

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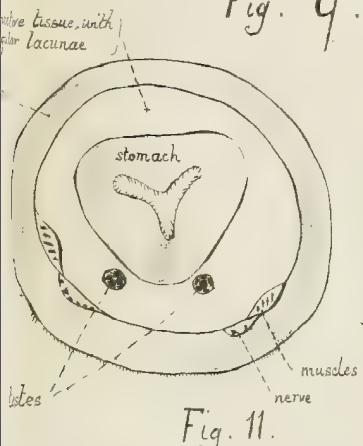

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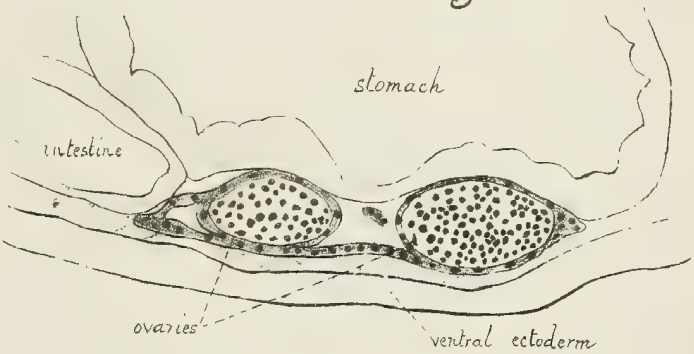

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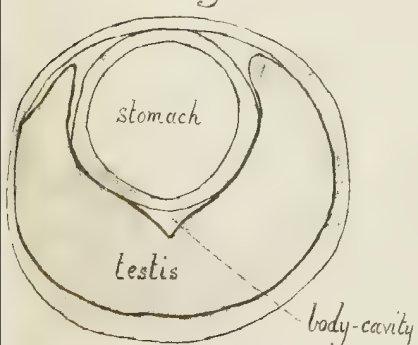

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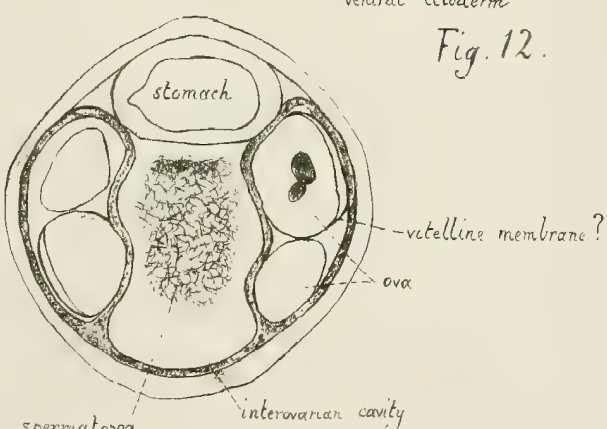

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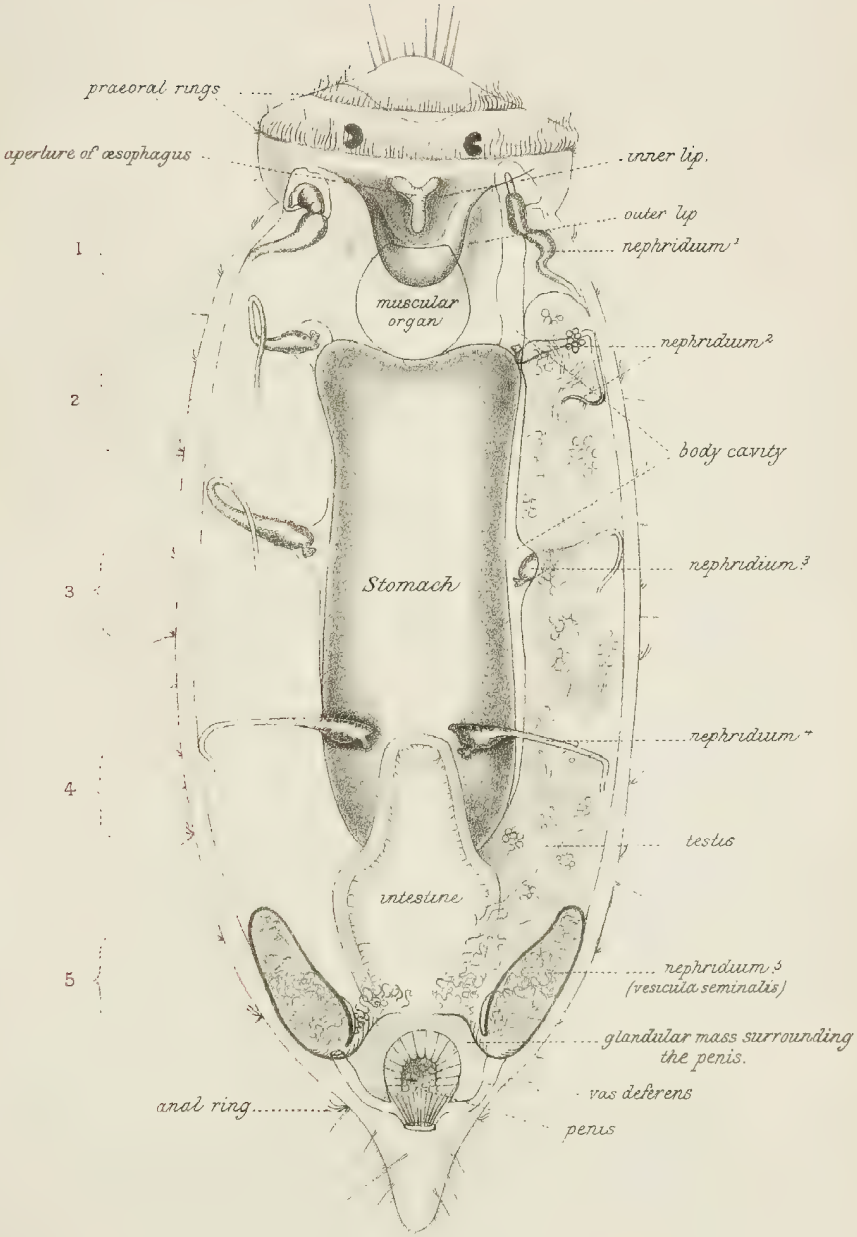

praeoral rings
aperture of œsophagus
inner lip.
outer lip
nephridium 1
1
muscular organ
nephridium 2
2
body cavity
Stomach
nephridium 3
3
nephridium 4
4
testis
intestine
5
nephridium 5 (vesicula seminalis)
glandular mass surrounding the penis.
vas deferens
anal ring
penis

Fig. 15.

Fig. 1.

Fig. 2.

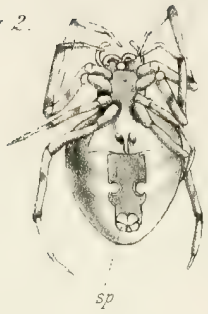


Fig. 3.

Fig. 8.

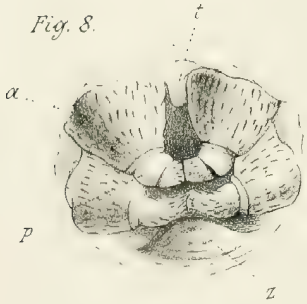
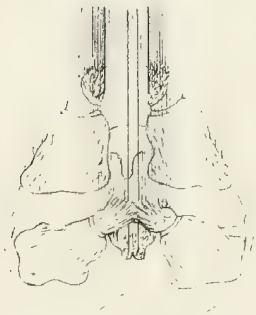


Fig. 9.

Fig. 13.



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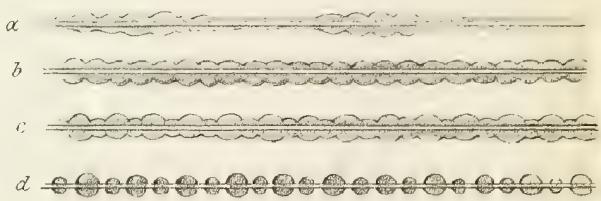

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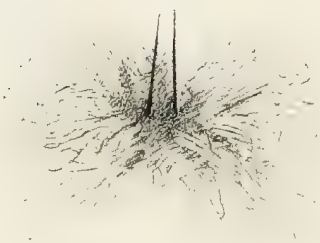

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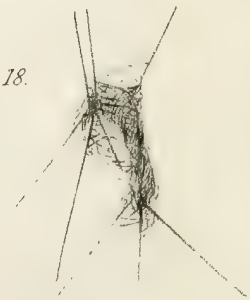

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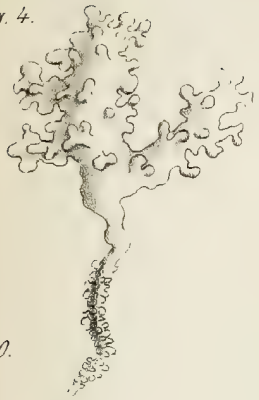


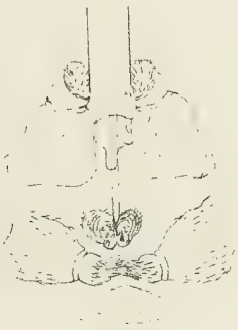
Fig. 5.

Fig. 6.

Fig. 7.

Fig. 10.

Fig. 11



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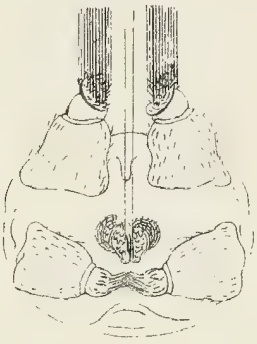


Fig. 15.

Fig. 17.

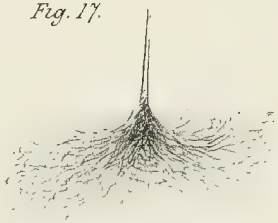


Fig. 19.

Fig. 20.

F. Huth, Lith^r Edin^r

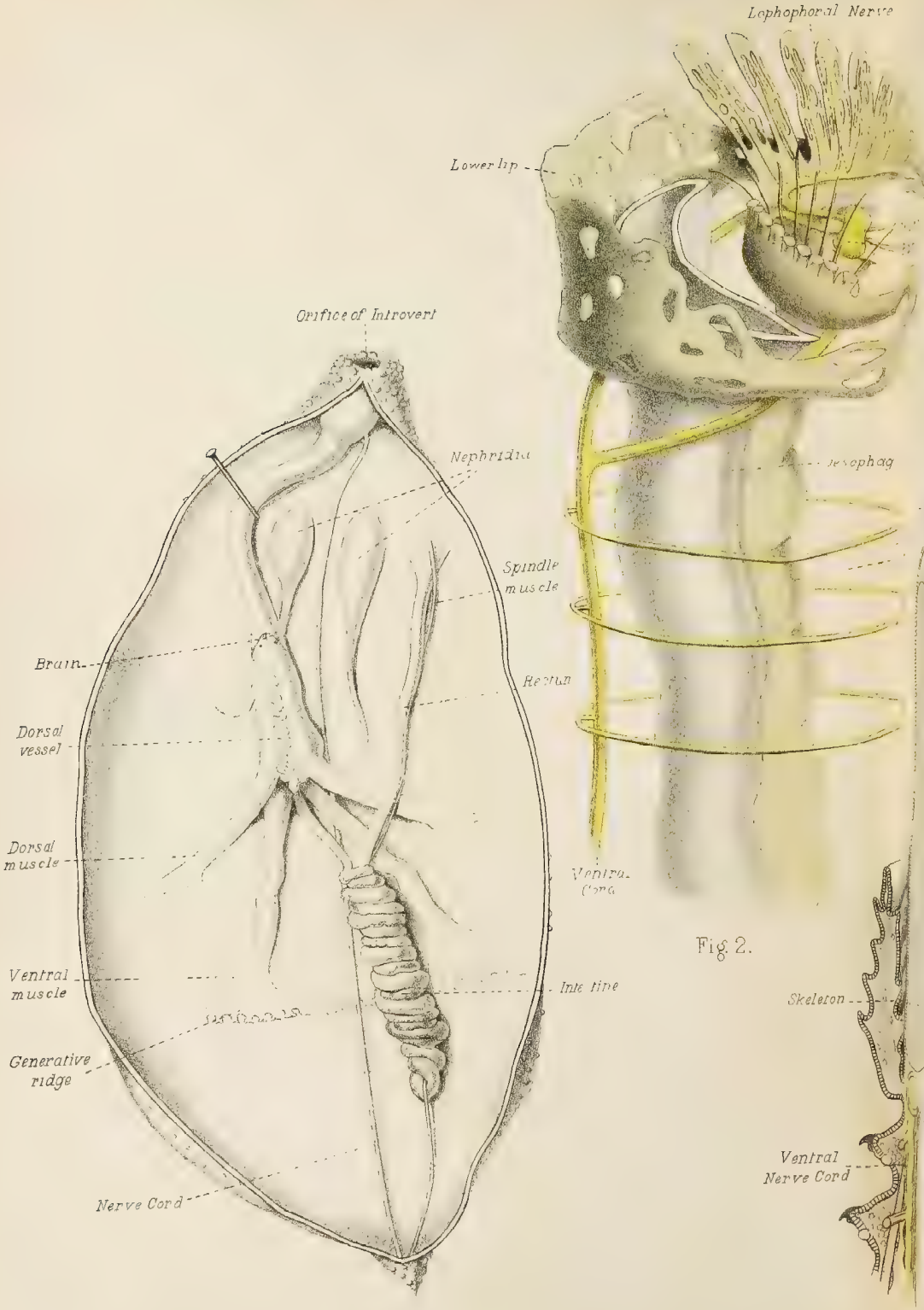
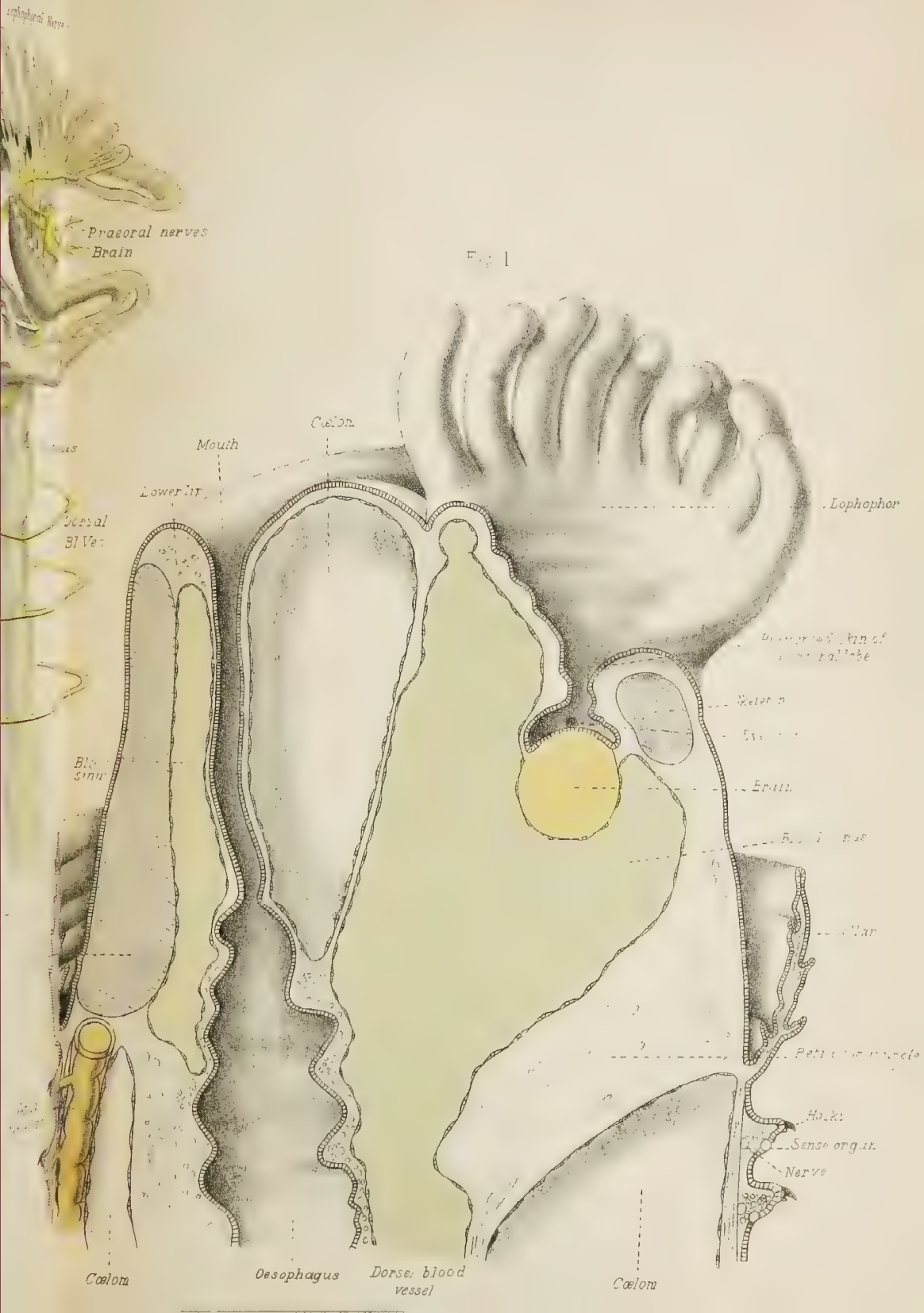

Lophophoral Nerve
Lower lip
Orifice of Introvert
Nephridia
Spindle muscle
Brain
Rectum
Dorsal vessel
Dorsal muscle
Ventral muscle
Intestine
Generative ridge
Nerve Cord
Oesophag
Ventral Cord
Skeleton
Ventral Nerve Cord

Fig. 3

Fig. 2.


Praeoral nerves
Brain
Fig. 1
Cœlom
Mouth
Lophophor
Brain
Hooks
Sense organ
Nerve
Cœlom
Oesophagus
Dorsal blood vessel
Cœlom

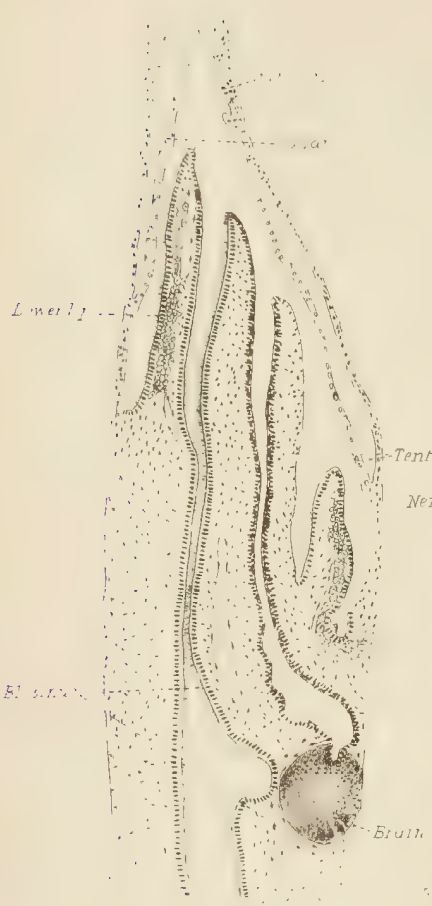


Fig. 4

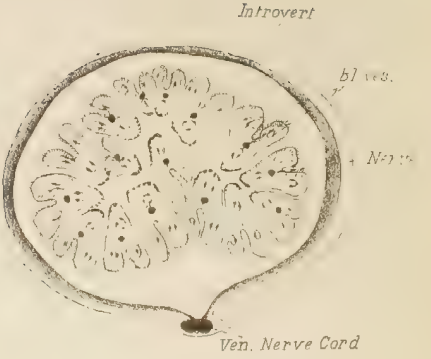


Fig. 5

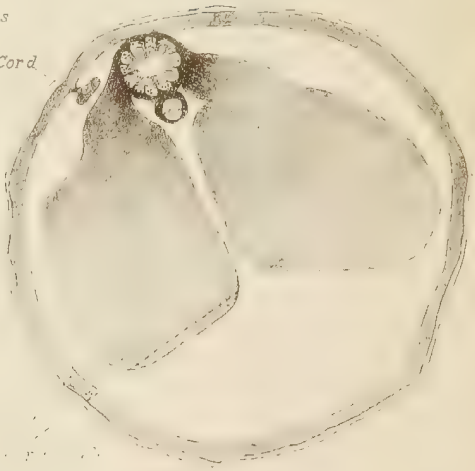


Fig. 3

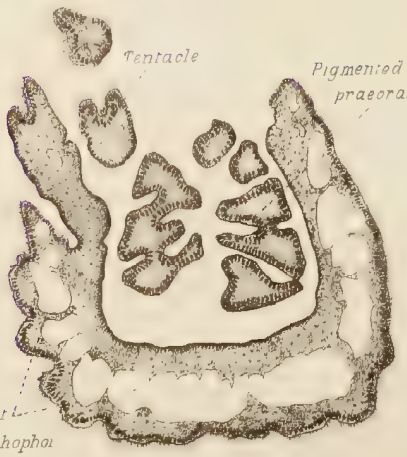


Fig. 7

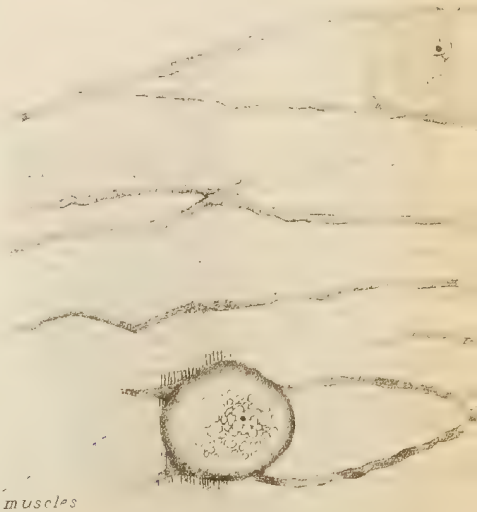
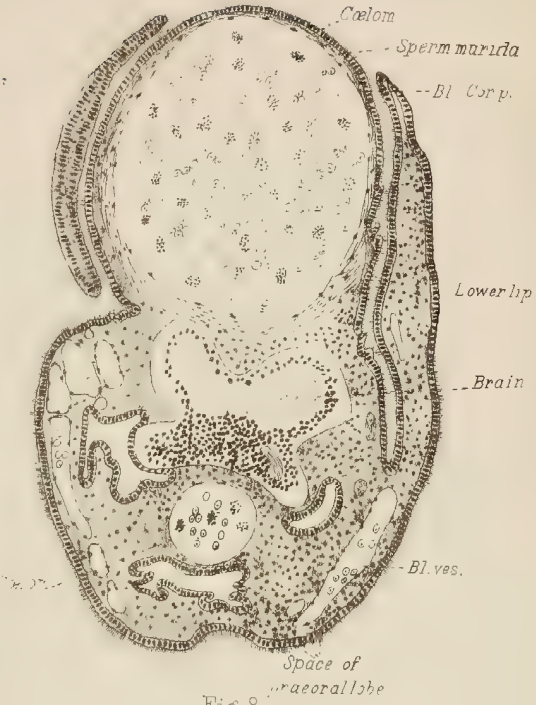


Fig 11

Fig 6



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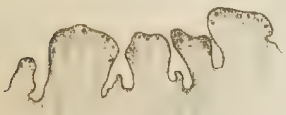

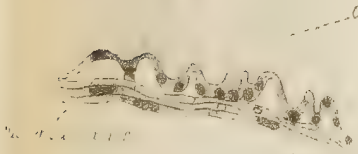

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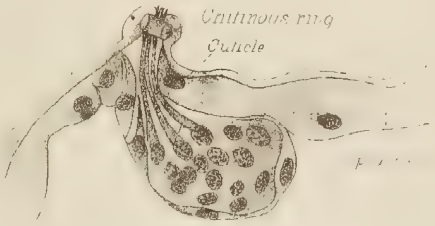

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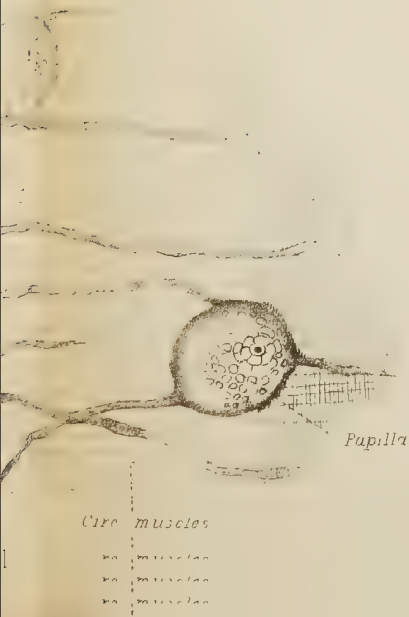


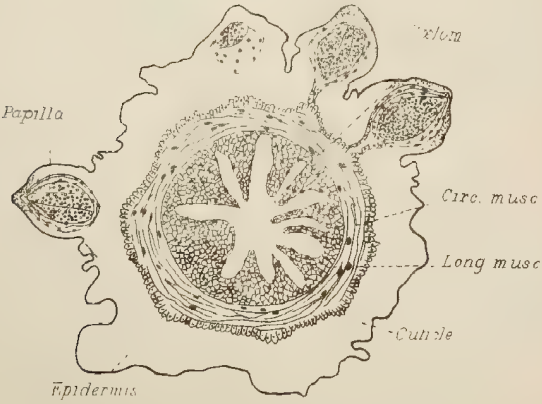


Fig 13

Lith. & Imp. Camb Sci. Inst Co.

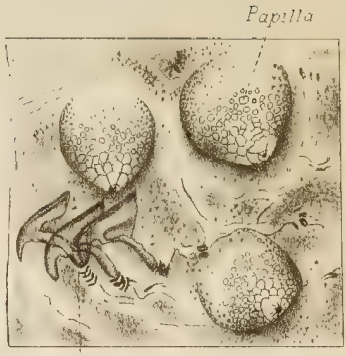


Fig 15

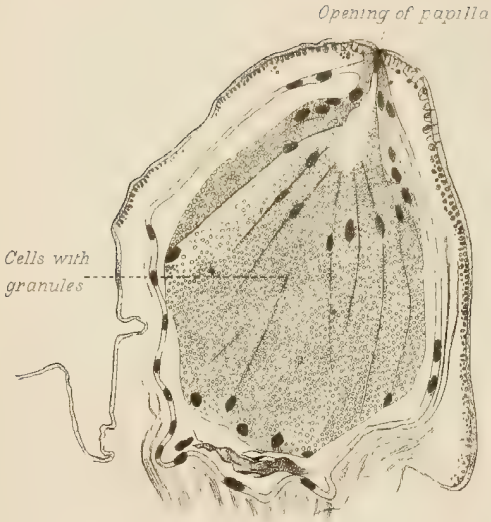
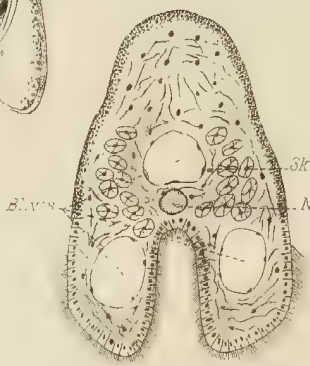


Fig 14



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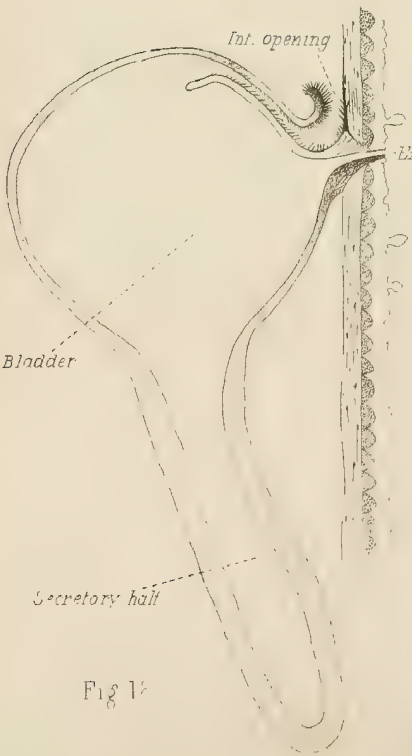

Fig 1½

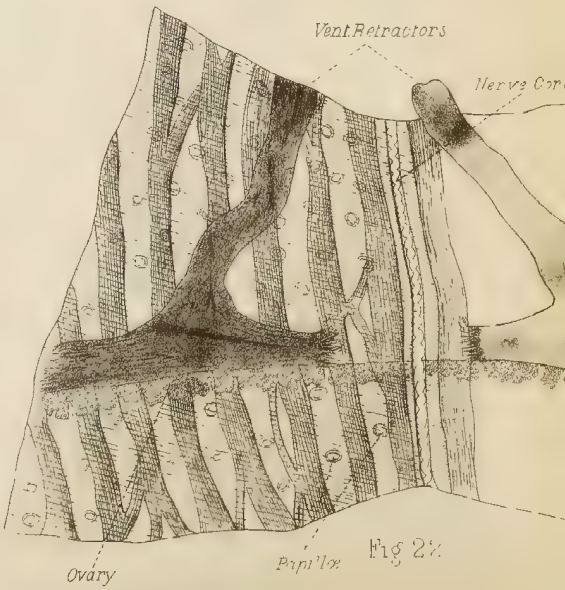

Fig 2½

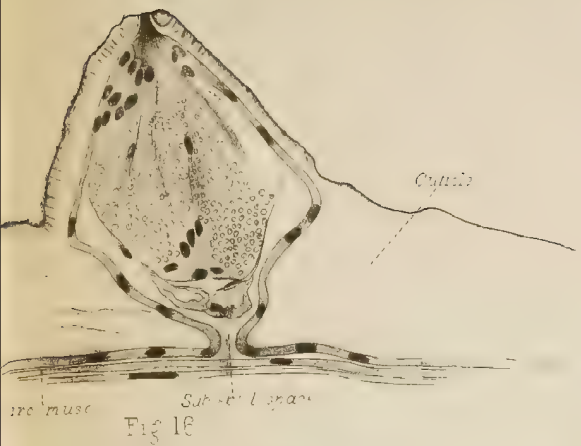

Fig 18

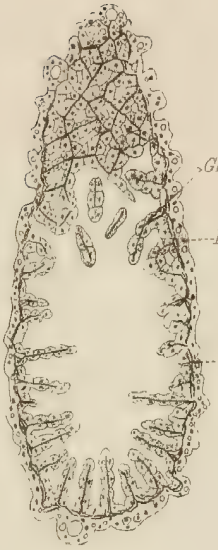

Fig 19

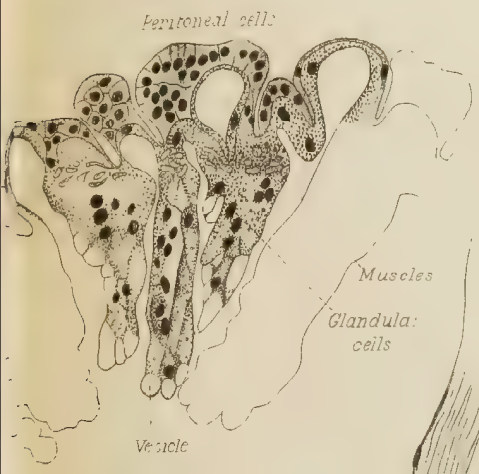

Fig 20

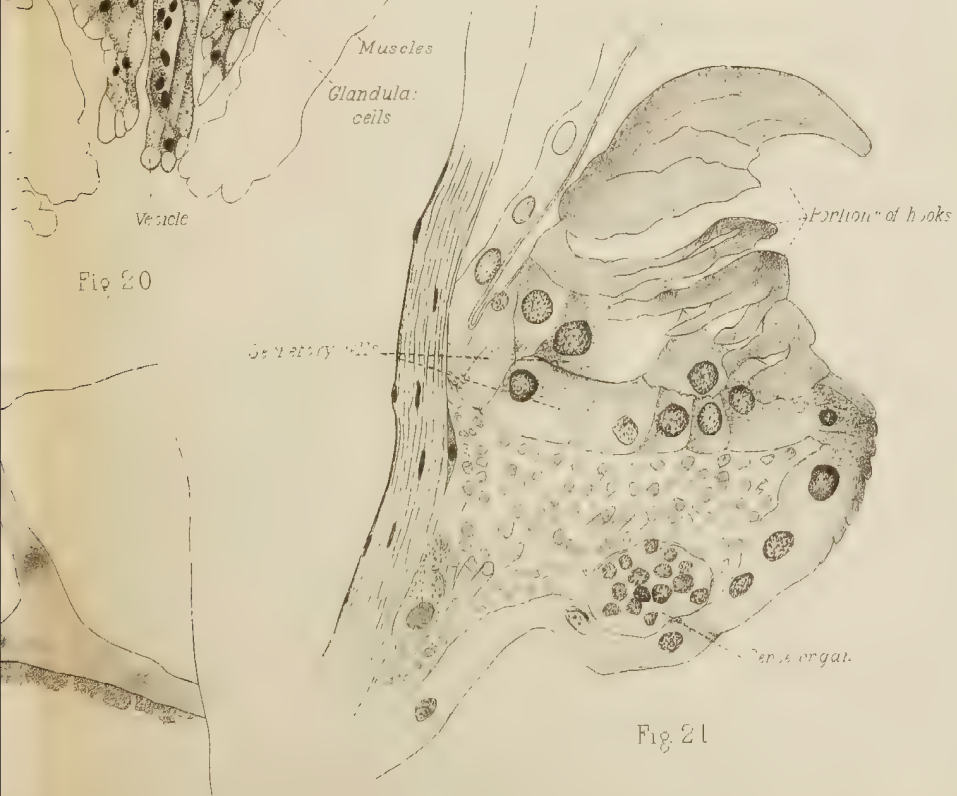

Fig 21

Lith & Imp. Camb. Sci. Inst Co.

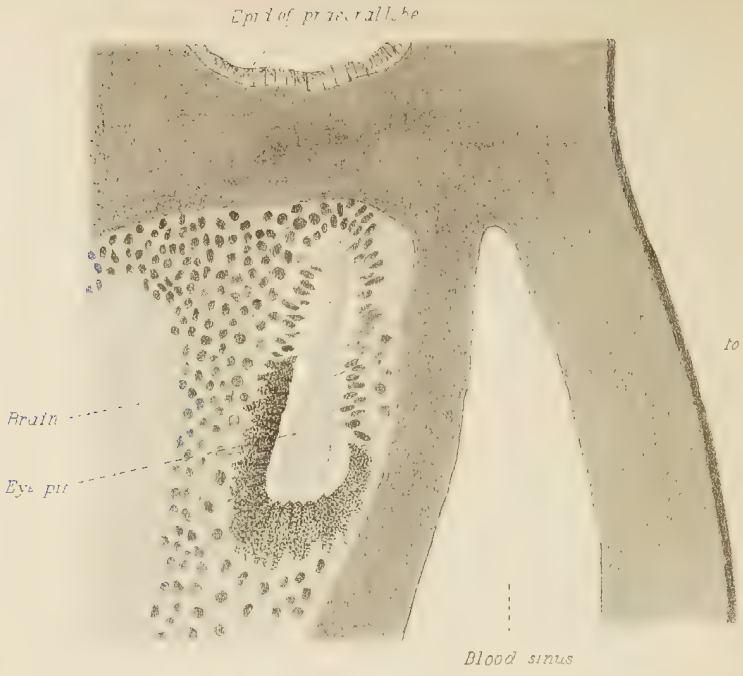

Fig 23.

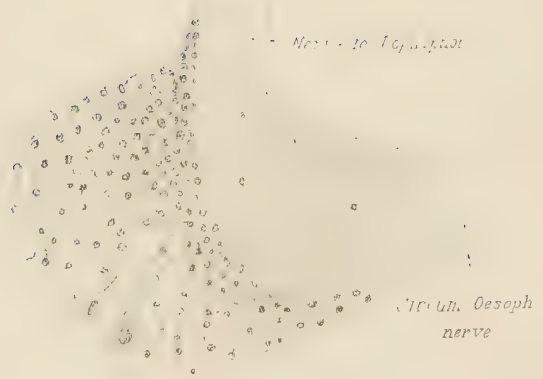

Fig 24

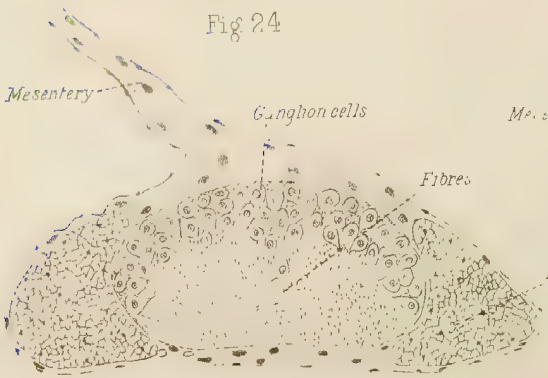

Fig 29

Fig 28

Fig 28

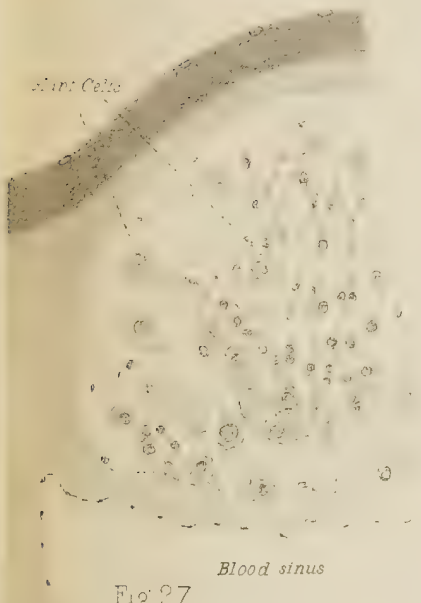

Fig 27.

Fig 29

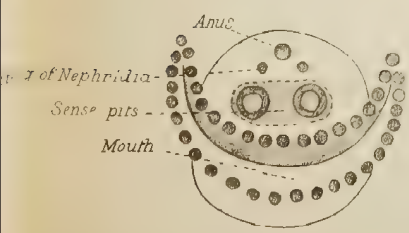

Fig 31

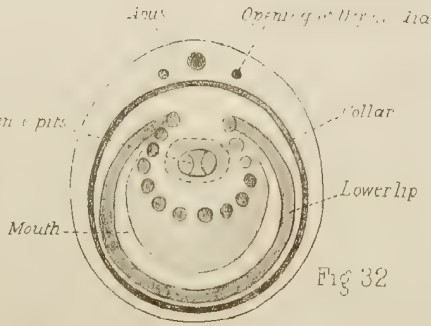

Fig 32

Lith. & Imp. Camb. Sci Inst Co.

On the British Species of Crisia.

By

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Fellow and Lecturer of King's College, Cambridge.

With Plate XI.

This paper will be followed by a further memoir, which will treat of the development of the ovicells and of the embryos in Crisia. I have already published a preliminary note[1] on this subject, and I hope to be able to complete the preparation of the more detailed paper without much delay.

It has often been pointed out that the subdivision of the Cyclostomatous Polyzoa into genera and species is attended with peculiar difficulties. The character of the zoœcia remains remarkably constant throughout this group, the systematic study of which is not facilitated by the presence of subsidiary structures, such as the opercula, avicularia, and vibracula, which in the Cheilostomata form so valuable a means of distinguishing the species.

The task of finding satisfactory specific characters within the limits of the genus Crisia is not less difficult than in other genera of Cyclostomata, as is seen clearly enough by examining the numerous works which have already been devoted to this genus. Smitt, for instance, in his critical analysis of the Scandinavian forms, has asserted that the delicate C. geniculata is connected by a continuous series of intermediate forms with the coarse form which he calls C. denticulata, and which he regards as the extreme point which has

[1] 'Proc. Cambridge Philosoph. Soc.,' vol. vii, part 2, 1890, p. 48.

been reached in the evolution of the genus. In his later works he consistently refers to the latter "species" as Crisia eburnea, forma denticulata, and is of opinion that the "species" recognised by other authors are, for the most part, merely partially fixed points in a continuous series. Most other writers, on the contrary, regard these forms as so many distinct species.

In many of the characters used for distinguishing the several species of Crisia from one another—such as the mode of branching, the number of zoœcia in an internode and their individual shape, the position of the ovicells, &c.—each species may vary within wide limits about a certain average. The most satisfactory specific characters appear to me to be furnished by the ovicells; and in this respect I am only confirming the results previously arrived at by Waters[1] for other Cyclostomata. Indeed, I believe that in many cases the species cannot be certainly identified unless ovicells are present. Unfortunately, in the great majority of works referring to Crisia, the information given with regard to these structures is of the most unsatisfactory character. Many writers, for instance, have mentioned the existence of "pear-shaped" ovicells in certain species; but this character is of generic much more than of specific importance, and the same remark might be made with regard to many of the other characters which have been ascribed to the different species.

The importance of the form of the aperture of the ovicell, as a specific character, has almost entirely escaped the notice of previous writers.[2] Busk[3] has merely stated that the existence of a tubular aperture on the ovicell is a generic character of Crisia.

[1] "Ovicells of Cyclostomatous Bryozoa," 'Linn. Soc. Journ. Zool.,' vol. xx, p. 275, and in other places.

[2] Waters has, however, called attention to the importance of this character in several works. See 'Quart. Journ. Geol. Soc.,' vol. xl (Nov., 1884), p. 676.

[3] "Report on the Polyzoa," Second Part, '"Challenger" Rep., Zool.,' vol. xvii, part 50, p. 2.

A comparison of the ovicells (and especially of their apertures) of various forms of Crisia has led me to the conclusion that the British fauna includes more species of that genus than are usually recognised. Although the constant occurrence of a particular form of ovicell might possibly be explained by the assumption of a definite correlation between the variations of the zoœcia and of the ovicells (the ovicell being regarded as a modified zoœcium), I do not think that this would give a sufficient explanation of the facts. I find, indeed, that the essential characters of the ovicells are extremely constant, in spite of the occurrence of variations of no inconsiderable magnitude in other parts of the colony.

The following specific diagnoses, which are necessitated by the results which I have arrived at, have been drawn up on the model of those given by Hincks in his well-known 'History of the British Marine Polyzoa.' New lists of synonyms appear to me to be also necessary, in spite of the recent appearance of Miss Jelly's admirable catalogue,[1] to which I must express my great indebtedness. My lists do not profess to be more than a selection of those works in which particular species have been described or figured in sufficient detail to make their identification fairly probable. In many cases I have been obliged to give up the attempt to identify the species to which the description refers.

C. denticulata, Lamarck. Plate XI, figs. 1—3.

Zoarium large, erect, of rather straggling habit; the average height of well-grown colonies about one inch; the branches well separated from one another, and with very little tendency to curve inwards. Internodes broad and flattened, but usually with a slight convexity running longitudinally along their anterior face, frequently with a double curve of such a character that if the lower part of the internode is convex towards the right side (e. g.) the upper

[1] E. C. Jelly, 'A Synonymic Catalogue of the Recent Marine Bryozoa,' London, 1889.

part is convex towards the left side; in most cases with an odd number of zoœcia, the dominant number of which appears to be 11. Branches arising fairly high in the internode, usually from the 3rd, 4th, or 5th zoœcium of either side; nearly always given off in perfectly regular alternation on opposite sides of the axis. Each internode with an odd number of zoœcia is normally provided with a single branch, while the even-numbered internodes are, with rare exceptions, branchless. Joints of the zoarium and of the rootlets nearly always jet-black, except in the youngest parts of the colony. Basis rami situated very low down on the zoœcium, and appearing as if wedged in between the zoœcium which bears it and the next zoœcium below it on the same side. Zoœcia entirely adnate with the exception of a short portion, of variable length, which bears the aperture, and which is bent forwards; a pointed projection sometimes occurring at the outer and upper angle of the aperture. Ovicell large, always high in the internode, usually near the end of a branch, and, like the zoœcia, more thickly covered with pores than in the other British species; its aperture inconspicuous, not borne on a prominent tube. Rootlets usually with black joints, which occur at more frequent intervals than in C. ramosa. (See also measurements on p. 159.)

C. luxata.—

(1) Fleming.—'Hist. of Brit. Animals,' Edinburgh, 1828, p. 540.

(2) Couch.—'Cornish Fauna,' part iii, Truro, 1844, p. 99, pl. xviii, fig. 3.

C. denticulata.—

(3) H. Milne-Edwards.—"Mém. sur les Crisies," 'Ann. Sci. Nat.,' 2e sér., 'Zool.,' tome ix, 1838, pl. vii, fig. 1.

(4) Johnston.—'Brit. Zoophytes,' 2nd ed., London, 1847, p. 284, pl. l, figs. 5, 6.

(5) Carus.—'Prodromus Faunæ Mediterraneæ,' vol. ii, Stuttgart, 1889, p. 39.

C. denticulata (pars).—

(6) Busk.—'Cat. Marine Polyzoa Brit. Museum,' part 3, 1875, pl. iv, figs. 1—4.

(7) Hincks.—'Hist. Brit. Marine Polyzoa,' London, 1880, p. 422, pl. lvi, figs. 7, 7*a*.

C. eburnea, Linn. Plate XI, fig. 6.

Zoarium forming dense tufts, usually attached by a single stem, the base of which does not, in most cases, develop many rootlets; the average height of well-grown colonies from ½ to ¾ inch; the branches characteristically curved inwards. Internodes usually short, somewhat flattened; in most cases with an odd number of zoœcia, the dominant numbers being 5 and 7. Branches generally arising from the lowest zoœcium in an internode, sometimes higher up; one branch is normally developed from each odd-numbered internode, even-numbered internodes being ordinarily branchless. On the main stem or the principal branches, the branches come off in regular alternation on opposite sides: nearer the growing-points, they are arranged in compound helicoid cymes, of the formula[1]—

$$(n + r_1) +$$
$$\quad \lfloor = (n + r_1) +$$
$$\qquad \lfloor = (n + r_1) +$$
$$\qquad\qquad \text{\&c.}$$

Joints yellow, or colourless near the growing-points, sometimes becoming dark brown in the older parts of the colony. Basis rami short, not wedged in between two zoœcia. Zoœcia almost entirely adnate, the upper portion, which bears the aperture, free, bent forwards nearly at right angles to the lower part; frequently a conspicuous pointed process on the outer side of the aperture. Ovicell large, curved inwards, usually replacing the second, or, less often, the third zoœcium of an internode; its aperture conspicuous, elongated from side to side, borne on a very distinct tube, which is wider at its base than at its summit. Rootlets usually developed in very small numbers. (See also measurements on p. 159.)

C. eburnea.—

(4) Johnston.—P. 283, pl. l, figs. 3, 4.

(5) Carus.—P. 38.

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[1] This method of representing the branching is explained on p. 146. In the above formula n would usually be 5, less often 7 or higher numbers.

(8) Smitt.—"Om Hafs-Bryozoernas utveckling och fettkroppar," 'Öfvers. af K. Vet.-Akad. Förhandl.,' 1865, No. 1, p. 9, pl. i, figs. 15—18.

C. eburnea (pars).—

(9) Smitt.—"Krit. förteckn. öfver Skandinaviens Hafs-Bryozoer," I, 'Öfvers. af K. Vet.-Akad. Förhandl.,' 1865, No. 2, pl. xvi, figs. 10, 11, 13—19.

(6) Busk.—Pl. ii, figs. 1, 2; pl. v, figs. 1, 2.

(7) Hincks.—P. 420, fig. 21 (p. 416).

C. eburnea, forma eburnea.—

(10) Smitt.—"Bryozoa marina in regionibus arcticis," 'Öfvers. af K. Vet.-Akad. Förhandl.,' 1867, No. 6, pp. 444, 461.

(11) Smitt.—"Recensio Syst. Bryozoorum Novaja Semlja," ibid., 1878, No. 3, p. 12.

(12) Smitt.—"Recensio Bry. e mari arctico," ibid., 1878, No. 7, p. 23.

(13) Freese.—"Beschr. Ostsee Bryozoen," 'Arch. f. Naturg.,' 54, Jahrg., Bd. i, 1888, p. 31, pl. ii, fig. 18.

C. aculeata, Hassall. Pl. XI, fig. 4.

Zoarium of very delicate habit, resembling that of the next species, from which it may be distinguished by its much slenderer appearance; the average height of well-grown colonies from ½ to ¾ inch, the branches with very little tendency to curve inwards. Internodes usually short, often consisting of five or seven zoœcia; but much longer internodes, with more numerous zoœcia, may occur, especially at the ends of the branches. Branches usually arising from the 1st or 2nd zoœcium of either side of an internode, but sometimes (especially in the case of internodes near the ends of the branches) higher up: an internode (especially a peripheral one) may bear two or more branches. In nearly all colonies, in addition to the ordinary branches, some of the internodes bear long, jointed spines, which are curved inwards over the anterior side of the branch; these spines are most often developed from the lower zoœcia of an internode, or at the apices of the terminal internodes. Joints yellow, or colourless near the growing-points. Basis rami usually short, not wedged in between two zoœcia. Zoœcia with a conspicuous, free, tubular portion, bearing the aperture; this portion is curved forwards,

but not as in the last species; it is usually lost in the zoœcia of the lower parts of the colony. Aperture circular, with no projection on its outer side. Ovicell small, fairly high in the internode, prominent near its upper end, and falling away very suddenly to the aperture, which lies on the surface of the zoœcium next above the ovicell on the same side of the internode; this zoœcium curves round the back of the ovicell, and always acquires a characteristic relation to the aperture of the latter; this aperture is inconspicuous, and is never borne on a distinct tube. Rootlets resembling those of C. ramosa. (See also measurements on p. 159.)

C. aculeata.—

(14) Hassall.—"Cat. of Irish Zoophytes," 'Ann. and Mag. Nat. Hist.,' vol. vi, 1841, p. 170, pl. vii, figs. 3, 4.

(15) Supp. to 'Cat.,' ibid., vol. vii, 1841, p. 366.

(4) Johnston.—P. 285.

(16) Smitt.—"Bidr. till känn. om Hafs-Bryozoernas utveckling," 'Upsala Univ. Årsskrift,' 1863, p. 3.

Smitt agrees with van Beneden (20) in stating that the ovicells are completely closed.

(17) Joliet.—"Cont. à l'hist. Bryozoaires, Cotes de France," 'Arch. Zool. Exp. et Gén.,' vol. vi, 1877, p. 286.

C. eburnea, var. aculeata.—

(6) Busk.—P. 4.

(7) Hincks.—P. 421, pl. lvi, figs. 5, 6.

(18) Jullien.—"Liste des Bry. rec. à Étretat," 'Bull. Soc. Zool. France,' t. vi, 1881, p. 14.

(19) Vine.—"Rep. on Recent Marine Polyzoa," 'Brit. Association Report,' Aberdeen Meeting, 1885, p. 588.

C. eburnea.—

(3) Milne-Edwards.—Pl. vi, fig. 2.

? (20) P. J. van Beneden.—"Rech. sur l'Anat. . . . . Bryozoaires . . . . Ostende," 'Nouv. Mém. de l'Acad. de Bruxelles,' t. xviii, 1845, pl. iii, figs. 12—16.

Van Beneden states that the ovicells are closed on all sides; and this statement is more likely to have been made of C. aculeata (in which the aperture of the ovicell is very inconspicuous) than of C. eburnea. The specimens figured are by no means unlike C. aculeata, but they have no spines.

? C. eburnea (pars).—

(9) Smitt.—Pl. xvi, figs. 12*a*, 12*b*.

On p. 135 of Smitt's paper it is explained that these figures represent young ovicells (of C. eburnea), without tubular apertures. It may, however, be remarked that an ovicell, with the contents shown in fig. 12*b*, would probably have had a well-developed tubular aperture if it had really belonged to C. eburnea; and, further, that there is evidence (see above, No. 16) that Smitt has worked at the ovicells of C. aculeata. Ibid., table of formulæ, Nos. 2, 3 (see explanation of the formulæ), and probably some of the later formulæ.

? C. denticulata (pars).—

(6) Busk.—Pl. iii, figs. 1—6.

Notice the spine in fig. 6. In the other figures, the character of the branching and of the basal internodes, and the small number of the pores appear to me to prove that this plate does not refer to C. denticulata, and that it probably refers to C. aculeata.

C. ramosa, n. sp. Pl. XI, figs. 10, 11.

Zoarium erect, often of rather straggling habit; the average height of well-grown colonies about $\frac{3}{4}$ inch; the branches (in well-grown specimens) arranged in fan-shaped systems, owing to the large number of branches given off by the terminal internodes, and with little or no tendency to curve inwards. Internodes often much flattened, of very variable length; often very long, and consisting of numerous zoœcia; in this case often with a well-marked double curve, as in C. denticulata (and, to a less extent, in other species Branches developed in greater numbers than in any of the other British species; even in the lower parts of the colony the internodes commonly bear two branches, while the terminal internodes, and especially those which bear ovicells, may give rise to as many as four or five branches, which do not necessarily come off alternately on opposite sides of the stem. The lowest branch of an internode very commonly comes off from the second zoœcium of one side; if the lowest branch arises from the first zoœcium of the internode, the next branch is usually given off by the third zoœcium of the opposite side. Joints yellow, or colourless near the growing-points, never black. Basis rami long, usually reaching the aperture of the

zoœcium next below it on the same side, unless it is borne by the lowest zoœcium of an internode. Zoœcia usually with a long, free, tubular portion bearing the aperture; this portion is distinctly curved forwards, but is usually lost in the older parts of the colony; in other cases this tubular portion is not developed to more than a very slight extent. Aperture circular, without any pointed projection on its outer side. Ovicell very large, and more regularly pear-shaped than in any of the other species; usually a little higher in the internode than in C. aculeata, but in some cases it may occupy as low a position as that of the fourth member of the internode; it is perhaps most commonly in the position of the 6th—8th member; its aperture circular, borne on a long and very conspicuous funnel-shaped tube, which is considerably wider at its summit than at its base. Rootlets often developed in considerable numbers, sometimes attaining a great length (nearly an inch), and composed, for the most part, of long segments, separated by yellow or colourless joints. (See also measurements on p. 159.)

(The following list includes references to several forms of Crisia which, as explained below, I do not believe to be identical with C. ramosa.)

? C. cribraria.—

(21) Stimpson.—"Synopsis of the Marine Invertebrata of Grand Manan [Bay of Fundy]," 'Smithsonian Conts. to Knowledge,' vol. vi, 1854.

This species may be identical with C. ramosa, in which case my own specific name will have to be given up. The zoœcia are described as being "so crowded as to form often two or three longitudinal rows, in which they are usually opposite" (p. 18). I do not see how such a statement could be made of C. ramosa. The figures given (pl. i, figs. 8*a*—*c*), although not unlike that species, are not drawn with sufficient care to enable a satisfactory conclusion to be arrived at.

? C. arctica.—

(22) M. Sars.—"Geol. og Zool. Jagtt. anst. p. en Reise Trondhjems Stift.," Christiania, 1863.

The zoarium of this form is said to reach the height of 30 mm.; the branches and the zoœcia are straight, or nearly straight; the internode possesses, on each side, two to three, often eight to twelve, rarely twenty to twenty-one zoœcia. The species is said to resemble C.

denticulata and C. cribraria. It differs, according to Sars' description, from my own specimens in the following respects.

The zoœcia are fused with one another along their whole length, so that the upper part, with the aperture, is not free. The outer and upper angle of the young zoœcia may bear a small knob (never observed in C. ramosa). The joints are usually uncoloured, but sometimes brown-grey in the older branches (usually yellow in C. ramosa). The ovicells are always in the axils of the branches, and they are not described as having an aperture (which can hardly be overlooked in C. ramosa).

On the whole, Sars' description suggests a form like C. denticulata or C. elongata, M.-Edw. It is, perhaps, the form figured by Smitt (**9**) in pl. xvi, fig. 20. The "basis rami" in this figure is unlike anything I have ever seen in C. denticulata, although resembling that of C. ramosa.

C. eburnea (pars).—

(**2**) Couch.—P. 99.

Some of the larger specimens mentioned by Couch probably belonged to this species: the ovicells are "somewhat urn-shaped with narrow tubular necks, which are not placed in the centre." This description probably refers to C. ramosa, although the "young specimens" in which the branches "all arch inwards" doubtless belonged to C. eburnea. The magnified figure (pl. xviii, fig. 2), which is not good, may be identified as C. aculeata by the presence of a spine; and the figure next to it (natural size) is probably either that species or C. ramosa.

? C. eburnea (pars).—

(**9**) Smitt.—Pl. xvi, fig. 9, and p. 135 (fig. 6). (These figs. may refer to C. aculeata.)

? C. eburnea, var.—

(**6**) Busk.—Pl. v, figs. 5—10.

? C. denticulata (pars).—

(**6**) Busk.—Pl. ii, figs. 3, 4.

(**9**) Smitt.—'Table of Formulæ,' Nos. 14—17, and probably some of the earlier numbers (e.g. 12 and 13), which are said to belong either to C. eburnea or to be transitional from this form to C. denticulata. It is hardly possible that a form with so many branches arising from the same internode as in No. 17, for instance, was really C. denticulata.

(**23**) Smitt.—"Floridan Bryozoa," Part 1, 'Kongl. Svenska Vet.-Akad. Handl.,' B. x, No. 11, 1872, pl. i, figs. 1—5.

I do not feel certain that the form described in (**23**) is really identical with C. ramosa, although it can hardly be regarded as C.

denticulata. The form of the zoœcia is very similar to that found in C. ramosa; but, on the contrary, the ovicells do not agree with those of the latter. If the left side of fig. 5 represents a young ovicell (probably somewhat broken), the ovicells are even less like those of C. ramosa in their early than in their fully developed condition. Is this form possibly identical with the one described by Stimpson (21) under the name of C. cribraria?

(7) Hincks.—P. 423.

The statement that the ovicells of C. denticulata have "a tubular orifice at the top" was possibly made after an examination of C. ramosa; especially as, on the same page of Hincks's work, occurs C. denticulata, var. *α* (to which pl. lvi, fig. 9, presumably belongs); and there can be little doubt that this is really C. ramosa.

C. denticulata, var. tenuis.—

(24) Vigelius.—"Cat. of the Polyzoa ... Willem Barents," 'Nied. Arch. f. Zool. Supplementb.,' i, 1881–2.

This form is said to correspond closely with Hincks's unnamed variety just referred to. It is, however, impossible to accept tenuis as a specific name, since the name C. tenuis had been applied by MacGillivray to an Australian species before the appearance of the paper by Vigelius (see F. McCoy, "Prodromus of the Zool. of Victoria," 'Decade' iv, pl. xxxix, Melbourne, 1879.

? C. fistulosa.—

(6) Busk (non Heller).—P. 5, pl. vi A, figs. 1, 2.

Even if this form is identical with the species under consideration it is better to drop Busk's name, since the specific name fistulosa was originally applied by Heller to a form which is clearly not the one described by Busk (see Waters, No. 25).

Through the kindness of Mr. R. Kirkpatrick I have been enabled to refer, at the British Museum, to a specimen of the form described by Busk; and I have also to thank Mr. Kirkpatrick for having subsequently given me further information on the same subject. The specimen in question is labelled "C. fistulosa, Hell., locality unknown. Lesina?" I am informed by Mr. Kirkpatrick that the label is in Mr. Busk's handwriting, with the possible exception of the last word; and that the specimen is probably really from the Mediterranean.

The specimen in the British Museum is even more like my own species than is obvious from Busk's description, which, in Mr. Kirkpatrick's opinion, was probably taken from that specimen. As many as five branches may come off from the same internode, and some of them higher than the sixth zoœcium, which, according to Busk, is their upper limit. The ovicells, of which only two could be satisfactorily examined, agree fairly well with those of the Plymouth form. Their

diameter is about ·45 mm. Mr. Kirkpatrick further informs me that the distance from aperture to aperture is ·4 mm., and that the total length of the zoœcium is about ·7 mm. Although these numbers are distinctly smaller than the average measurements of corresponding structures in C. ramosa, I am inclined to believe that my own specimens belong to the same species as the one in the British Museum.

Waters (**25**), in 'Ann. and Mag. Nat. Hist.,' 5 ser., vol. iii, 1879, p. 269, pl. xxiii, fig. 4 ("Bryozoa of the Bay of Naples"), identifies C. fistulosa, Busk, with what he calls C. elongata, var. angustata. I cannot, however, believe that C. ramosa is identical with the form described by Waters. Although the number of zoœcia in the internode in C. ramosa may be large, this species could hardly be characterised as having fourteen to twenty-six zoœcia in the internode; nor does the description, "branches arising usually from the fifth to eighth zoœcium of a branch, and at about the same distance a fresh branch grows on the other side," correspond with the branching of C. ramosa. As Mr. Kirkpatrick has pointed out to me, Waters' statement that the zoœcia are ·04 mm. apart was no doubt due to an oversight.

For further remarks on C. fistulosa, Busk, see Vine (**19**), p. 589.

The characters of the ovicell are so constant in my specimens that, taken in conjunction with other facts, I cannot resist the conclusion that this form deserves recognition as a species. Although it is obviously alluded to in some of the works just quoted, I cannot identify it with certainty with any form which has hitherto received a specific name; and I therefore suggest for it the name C. ramosa, in allusion to the large number of the branches given off by a single internode.

C. ramosa has been found in large numbers at Plymouth, where it is certainly the commonest of all the forms of Crisia.

While the identification of fully developed colonies of Crisia —in those cases at least where ovicells are present—cannot often be a matter of doubt, it may be extremely difficult to identify the species to which a small fragment of a colony or a young zoarium belongs. The greatest difficulty is found, in these cases, in distinguishing C. eburnea from C. aculeata, or the latter species from C. ramosa. The characters of the several species can be best brought out by a careful comparison, under a series of distinct heads, of their more obvious external features.

Habit of Zoarium at Different Seasons; Regeneration.

A very slight acquaintance with the British forms of Crisia enables one to distinguish at a glance, in most cases, the species to which a given specimen belongs. C. denticulata is characterised by the coarseness of its general habit; by the regular dichotomous appearance of the branching, as seen by the naked eye; and by the fact that the branches diverge from one another to such an extent that they are separated from one another by considerable interspaces at their ends. In C. eburnea the branches are inflected towards the axis of the colony, and are so closely massed together that it is impossible to study the exact character of the branching without first disentangling the branches. On flattening the specimen out on a slide the cymose character of the branching is at once apparent. C. aculeata possesses a characteristic delicacy of habit ("of a slenderer habit than C. eburnea, which the species closely resembles"[1]); and it may be compared, in external form, to a C. eburnea which has become of much laxer and slenderer habit than usual, and in which comparatively few branches have been developed. The branches are much straighter than in C. eburnea. C. ramosa is extremely similar, in general appearance, to C. aculeata, but is of distinctly coarser habit; the branches are very straight, and the number of the branches to which the internodes near the growing-points give rise results, in actively growing colonies, in the formation of fan-like systems of branches. The long tubular apertures of the zoœcia (if developed) give a characteristic appearance to the species, which cannot, however, in all cases be distinguished by the naked eye from C. aculeata.

The above remarks apply especially to colonies in their fully developed condition; but the appearance of any species depends largely on the time of year at which it was found. Many of the specimens of C. eburnea found in the early spring are provided with numerous ovicells, the ultimate fate of which seems to have hitherto attracted no attention, although

[1] Johnston, G., 'A Hist. of the British Zoophytes,' ed. 2, p. 286.

there can be no doubt that these structures disappear after the end of the breeding season. I have looked in vain for any signs of the absorption of the ovicells in Crisia; and the following facts probably imply that they are simply thrown off from the colony after the liberation of the embryos which have been produced in them.

The typical spring form of C. eburnea possesses a conspicuous main stem, which forms an obvious central axis, from which the rest of the colony comes off as a series of branches, developed in regular alternation on opposite sides, and decreasing in size fairly regularly from the base to the summit of the colony. The main stem consists of perhaps eleven or twelve internodes, each of which normally gives rise to a branch; and the branches themselves are usually provided with a profusion of ovicells, many of which are still in process of development, and most of which are near the ends of the branches.

In a colony of the same species found in May most of the ovicells were at some distance from the ends of the branches, owing to the development of several (7—8) zoœcia above the ovicells; and the branches which bore ovicells had, in most cases, completely finished their growth: very few ovicells, and these of a weakly appearance, were being developed. Most of the branches ended in slender internodes, in which growth was no longer taking place, as was shown by the fact that no growing-points were left. The exhaustion of the colony was further shown by the fact that some of the terminal internodes consisted of no more than two or three zoœcia, with no growing-points.

In the summer (August) large and highly branched colonies with active growing-points are found, but they are normally without any trace of ovicells. In many of these cases it may be noticed that the main stem has been broken, and is merely represented by its basal portion. The rest of the colony will, in this case, probably consist of a small number of large branches given off from the remains of the stem or of its lateral branches, and in many cases the sharp contrast between

the clean white appearance of these highly branched parts of the colony and the dirty-brown appearance of the stump of the main stem, covered as it is by foreign growths of various kinds, will give rise to the suspicion that the former have been developed at a later period than the latter, and that the latter are the remains of colonies which developed ovicells at an earlier period of the year.

Smitt[1] has called attention to the fact that the free tubular portion of the zoœcium of C. geniculata is sometimes relatively transparent, and that it is separated by a sharp line from the basal, more highly calcified part, and he suggests that this transparent portion has in these cases been regenerated. He further points out[2] that in Aetea argillacea (=Aetea truncata, forma abyssicola elongata[3]) this process of regeneration seems to be periodic, since a zoœcium consisting of portions of three different ages was in one case observed by him; and that in Farrella fusca (=Vesicularia fusca[4]) the zoœcium may attain twice its normal length by the occurrence of this regenerative process.[5] Milne-Edwards[6] had previously pointed out that the zoœcia were able to form rootlets at an advanced period of their existence.

There can be little doubt that Smitt's suggestion is a correct one. In C. eburnea the older parts of the colony are frequently covered with an encrusting red seaweed, the presence of which has no doubt been responsible for the "rose-red" colour which has been mentioned by Johnston[7] and others as a feature which sometimes characterises the species. In certain specimens found in April the basal parts of the colonies were completely covered by this encrusting growth, while in various

[1] 'Öfvers. af K. Vet.-Akad. Förhandl.,' 1865, No. 2, p. 128.

[2] "Om Hafs-Bryozoernas utveckling och fettkroppar," 'Öfvers.,' &c., 1865, No. 1, pp. 29, 30.

[3] 'Öfvers.,' &c., 1867, No. 5, p. 280.

[4] 'Öfvers.,' &c., 1866, pp. 502, 505.

[5] Ibid., pl. xiii, fig. 39, and explanation of figure.

[6] 'Ann. Sci. Nat.,' 2e sér., "Zool.," tom. ix, 1838, p. 196.

[7] 'British Zoophytes,' ed. 2, p. 284.

parts perfectly white growing points or new apertures were making their appearance. Similar phenomena of regeneration have been repeatedly observed in all the species which I have examined. Thus the first glance at an ordinary colony of C. ramosa will suffice to show that the tubular ends, so characteristic of the young zoœcia, are absent in the lower parts of the colony, where they have been either broken off or absorbed. The zoœcia which are in this condition are closed by an obliquely placed diaphragm, as described in Crisia and other Cyclostomata by Waters,[1] Pergens,[2] and others. On staining a specimen of C. ramosa without decalcification, it is at once obvious that these diaphragms are used for the closure of zoœcia which contain brown bodies but no functional polypides. They are placed at the point where the zoœcium normally becomes free from the internode, and the free portion becomes gradually broken away or absorbed down to the point where the diaphragm is situated. In the younger parts of the colony, where the zoœcia possess free tubular ends, no diaphragms are present, and functional polypides or obvious buds, together with the brown bodies formed by the death of the last polypides, are found in nearly all the zoœcia.

The individual life of the zoœcium has not, however, necessarily come to an end with the formation of one of these diaphragms, as may be easily proved by the examination of suitable spring colonies which have been stained with borax carmine without decalcification. Whilst zoœcia in which no regeneration is taking place are closed by a diaphragm and appear perfectly unstained, the red colour of the regenerating parts is obvious at the first glance. The first indication of the renewed activity of a zoœcium is given by the fact that some of the cells below the diaphragm have acquired the power of

[1] A. W. Waters, "Closure of the Cyclostomatous Bryozoa," 'Linn. Soc. Journ. Zool.,' vol. xvii, 1884, p. 400; "Fossil Cyclostomatous Bryozoa from Australia," 'Quart. Journ. Geol. Soc.,' vol. xl, 1884, p. 675.

[2] Ed. Pergens, "Revision des Bryozoaires du Crétacé figurés par d'Orbigny," 1e partie, "Cyclostomata," 'Bull. de la Soc. Belge de Géol.,' &c., tome iii, 1889, p. 317.

taking up colouring matters; slightly later a young polypide bud is seen below the diaphragm, which is then absorbed, the zoœcium growing out (in C. ramosa) into a long tubular portion, at the end of which is the aperture.[1] In C. ramosa the free portions of regenerated zoœcia are sometimes considerably longer than the normal length of the tubular portion. In one case the regenerated portion, which was completely free from the branch, was ·69 mm. long.

It is well known that new stems are given off from various parts of the rootlets.[2] These rootlets are usually developed from the backs or sides of the zoœcia, especially of those near the base of the colony. But in cases where regeneration is actively taking place the tip of a branch may grow out into a rootlet, or a rootlet may take the place formerly occupied by a zoœcium, usually one of the terminal zoœcia of an internode in this case.[3] The rootlet thus formed may grow for a considerable distance, and finally produce a new stem as a lateral branch; or the new stem may be the actual prolongation of the rootlet, which, after a longer or shorter course, assumes the characters of a stem. In other cases a new growing-point is formed from an old joint at the point where a lateral branch or an axial internode has previously been lost; or it may be formed from the apex of an internode in which the fracture has taken place across the middle of the internode, instead of at an axial joint. The result of this is that it is very common to observe an old brown stem from which start new internodes (lateral or axial), which are shown, by reason of the perfectly white appearance of their ectocyst, to have been formed at a much later period than the brown part of the stem. In one or two cases a growing-point had started from the proximal side of a broken joint, and had then given rise to a stem which grew in a direction directly opposite to that of the internode from which it was developed. These cases are somewhat analogous to the

[1] This is the process which was observed by Smitt in C. geniculata.

[2] Cf. Smitt, "Krit. Fört.," i, 'Öfvers.,' &c., 1865, p. 122.

[3] These statements refer, for the most part, to C. eburnea and to C. ramosa.

one described by Smitt,[1] in which a "basis rami" had given rise to a normal branch, and also to a growing-point directed straight downwards from its base, which was formed by the proximal end of the "basis rami," from which it was separated by a joint.

Although regenerated lateral branches may start from the old lateral joints, it is not uncommon to find that they are given off from near the end of the old internode, instead of in their normal position lower down; this is due to the fact that the aperture of an old zoœcium has become a growing-point.

In colonies in which the process of regeneration is commencing, it is frequently noticed that the young growing-points are appreciably smaller than the normal ones. These small growing-points naturally give rise to slender zoœcia and branches, which, however, as they grow longer, acquire fresh strength, and soon regain their normal diameter. The regenerated parts of a colony are, consequently, often joined to the older parts by slender bases, in which, moreover, the basal internodes may consist of an unusually small number of zoœcia. In both these respects they resemble colonies which are developed directly from the larva, or from a growing-point which starts from the rootlet of an old colony.

It is important to notice that, so far as my observations go, the regenerated parts of a colony always retain the same specific characters as the older parts. I have looked in vain for any indications which might have been given by regenerating colonies that the forms of Crisia described above as distinct species might be merely different phases of the same species.

The general life-cycle of C. eburnea may probably be summarised as follows:—The breeding season is at its height in April and May; and at about this period it is not difficult to find young individuals which consist of a single zoœcium attached by a disc-like base, and which have resulted from the metamorphosis of a free larva; small colonies are soon formed by these primary zoœcia. At first, rootlets may be altogether absent, and in many colonies they are developed very sparingly;

[1] Loc. cit., p. 125.

but when formed, some of them give rise to fresh stems, which are the starting-points of new colonies. Or, again, some of the specimens found in the summer have resulted from colonies which developed ovicells in the earlier part of the year, and which, after losing these structures, again burst out into renewed growth; in some cases leaving a single ovicell on the colony as some indication of their past history. In the spring, ovicells, when present at all, are found in large numbers, and those well-developed colonies which do not possess them at this period are probably in most cases of the male sex. Thus, in order to find spermatozoa in April, it was generally quite sufficient to select any colony in which there were no ovicells, while spermatozoa were not discovered in any of the cases in which ovicells were present.

In the early spring the discoloured stumps of colonies which grew during the preceding year are found; from various parts of these, new growing-points are developed, and give rise to the colonies found at a slightly later period. The production of the enormous number of embryos then developed seems to exhaust the energy of the colony, whose growth practically ceases for a time, many of the branches being thrown off. After a period of rest, growth recommences with great vigour, and by the middle of the summer large and highly branched colonies are again found, although now, as a rule, with no ovicells.

Number of Zoœcia in the Internode, Mode of Branching, &c.

Most of the previous accounts of Crisia merely mention the limits between which the number of zoœcia in the internode may vary in the several species. Thus Hincks[1] says of C. eburnea, "3—9 cells in an internode;" while Johnston[2] is a little more explicit, stating that "there are from two to five, sometimes seven, and very rarely even nine, cells in each internodial space" in the same species. It appears to me that it is quite impossible to define accurately the several species

[1] 'British Marine Polyzoa,' p. 421.

[2] 'British Zoophytes,' ed. 2, p. 284.

without paying careful attention both to the number of zoœcia in the individual internodes and to the character of the branching. Smitt[1] is the only writer who has done this in a thoroughly satisfactory manner, and it will be convenient to make use of a modification of a graphic method of representing the characters of the colony which he was the first to introduce.[2]

In this method the limits of each internode are indicated by brackets, in which is a number denoting the number of zoœcia in the internode; r indicates a branch, the position of which is further shown by means of a number: thus ${}_1r$, e. g., indicates a branch given off from the first (lowest) zoœcium of an internode on the left side, while r_2 indicates a branch given off from the second zoœcium on the right side of the internode; finally x indicates the growing-point, and *Ov.* an ovicell. A key to the method may be obtained by referring to fig. 6, the formula of which is included on the formula on p. 154, as explained on that page.

Thus many of the characteristic features of C. denticulata (figs. 2, 3) may be represented by the formula—

$$(8)+(9+{}_3r)+(10)+(9+r_2)+(9+{}_3r)+(11+r_4)+(11+{}_3r)+(13+r_5)+(9+{}_3r)+(8+x)$$
$$=(13+{}_5r)+(10)+(7+r_2)+(4+x)$$
$$=(5+x)$$
$$=(11+{}_5r)+(3+Ov.+5+r_4+x)$$
$$=(x)$$
$$=(11+{}_4r)+(x)$$
$$=(4+x)$$
$$=(11+r_5)+(10)+(11+{}_4r)+(8)+(x)$$
$$=(5+Ov.+2+{}_3r+x)$$
$$=(3+x)$$
$$=(10)+(9+r_2)+(5+Ov.+5+x)$$
$$=(9+Ov.+6+r_4+x)$$
$$=(8+x)$$

[1] 'Öfvers. af-K. Vet.-Akad. Förhandl.,' 1865, p. 115.

[2] Loc. cit., p. 139.

—representing the axis of a branch given off by the main stem of a colony, together with all the ramifications of two of its secondary branches.

It will be noticed that nearly every internode develops a single branch, and that the branches come off in regular alternation on opposite sides of consecutive internodes of every axis. Although the number of zoœcia in the internode is very variable, eleven may be regarded as the number most characteristic of the species.

The above formula further shows that every branch-bearing internode whose development is complete possesses an odd number of zoœcia, while in completely developed internodes which bear no branch the number is even. Although this rule is not quite absolute, it is difficult to find any exception to the striking rule that a branchless internode has an even number of zoœcia; or, conversely, that an internode with an even number (whether this number is large or small) of zoœcia bears no branch. It may be pointed out that even if the branches have been broken off, their previous presence can be ascertained by the existence of the basal articulation from which they formerly sprang.

It may further be noted that a lateral branch is, with very rare exceptions, produced on the side of the basal zoœcium of the internode (Pl. XI, fig. 2).

The regular alternation of the zoœcia of the axis of any branch is not disturbed by the development of an axial joint; and the last zoœcium of the internode below the joint nearly always projects beyond the penultimate zoœcium (which belongs to the other side) in the form of a free tube (fig. 2). Since the branch-bearing internode has an odd number of zoœcia, and since the branch is developed on the side of the basal zoœcium, it follows that the last zoœicum, which is produced into a free tube, will also be on the same side as the branch. A moment's consideration will show that the basal zoœcium, the branch, and the terminal ("produced") zoœcium, in any internode, will normally be on the opposite side to that on which these structures are situated, both in

the internode below it and in the internode above it on the stem.

But if an even-numbered internode is developed (fig. 2), its last zoœcium will of course be on the same side of the stem as the last zoœcium of the preceding internode; and consequently the basal zoœcium and the branch of the internode above it will be on the same side as its own basal zoœcium, and on the opposite side to the branch next below it; or, illustrating this by a formula, we shall, as a rule, find cases like $(13+r_5) + (8) + (7+{}_2r)$, as shown in fig. 2.

Thus, stating the same fact in another way, an even-numbered and branchless internode may be intercalated in the stem without disturbing the alternate origin of the branches on opposite sides. The same is true of those cases where two even-numbered internodes occur consecutively on the same axis.

The more closely one investigates unusual methods of branching in this species, the more obvious does it become that the growth of the colony is regulated by some well-defined law, which finds one of its expressions in the preceding rule.

Thus it will be seen, by reference to figs. 2, 4, 6, and 11, that the basal zoœcium of a lateral branch is on the abaxial side of the latter in all the four species referred to; and further, that the branch given off by the basal internode of an axis is also on the abaxial side. This is obvious enough for C. denticulata, from the formula on p. 146, where it will be noticed that, in the one case in which the basal internode has an even number of zoœcia, the second internode develops the first branch, and that that branch (and of course the basal zoœcium) is on the abaxial side.

On two occasions abnormal branching of the type $(9 + {}_3r) + (13) + (11 + {}_3r)$ was noticed. Here an odd-numbered branchless internode occurs; but such cases seem to be rare. Since the number of zoœcia in the branchless internode is odd, it follows that the basal zoœcium, and consequently the branch, of the third internode will be on the same side as in the first internode.

In another case the formula $(15 + r_4) + (9) + (10) + (9 + r_3)$ was obtained, and it is obvious that this is a further illustration of the same principle.

In an axis, part of the formula of which was $(13 + r_5) + (14 + {}_2r + r_5) + (11 + {}_4r)$, one of the internodes had two branches, the first developed on the side of the basal zoœcium, and the second on the opposite side. Since the number of zoœcia in this internode was even, the regular alternation of the branches was not disturbed. Cases of this kind appear to be extremely rare.

Another abnormal case, from a young colony, had the formula—

$$+(5+r_2)+$$
$$\quad\quad\quad

internodes have an odd number of zoœcia, and in which, further, the branch and the basal zoœcium are, in each internode, on the same side. The third internode which is completely figured has 10 zoœcia, and possesses no branch. It must, however, be pointed out that in his fig. 1 *a* (C. denticulata, under slight magnification) Milne-Edwards represents most of the internodes as having an even number of zoœcia; but it may probably be assumed that in this figure, which gives an excellent representation of the general appearance of the species, sufficient attention has not been paid to the details of the arrangement of the zoœcia. Again, Busk[1] figures, in the same species, two complete internodes, one of which has thirteen zoœcia and a branch, and the next has twelve zoœcia and no branch.

The relations above described are perhaps capable of being, to some extent, explained in the following manner. In the species of Crisia which I have examined, and, I have very little doubt, throughout the genus, the base of an internode, whether axial or lateral, is simply the basal part of the lowest zoœcium of that internode, that part having been separated by the development of the joint from its upper or distal part. This will be intelligible on referring to Pl. XI, fig. 1, representing an axial internode in which only two zoœcia are completely separated from the growing-point. The lowest zoœcium of the internode is seen to be divided into two parts by the horny joint; and the lower of these two parts forms the articulation to which the younger internode is attached. In examining the formation of the joint (whether axial or lateral) in stained specimens it is at once obvious that the alimentary canal of the youngest zoœcium of the internode at first extends, through the tubular joint, into this lower portion; confirming the statement made above with regard to the morphology of the base of the internode.

It is thus clear that the occurrence of an axial joint in no ways disturbs the alternation of the zoœcia (see any of the figures). The last zoœcium of the older internode would

[1] 'Cat. of Mar. Pol. in Brit. Museum,' Part III, "Cyclostomata," pl. iv, fig. 2.

overlap, and be fused with the next zoœcium higher up on the same side if it were not for the development of the joint; which is, however, formed in such a position across a zoœcium as to leave the preceding zoœcium in the characteristic "produced" condition which has already been described. In the ordinary type of branching, where successive internodes produce branches in regular alternation on opposite sides, the number of zoœcia must be odd if the branch is to be produced on the side of the basal zoœcium in each internode. The formation of a new axial internode practically amounts to the transverse division of a zoœcium, while the formation of a branch may be expressed as due to the longitudinal division of a zoœcium (at the growing-point). Suppose that the right side of an axis bears a branch (as in the lowest internode shown in fig. 2). The tendency of the growing-point to produce new branches alternately on opposite sides would normally result in the production of a branch from the left side of the next youngest internode; but if a lateral branch has not been produced by the time that a new axial joint is to be formed, that axial joint would be, as a matter of fact, normally developed from a zoœcium of the left side, as at the base of the third internode in fig. 2; and this implies the existence of an even number of zoœcia in the second internode. The production of an even-numbered internode may thus be regarded as due to the alternate predominance of the two sides of the growing-point. The development of a lateral branch on the right side (e. g.) has apparently the effect of leaving the left side of the growing-point with an excess of vigour; so that when a new internode is formed—whether by the transverse division of a zoœcium to form an axial joint, or by its longitudinal division to form a lateral branch—it is the left side (in this particular case) of the growing-point by which this division is effected. Division in the transverse direction results in the formation of an even-numbered internode, while the production of a lateral branch on the left side of the next succeeding internode restores the function of producing another axial joint to the right side of the growing-point.

That there are exceptions to this rule has been shown above by the description of odd-numbered branchless internodes; but it must be remembered that these cases are rare.

From what has already been said of the laws which regulate the growth of Crisia, it is obvious that a representation of a colony can easily be reconstructed from a formula of the character introduced by Smitt; and no further justification is required for the use of such formulæ.

In some specimens of C. denticulata the average number of zoœcia in an internode may be higher than in the one described; and the numbers 13, 15, 17, and even 19 are by no means uncommon. It may often be noticed that, although internodes consisting of any given number of zoœcia do not seem to be arranged in any definite order in the colony, an individual colony may be characterised by the frequent occurrence of internodes with that number of zoœcia. Thus if the dominant number, in any particular case, be 11—and this seems to me the most common case—variations in the number of zoœcia in the internodes of that colony will apparently take place about the number 11 as a mean; so that, although internodes of 9 or 13 zoœcia are common, there may be none of so many as 15 zoœcia. But if the colony have many internodes of 15 zoœcia, for instance, then it will probably be found that some of the other internodes have 17 or 19.

If the growth of the branch be complete, so that no more axial joints are to be formed, the terminal internodes, and especially those which have produced ovicells, may have a larger number of zoœcia than the internodes of the rest of the colony; and the number of zoœcia formed before the growing-point exhausts its activity does not appear to be regulated by the laws which govern those internodes which are not terminal. But even the terminal internodes normally produce no more than a single branch (cf. C. aculeata and C. ramosa), the cases mentioned on p. 149 being the only ones in which two branches were noted to come off from the same internode.

The articulations of the lateral branches of this species are

alone sufficient to distinguish C. denticulata from the other British forms. They are situated at a very low level on the zoœcia which bear them, and each "basis rami" (Smitt) appears to be wedged in between two consecutive zoœcia (fig. 3), instead of being, as in other species, distinctly apposed to the outer side of one zoœcium (figs. 4, 6, 11). The branches usually originate from z_3,[1] z_4, or z_5; less commonly from z_2 or from z_6.

The joints, both of the zoarium and of the rootlets, of this species are in nearly all cases of a jet-black colour, as recognised by most of the previous writers.[2] The young joints are, as in other species, uncoloured; but the black colour is in almost all cases very speedily acquired. Smitt and Busk do not mention this as a specific character, no doubt because they have given wider limits to the species than are accepted by most writers.

The ovicell[3] in all species replaces an ordinary zoœcium, and in this particular species it is usually borne on a lateral branch, and in most cases is situated at some distance above a joint. In the instances given in the formula on p. 146 the ovicell replaces the 4th, the 6th, or the 10th zoœcium of an internode. I have never seen it lower than 4th nor higher than 13th. It is usually very near the end of a branch, and this feature is well shown in pl. iv, figs. 2 and 4, of Busk's British Museum Catalogue (Part III). In one of my cases, however, thirteen zoœcia occurred above the ovicell, and eleven below it, and very rarely a joint may be developed above it. If the ovicell-bearing internode develops a branch, that branch is very seldom given off from a position higher than the zoœcium which corresponds to the ovicell on the opposite side of the branch.

[1] I.e. from the third zoœcium of either right or left side: the side from which a branch comes off has no significance unless considered in relation to other characters.

[2] Cf. Fleming, J., 'Hist. Brit. An.,' p. 540; Johnston, A., 'British Zoophytes,' 2nd ed., p. 284; Hincks, T., 'Brit. Mar. Polyzoa,' p. 423; &c.

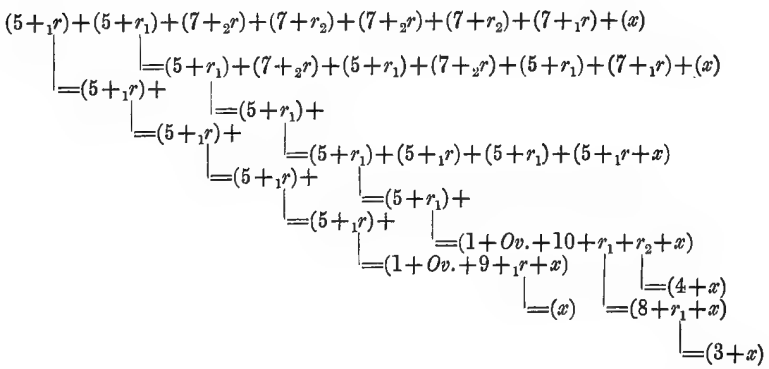
[3] See also p. 169.

The calcareous matter of the ectocyst is considerably thicker in C. denticulata than in any of the other British species.

C. eburnea. Fig. 6.

Although this species is not likely to be mistaken for C. denticulata, I believe that it is more nearly allied to that species than are any of the other British forms. This is shown by the flatness of the internodes, by the fact that each internode has normally one branch, and by the characters of the apertures of the zoœcia.

The branching may be illustrated by the formula[1]—



—representing the partial formula of a branch of a colony found in April, in which ovicells were very numerous. The ovicell-bearing internode on the right side of the formula is the one which has been represented in Pl. XI, fig. 6.

The tendency of the branches of this species to arrange themselves as unilateral sympodes is here most marked; and the formation of these helicoid cymes—again borrowing a botanical term—is one of the most characteristic features of C. eburnea. This was recognised by Johnston,[2] who says of this species, "Polypidom much branched, the primary divisions alternate, spreading; the secondary from one side only." It will further be noticed that in parts of a colony in which this

[1] See explanation of this graphic method given on p. 146.

[2] 'Brit. Zoophytes,' ed. 2, p. 284.

method of branching is well developed, the internodes composing the sympode are usually made up of five zoœcia, and that, although the branching may, in other parts of the colony, take place from z_2 (or rarely from z_3 or z_4), well-developed helicoid cymes are invariably composed of internodes in which the branching takes place from z_1.

These helicoid cymes do not, however, agree with the method of branching defined under that term in text-books of botany, in that the main axes of the parts of the sympode are by no means suppressed. This is obvious enough from the formula, in which the first internode on the left side forms the basal member of a helicoid cyme developed on the left side of the branch; but it is, at the same time, the basal member of a long axis, which develops new cymes alternately on opposite sides; and the same is true of the other constituents of the sympodes. Thus each of the branches indicated in the formula, with the exception of those which are quite near to the growing-points, is again the basal member of a helicoid cyme; and these cymes are consequently given off alternately on opposite sides, not only by the internodes of the main stem, but also by the internodes of its branches of the second, third, and other orders. The number of members of which these helicoid cymes are composed decreases fairly regularly in a centrifugal direction.

Each internode is typically provided with one branch, and at the same time is composed of an odd number of zoœcia, just as in C. denticulata. It is not uncommon, however, to find branchless internodes, whose position in the colony may be illustrated by the formula—

$$(5 + r_1) + (6) + (5 + {}_1r);$$

and, just as in C. denticulata, these branchless internodes nearly always consist of an even number of zoœcia, most commonly of four or six, less often of two or eight. Exceptions to this rule are somewhat less rare than in C. denticulata, which this species so closely resembles in its method of branching. The exceptions are more common at the base

of the colony than elsewhere. The branch is developed on the same side as the basal zoœcium of an internode, and the last zoœcium is usually somewhat produced. In very rare cases, of which the specimen represented in fig. 6 is an example, two branches may be developed from the same internode.

The articulations which bear the lateral branches are relatively short; even when the branch is developed from z_2 or z_3 the "basis rami" is never wedged in between two zoœcia, as in the last species; and the joint which bears the branch is nearer to the aperture of the zoœcium which has developed it than in C. denticulata.

The number of zoœcia is typically five or seven, the former number being especially characteristic of the members of a helicoid cyme. As in C. denticulata, the definiteness with which the colony grows is frequently indicated by the regular repetition of the same forms of internode in a branch. Thus the greater part of the main axis of the branch whose formula is given on p. 154 is composed of internodes of the type $(7+r_2)$; in the main axis of the branch given off by the second internode of that stem, $(5+r_1)$ alternates regularly with $(7+{}_2r)$ until the end of the axis is nearly reached; while in the next line but one will be seen the formula of a branch composed of units of the type $(5+r_1)$. The regular repetition of internodes of the type $(5+r_1)$ in the formation of most of the helicoid cymes is a further illustration of the same thing. In many other cases, however, no such regularity of arrangement was noticed. In a colony found at Plymouth in August, the dominant number of zoœcia was seven, although internodes with five zoœcia were not uncommon. But, in correlation with this increase in the normal number of zoœcia, it was found that several internodes of nine zoœcia occurred, and two of eleven.

In the terminal internodes the number of zoœcia may be larger; in one case observed it was as high as twenty, no growing-point being left.

The ovicell most commonly replaces the second zoœcium of a lateral branch (fig. 6), and is consequently the basal member of its own (axial) side; in other cases, however, the ovicell may

replace the third zoœcium above a joint (and it is then abaxial), but it is very rarely found higher in the internode. A branch is never given off by an ovicell.

As the age of the ovicell increases, fresh zoœcia continue to be added above it up to a certain point. The old ovicell seems to be always surmounted by a considerable number of zoœcia; in the specimen shown in fig. 6 there are, in addition to two incompletely formed zoœcia—the last that this branch would have produced—ten zoœcia above the ovicell. It must be noted that in this and other similar cases all zoœcia which are further from the joint than the ovicell are described as being above the latter. The second zoœcium of the right side in fig. 6 may not, at first sight, appear to be in this position, although an examination of the lower end of the ovicell at once shows its real place in the series.

A joint is seldom developed above the ovicell, and the growing-point usually completely exhausts its power of developing fresh zoœcia after a certain period.

The joints of this species are pale-coloured, or more usually yellow. In old parts of the colony the joints may become very dark, or almost black; this is especially true of those parts which form the starting-point for the regeneration of fresh branches. The joints are probably never so dark as they are normally in C. denticulata.

Smitt, in his valuable paper on Crisia,[1] gives a series of formulæ illustrative of the branching, &c., of the forms of this genus, and many of these formulæ illustrate in a most instructive manner the tendency of some at least of the species of Crisia to develop even-numbered internodes without branches. In his explanation to No. 8 of this series Smitt expressly points out that, in Nos. 4—8, shorter branchless internodes may alternate with longer internodes which have developed branches. It is a noteworthy fact that the greater number of the branchless internodes shown in these formulæ have an even number of zoœcia, and that the number is odd in most of those internodes which have developed branches. This fact seems, however, to

[1] "Krit. Förteckn.," I, 'Öfvers. af K. Vet.-Akad. Förhandl.,' 1865.

have escaped Smitt's attention. It must further be pointed out that some of the exceptions to the rule which has been so much insisted on above are probably due to the fact that some of the formulæ refer to C. aculeata, as is admitted by Smitt in two of the cases.

A very interesting abnormality of C. eburnea is figured in Pl. XI, fig. 5. The internode in question was the penultimate internode of a branch of a thoroughly characteristic colony, in which no other abnormalities were detected. In addition to bearing two lateral branches in a very unusual position, at its upper end, this internode distinguished itself by producing three zoœcia arranged in a row along the middle of its front surface, giving it, when seen from this side, an appearance very much like an Entalophora, for instance. The back of this internode appeared normal, and it was not obvious that any of the three growing-points borne by the internode was constructed in such a manner that it would have reproduced the abnormality in the next following internodes.

C. aculeata. Fig. 4.

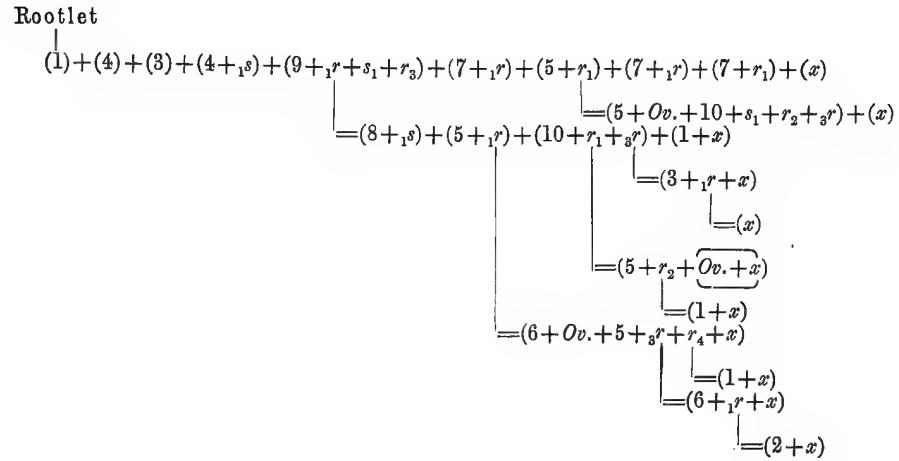
I believe this form, which is in many respects intermediate between C. eburnea and C. ramosa, and which was originally distinguished as a species by Hassall,[1] to be a perfectly good species. Nearly all recent authors have regarded it as a variety of C. eburnea; this view is taken, for instance, by Hincks,[2] Busk,[3] Smitt,[4] &c. Even Johnston,[5] although inserting it as a distinct species, adds that he cannot persuade himself that it is more than a variety of C. eburnea.

My belief in the specific distinctness of C. aculeata rests mainly on the characters of the ovicell; since a particular form of ovicell (shown in fig. 4) is invariably found on colonies of

[1] Hassall, A. H., 'Ann. and Mag. of Nat. Hist.,' vol. vi, 1841, p. 170.
[2] 'Brit. Mar. Polyzoa,' p. 421.
[3] 'Cat. of Marine Polyzoa in Brit. Museum,' part iii, p. 4.
[4] Loc. cit.
[5] 'British Zoophytes,' ed. 2, p. 285.

the aculeata type, and never occurs in any other type of colony.

The method of branching and the number of zoœcia in an internode are far less constant than in the last two species. Some of the characters of C. aculeata may, however, be illustrated by a formula, using the letter *s* to indicate the position of a spine, in addition to the symbols which have been employed in other cases.



The formula represents the whole of a main stem, given off from a rootlet, together with the whole of one of its lateral branches and a portion of another. In several important respects this formula differs from those which have been given of the preceding species. It is by no means uncommon to find completely formed internodes which have an even number of zoœcia; and these even-numbered internodes do not conform to the denticulata or eburnea type by being usually without branches. In some cases, indeed, an even-numbered internode has no branch; in other cases it has two branches, one on each side; in others again it may have one branch, or it may have a spine, which, as has often been pointed out, is a structure which may be regarded as a suppressed branch: like the true branches, the spine has horny joints at intervals, and is attached to the

zoœcium by means of a basal piece which is quite similar to that of a normal branch.

The spines shown in fig. 4 have been artificially bent backwards; in their normal position they curve over the front of the branches.

The number of spines developed on a colony is extremely variable; in a few cases spines are altogether absent, and the species could then hardly be distinguished with certainty from C. ramosa, were it not for the presence of the characteristic ovicells. Although, in one or two cases observed, an internode had developed spines on all or nearly all its zoœcia, it is not usual to find more than one or two spines on a single internode, while a large proportion of the internodes of a colony do not develop any of these structures. The spines most commonly occur on the lower zoœcia of an internode, and are commonly in the position—

$$(n + s_1 + r_2)$$
$$\text{or } (n + s_1 + s_2 + r_3);$$

being found on the abaxial side if the internode is, as is often the case, the basal member of a branch.

The spines may, however, be developed in other positions; thus it often happens that the last structure developed at the apex of a branch, before the growing-point ceases to grow, is a spine,[1] which is situated on the axial side of the last zoœcium, and is consequently in the position of the terminal zoœcium of the branch to the right of the ovicell in fig. 4.

In the specimens (most of them from Plymouth or Roscoff) which have come under my notice the presence of a single spine on a colony has been quite sufficient to enable the species to be identified with certainty as C. aculeata. It is perfectly true that the lower parts of the zoarium may have an eburnea-like appearance; but the colony, if well grown, seems always to acquire the aculeata form of the zoœcia and internodes towards the ends of the branches.

I have in no case found an ovicell of the type shown in fig. 6

[1] Cf. C. acuminata, Busk, '"Challenger" Rep.,' part 50, pl. iii, fig. 1.

(C. eburnea) on a colony which, from the presence of spines or from other characters, was found to belong to C. aculeata. I cannot admit that there is sufficient evidence to show that this form is merely a variety of C. eburnea. Both in the form of its zoœcia and in its method of branching it is totally unlike this form, although it is sometimes with difficulty distinguished from C. ramosa.

The branches of C. aculeata are usually slightly incurved, but not nearly to the same extent as in C. eburnea; and it does not possess the well-developed helicoid cymes of the latter species. Many of the internodes bear two branches, usually on opposite sides, but more rarely on the same side. In well-developed colonies the terminal internodes, and especially those which possess ovicells, are commonly provided with two branches.

The number of zoœcia in an internode is extremely variable; it is usually small in the lower internodes of a stem, such numbers as 1, 2, 3, and 4 being common in this position. The next parts of the stem, and the basal parts of the lateral branches given off by it often assume an eburnea-like appearance, the internodes consisting of 5 or 7 zoœcia. At the ends of well-developed branches the number usually becomes higher; a terminal internode with 22 zoœcia has been observed, although this number is higher than is usually the case. When the terminal internodes have many zoœcia they usually bear two branches; but if the number of zoœcia is still larger the number of branches may increase to as many as five.

The position of the branches is another very variable feature. In the lower parts of a colony the branching takes place commonly from z_1; while higher up, although some of the branches still come off from z_1, others are given off quite as commonly from z_2, and in many of these cases the zoœcium below the branch, and on the same side, bears a spine. Branching may, however, take place from the higher zoœcia of an internode, as from z_3 or z_4; and when several branches come off from the same internode, those which are last formed have a very high position in the internode. The

most striking case observed illustrating this point had the formula—

$$(7 + Ov. + 11 + r_1 + r_4 + r_5 + {}_6r + r_{10} + x).$$

It cannot fail to be remarked that the character of the branching is much more variable in this species than in C. eburnea.

The joints are usually yellow; the articulations which bear the branches are usually short, and are then very similar to those of C. eburnea; in some cases, however, they acquire the form characteristic of C. ramosa.

Near the ends of the branches, where most of the zoœcia have polypides, the ends of the zoœcia are, in most cases, long free tubes, and are thus strikingly different from those of C. eburnea. The free portions of the zoœcia are either gradually bent forwards from the point where they leave the branch, or they may be bent forwards at a distinct angle from this point. The curvature of the zoœcia is, in either case, different from that of C. eburnea. The zoœcia are distinctly longer and more "loosely aggregated" than in that species; and the branches are usually of slenderer habit (as recognised by Johnston[1]).

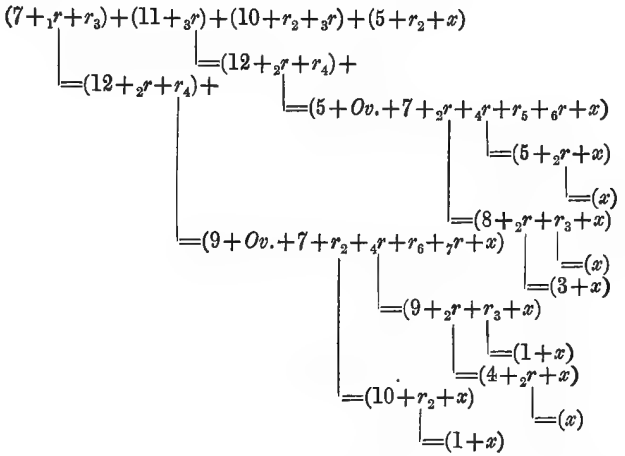
The ovicell is nearly always higher in the internode than in C. eburnea. In the average of a considerable number of observed cases the ovicell was in the position of the 5th—6th member of the internode above the joint, and thus replaced z_3 or ${}_3z$. In one case the ovicell replaced the 8th zoœcium, and in another it was the 3rd unit of the internode; in no case was it found lower.

The stem is not usually jointed above the ovicell; and fig. 4 is, consequently, a somewhat exceptional case. As in the preceding species, the ovicell is normally borne by a terminal internode; and a considerable number of zoœcia may be added above the ovicell.

[1] 'Brit. Zoophytes,' ed. 2, p. 286.

C. ramosa, n. sp. Fig. 11.

Some of the characteristics of this species are well exhibited by the formula[1]—



The branching is seen to be very similar to that of C. aculeata, but the tendency, already manifested by that species, to develop more than one branch from an internode, is here carried much further, so that a considerable proportion of the internodes have two branches each, while the terminal internodes, if the colony is well grown, will be found to have at least two each.

The rule relating to odd- and even-numbered internodes, so characteristic of C. denticulata and of C. eburnea, here breaks down altogether, as, indeed, was the case to a considerable extent in C. aculeata. Odd-numbered internodes are not much commoner than even-numbered ones, and either kind may produce one or more branches, or be altogether branchless. The first branch of an internode is, however—as in other species—nearly always developed on the side of the basal zoœcium, and the last zoœcium of an internode is very often

[1] It is obvious that, in the case of the ovicell-bearing internodes, some of the branches are given off above the ovicells. For the purposes of the formula, however, the ovicell is counted as an ordinary member of the internode. A branch is probably never developed from the ovicell itself.

situated on the side on which the last branch is developed, thus causing the position of the basal zoœcium of the next internode, and consequently of the first branch of that internode, to be on the opposite side.

Just as C. eburnea is, on the whole, characterised by branching from z_1, so this species may be said to branch normally from z_2, or to produce branches on the type $(r_n + {}_{n+2}r)$, where n usually represents z_2 or z_1.

The extent to which this must be taken as a general rule may be understood by the following analysis of the complete formula of a well-developed colony:

		Number of Cases.
(1)	Internodes with one branch, originating from z_2 . .	24
(2)	Branches arranged on the type $(r_2+{}_4r)$	5
(3)	„ „ „ $(r_1+{}_3r)$ or $(r_3+{}_5r)$ . .	5
(4)	„ „ „ $(r_2+{}_2r)$	1
(5)	„ „ „ $(r_2+{}_3r)$	5
(6)	„ „ „ $(r_1+{}_2r)$	1
(7)	„ „ „ $(r_3+{}_4r)$	2
(8)	One branch only, originating from z_1	2
(9)	„ „ „ z_3	8
(10)	„ „ „ z_4	7
(11)	„ „ „ z_5	3
	Total number of internodes which had developed branches	63

Only eight of the completely developed internodes were branchless. Thus in this particular colony, in which no ovicells were present, and in which no internode possessed more than two branches—

30 p. c. of the branching internodes bore two branches;
38 p. c. „ „ „ one branch, originating from z_2.
32 p. c. „ „ „ „ „ from other zoœcia.

100 p. c.

Or, adding together Nos. 1 to 4, the cases in which the branches come off from z_2, or in which the second branch is two zoœcia higher than the first, we find that these cases amount to 55·5 per cent. of the total number of branching internodes, and this may be taken as a case which does not exaggerate this feature of the branching.

Since some of the internodes which bore branches were immature, and had not had time to develop more than one branch, the figures would have been slightly different if the growth of the colony had been complete.

The symmetrical character of the branching noticed in other species is also found in C. ramosa. Thus the branches originating from an internode whose formula was $(14+{}_3r+r_5)$ developed altogether five internodes from which new branches were given off; in two of these cases the branch was borne by z_3, in two more by z_5, and in the last case by z_4; and other cases of the same kind may easily be found.

The symmetry of the branching comes out with special clearness in the case of some abnormalities, of which the formula given on p. 145 is an example. Two consecutive internodes of the main stem represented in the formula give off internodes whose formulæ are identical. One of these gives off, on its right side, a lateral branch consisting of a single long internode bearing an ovicell, and the other gives off a precisely similar branch on its left side. Both of these ovicells have the same deformity, having developed a constriction at a particular point near their upper end; and it will further be noticed that the symmetry extends, to some extent, to the branches given off by the internodes which bear these ovicells.

Fig. 12 represents an abnormal ovicell or zoœcium of a type found in more than one colony. The growing-point appears to have started with the intention of developing an ovicell, and then to have altered its original purpose, and to have developed the incipient ovicell into an abnormal zoœcium. This alteration of purpose may have been due to the failure of the young ovicell to develop the egg[1] which is normally found in the immature ovicell.

The point which immediately concerns us at present is that each of two consecutive internodes of the same stem of this particular colony developed lateral branches, one on each side of the stem, and that each of these lateral branches bore an ovicell of this peculiar "suppressed" form. The same colony

[1] 'Proc. Cambridge Philosoph. Soc.,' vol. vii, p. 48.

possessed two more of these suppressed ovicells, two ovicells showing other abnormalities, and several normal ovicells.

In another colony a normal ovicell, with a "suppressed" ovicell on a lateral branch on each side of it, was noticed.

In another case (fig. 13) a single internode bore no less than four ovicells, and the colony to which this belonged possessed, in different parts, four internodes, in each of which two ovicells had been developed. It may be noted that the occurrence of two ovicells, side by side, in the same internode, is described by d'Orbigny[1] in C. patagonica, apparently as a normal feature of the species.

These cases, and the general remarks which have been made with regard to the branching of various species of Crisia, show that the growth of the colony is even more definite in its character than would appear from a superficial examination, and that in each particular species the tendency to vary is subordinated to certain principles of growth, which give rise to the special symmetry which characterises the species.

The number of zoœcia which compose an internode is even more variable in C. ramosa than in any of the other species. Generally speaking, the number is smaller near the base of the colony, and larger near its periphery, although this rule is by no means absolute. The length of the internode depends mainly on the number of zoœcia it possesses. The longest which was measured was a terminal internode in which growth had ceased, and which consisted of 28 units, of which the 10th was an ovicell; its total length being slightly more than 7 millimetres. These long internodes usually show a well-marked double curve, like a much elongated S, just as was remarked in C. denticulata; and they commonly bear 3, 4, or even 5 branches.

The appearance of the internodes depends greatly on the condition of the zoœcia. Near the ends of the branches the zoœcia generally have very long tubular mouths, and, for the most part, contain a functional polypide. This is especially

[1] D'Orbigny, A., 'Voyage dans l'Amérique méridionale,' tome v, 4e partie, 1839 and 1846, p. 7, pl. i, fig. 1.

true of actively growing colonies found early in the year: at a later period, when growth is less energetic, the apertures may be much less prolonged, and in many cases they are not more prominent than in some specimens of C. denticulata, even in the case of those zoœcia which are not closed by a diaphragm. Lower in the stem the tubular mouths are, in most cases, lost; the zoœcium is closed by an oblique diaphragm, and no polypide is present. The internode is then a flattened structure, in which the apertures of the zoœcia project even less than in C. denticulata.

In an interesting abnormality found in August, two prominent tubular apertures occurred, side by side; the extra zoœcium being in the position which would normally have been occupied by a basis rami.

Busk[1] has made rather a point of the fact that in C. conferta the free tubular portion of the zoœcium is not a mere production of the peristome, but presents "the same puncturation as is seen on the rest of the cell." This is certainly the case in C. ramosa and in C. aculeata, and to a less extent in C. denticulata. C. eburnea is, in fact, the only species I have examined in which the tubular portion is usually merely a thin prolongation of the peristome.

The average position of the ovicell is somewhat higher than in C. aculeata; but that it varies greatly in position is obvious from the formula—

$$(4+Ov.+19+r_1+{}_2r+{}_4r+r_6)+$$
$$\qquad\qquad\qquad

fig. 11, and in both the above-cited formulæ in which the ovicell replaces z_3 and z_7 respectively.

The joints of this species are yellow, or more rarely brown. They are never black. Rootlets are very freely developed from the base of the stem, and they may attain a great length. They usually originate rather low on the zoœcia and from their lateral edges. As in other species, they become very firmly attached to stones and other objects, and form creeping stolons, from which (as well as from rootlets which are not attached in this way) fresh stems may originate. The colonies do not so often consist of a single main stem as in C. eburnea. It is frequently remarked that the longest and most branched parts of the colony are lateral branches, and not parts of the main stems.

Ovicells.—In C. ramosa (figs. 10, 11) the ovicells are considerably larger than in any of the other species (see figures, all of which are drawn to the same scale, and table of measurements on p. 159). They are regularly pear-shaped, their main axis being straight; they are much inflated above, their curvature diminishing gradually in all directions from their most prominent portion. The aperture is in the form of a distinct funnel-shaped tube, which is considerably smaller at its base than at its mouth; and the mouth of the funnel, the actual aperture of the ovicell, is more or less circular. In the shape of the aperture this species differs from all the other British forms.

The tubular aperture is of course not present in incompletely developed ovicells: an account of the development of the ovicells will be given in a forthcoming paper. It must also be noted that the aperture is liable to be broken away in old ovicells, and that in many cases, where the ovicells or their contents are not normally developed, the tube itself is not formed. In normal and completely developed ovicells the shape of the aperture is, however, a perfectly characteristic and constant feature.

C. aculeata (fig. 4), which in some other respects is so similar to C. ramosa, has a much smaller ovicell than that

species (compare fig. 4 with fig. 11).[1] Its shape is very characteristic, its most prominent portion being considerably nearer its distal end than in C. ramosa. From this point the ovicell slopes off very suddenly towards its aperture, and more gradually towards its base, although this latter slope is steeper than in C. ramosa. The aperture is not borne on a distinct tube, but it lies in a characteristic position on the zoœcium next above the ovicell, on the same side of the internode. This zoœcium curves forwards round the back of the ovicell, the aperture of which is situated on it at the point where it makes its appearance above the ovicell.

In C. eburnea (fig. 6) the ovicell is large—considerably larger than in C. aculeata. Since the base of the internode which bears it is distinctly curved inwards, the ovicell itself has the same curvature at its base, as is best seen when the ovicell is looked at from the side. The ovicell is well inflated, and slopes away more gradually from its most prominent point than in C. aculeata. The aperture is quite characteristic; it is borne on a tube-like structure, distinctly broader at its base than at its free end, and instead of being circular, as in C. ramosa, it is transversely elongated, its lower border being often slightly convex towards the centre of the aperture.

In C. denticulata (fig. 3) the ovicell is fairly large, and usually becomes level with the flat surface of the internode near its base, the distal portion of the ovicell being very prominent. The aperture is not situated on a well-developed tube; it is not, however, on the surface of a zoœcium, as in C. aculeata, but is situated between two zoœcia, and it is very nearly sessile on the top of the ovicell, as was the case in C. aculeata.

In all four species the aperture is connected with the top of the ovicell at the point where the latter joins the front surface of the internode.

The importance of the form of the aperture appears to have

[1] It must, however, be pointed out that the ovicell of C. ramosa may be smaller, and that of C. aculeata larger, than in the particular specimens figured.

been almost completely overlooked by all previous writers on Crisia. The aperture is often said to be absent, as indeed it may be in injured or abnormal ovicells. As will be seen from a later communication, a normal ovicell is, according to my observations, never without an aperture from the time when the ovicell is first developed at the growing-point to the time when embryos are ready to escape from the ovicell. The calcareous aperture is, however, throughout the development closed by a thin cuticular membrane, and the presence of this membrane sometimes makes it difficult to see the aperture in those cases in which this structure is not borne on a distinct tube.

On breaking open an ovicell (fig. 10) it will be noticed that the aperture leads into a space partially separated from the rest of the ovicell by a valve-like structure of calcareous nature. This valve has very definite relations to the structures found in the interior of the ovicell, as will be described in my subsequent paper. It springs from the posterior wall of the ovicell, and passes obliquely forwards, being also attached to the lateral walls of the ovicell in such a way as to leave a more or less oval opening connecting the main cavity of the ovicell with the aperture of the latter. The valve is most developed at the back of the ovicell, and gradually dies away laterally as it passes to the front wall of the ovicell, where it no longer forms a distinct ridge.

This valve is developed in all the four species which are specially discussed in this paper, but it appears to be less well developed in C. eburnea than in the other species.

Note on C. cornuta, Linn., and C. geniculata, M.-Edw.

Until quite recently I had devoted no particular attention to these forms, the specific identity of which appeared to be perfectly established by such statements as those of Smitt,[1] to the effect that they may both occur as branches of the same stem. But, having recently found some ovicells of C. geniculata, I cannot help believing that the two forms are speci-

[1] 'Öfvers.,' &c., 1865, No. 2, p. 128.

fically distinct, and a more careful examination of C. cornuta has convinced me that Smitt's statement may be explained in such a way that it is unnecessary to follow him in his conclusion.

Even if the two forms are not really distinct, it appears to me worth while to call attention to what would then be an interesting case of a definite variation of the ovicells correlated with the presence or absence of spines on the zoœcia.

C. geniculata consists typically of a series of internodes, each of which is composed of a single zoœcium; from opposite sides of this zoœcium arise a pair of branches which are not quite at the same level. An excellent figure of this form is given in Busk's 'British Museum Catalogue' (part 3), pl. i, fig. 2. On comparing this figure with fig. 7 on the same plate (representing C. cornuta), it will be seen that C. cornuta exactly resembles C. geniculata as far as those zoœcia which bear two branches are concerned; but that, as Busk points out (p. 3), one of the branches is usually replaced by a jointed spine.

It is obvious that spines will be absent in C. cornuta if two branches are developed from each zoœcium. Further, the spines are very readily broken off, and a close examination is then sometimes necessary to discover the small basis with which the spine articulates. From one or other of these causes I have several times observed branches of normal colonies of C. cornuta having a close resemblance to C. geniculata; and this may be the explanation of Smitt's statement referred to above.

In every case in which I have observed the ovicells—although I must add that I have not obtained many ovicells of C. geniculata—I have noticed the following characteristic differences between the two forms; a reference to Busk's figs. 2 and 10 (l. c., pl. i) shows that the forms examined by Busk were similar to those which I have myself found. Busk's fig. 4 (C. geniculata) does not, however, quite agree with the specimens which I have examined.

The ovicell of C. cornuta (fig. 9) is the basal and only member of its own internode; it bears a lateral branch on each side, these branches originating at not exactly the same level.

After the branches have been given off, the ovicell becomes perfectly free, and is in this part considerably inflated. The tubular aperture arises near the back of the ovicell, and is usually bent somewhat backwards from its point of origin; so that, in looking at the branch from its "front" surface, the base of the tubular aperture is nearer to the observer than its distal end.

In C. geniculata, on the contrary, a common arrangement is as follows:—The basal member of the internode is an ordinary zoœcium (figs. 7 and 8), which gives rise to the ovicell as the second member of the internode. Immediately above the ovicell is another zoœcium, which gives off a lateral branch near the level of the upper end of the ovicell. The basal zoœcium itself gives off a branch on the opposite side to the ovicell. The internode may thus be represented as—

$$\begin{matrix} (1+Ov.+1) \\ | \qquad\quad | \\ {}_1r \qquad r_2 \end{matrix}$$ (counting the ovicell as the basal member of its own side).

The ovicell itself is distinctly smaller than in C. cornuta, and is not much inflated at its upper end. Its tubular aperture is most distinctly bent forwards from its base, sometimes at a very sharp angle, and the actual aperture is smaller than in C. cornuta. Moreover, the ovicell is not free, as in the latter species; the upper zoœcium of the internode being closely attached to its back along the greater part of its course. This zoœcium ultimately becomes free from the ovicell, and curves forwards above the upper end of the latter.

In other cases the ovicell may be the third member of the internode, each of the two zoœcia below it giving off a branch; and two zoœcia, each bearing a branch, may occur above the ovicell. The commonest arrangement seems to be either that given in the above formula, or the occurrence of three branch-bearing zoœcia, one of which is below the ovicell and the other two above it (cf. Busk's fig. 2). The ovicell is, in any case, not the lowest member of the internode, and one or two zoœcia are always attached to its back.

C. geniculata is a slenderer and more delicate form than

C. cornuta, its zoœcia being distinctly longer and thinner than in that species; and spines seem to be never developed. As already remarked, however, parts of the colonies of C. cornuta may be devoid of spines.

Breeding Period and Occurrence of Species.

The specimens from which the following statements are made have been received at various periods from February to the end of August. I have to offer my best thanks to those who have most kindly assisted me by supplying me with material; and especially to the staff of the Marine Biological Association, Prof. H. de Lacaze-Duthiers, and Mr. J. Sinel.

The dominant species at Plymouth is certainly C. ramosa; although, strangely enough, I have not been able to obtain this form from any other place, except from a bottle found in the Morphological Laboratory at Cambridge. The contents of this bottle came either from the Channel Islands or from Arran!

At Plymouth, C. ramosa is found commonly at depths from 4 to 30 fathoms. It is particularly fond of growing on stones, but is found on other objects—e. g. glass bottles, shells, red seaweeds, Cellaria, and sponges. When it grows in the last position it appears to be in danger of being killed by the sponge, which grows over its branches. The Crisia is, however, generally able to keep pace with the growth of the sponge, so that only the basal parts of its colonies are killed, or at least prevented from having functional polypides by the sponge. The specimens growing at 4—6 fathoms were usually much more luxuriantly branched than the few specimens which I received from 20—30 fathoms; and ovicells were obtained only from those growing under the first set of conditions.

C. eburnea is also common at Plymouth, but is almost always found on red seaweeds or on Sertularia. The restriction of various species of Crisia to particular seaweeds, &c., has been often noted by previous observers.

Winther[1] has stated that, in the Danish forms of this species,

[1] G. Winther, "Fortegnelse over de i Danmark hidtil fundne Hav-Bryozoer," 'Naturh. Tidsskrift' (Kjøbenhavn), 3 Raekke, vol. xi, 1877–8, p. 7.

the effects of the brackish water of the Baltic can be easily observed by comparing colonies found in different localities. Those which are nearest to the Baltic are said to have internodes consisting typically of three zoœcia; in those most exposed to the North Sea the internodes have seven zoœcia; and in colonies from intermediate localities they have five zoœcia. I have not been able to observe any definite correlation between the character of the colony and the conditions under which it was growing.

C. aculeata is less common at Plymouth than either of the preceding species; it was found on stones, red seaweeds, and sponges, usually from 4—5 fathoms.

C. cornuta was fairly common, mostly on red seaweeds; while C. denticulata was seldom found at Plymouth.

By the kindness of Prof. de Lacaze-Duthiers I received a large supply of Crisia from Roscoff in June. The species most common at Roscoff appear to be C. aculeata, C. denticulata, and C. cornuta. C. geniculata was less common, and only a few fragments of C. eburnea were found.

From Mr. J. Sinel I have received numerous specimens of C. denticulata and C. cornuta found at Jersey; and a smaller supply of C. eburnea, C. geniculata, and C. aculeata. The Jersey specimens of C. denticulata were found between tidemarks, while Smitt[1] states that C. denticulata is pre-eminently a deep-water form. It is, however, probable that Smitt's specimens did not really belong to this species.

I have also obtained specimens of several species from Guernsey and the Scilly Islands.

Smitt's valuable contributions to our knowledge of the Polyzoa have been devoted, so far as they concern the genus Crisia, to showing that the "species" which have been distinguished in this genus are in reality "forms" of a single species.

In one of his later papers[2] Smitt remarks, speaking of the forms of Crisia discovered in the expedition to which his paper

[1] 'Öfvers.,' &c., 1865, No. 2, p. 138.

[2] "Recensio syst. . . . . Bryozoorum . . . . Novaja Semlja, &c.," 'Öfversigt. af-K. Vet.-Akad. Förhandlingar,' 1878, No. 3, p. 12.

refers, that he has united all these forms in a single species; and adds, "Auctores vero si sequi volumus, unamquamque fere coloniam speciem distinctam habebimus."

Although not in the least denying the difficulty of finding satisfactory specific characters other than those derived from the ovicells, the result of my investigation has been to convince me that Smitt has gone too far in denying the specific value of certain of the forms of Crisia. My results may possibly have to be explained by a suggestion which Smitt himself throws out, to the effect that although the series represented by the various forms of Crisia living in different localities is one in which practically none of the stages in the evolution of the species have been lost, "vivit multis in locis altera vel altera forma tam constans, ut species bene distincta facile censeatur."[1] Unfortunately, all the localities from which I have been able to obtain Crisia are comparatively close to one another; but I have found no essential differences between the forms of the same species from different localities.

Until it can be shown that any two or more of these forms can be developed as branches from the same stem, or as stems from the same rootlet, or at least that they can be produced as descendants of the same form, it appears to me that it will be impossible to deny to them the rank of species.

C. eburnea begins to breed at Plymouth as early as February; ovicells are present in great numbers during March, April, and May. Towards the end of the latter month they disappear, and are not normally present on colonies found in the summer. March and April appear to be the months when ovicells are most common.

C. ramosa commences to breed (at Plymouth) in April; a few of the colonies found at this period have young ovicells. In May young ovicells are very common; and the breeding period continues from this time until August at any rate. Immature ovicells may be found even at this time, but they are then becoming uncommon. The breeding season is probably at its height in May and June.

[1] 'Öfvers.,' &c., 1867, No. 6, p. 461.

C. aculeata.—A large proportion of the specimens found at Roscoff in June possessed numerous ovicells. At Plymouth ovicells were also found in April and May. The breeding season is probably much the same as in the last species.

C. denticulata.—The only specimens obtained in which ovicells were common were found in Guernsey and Jersey in the summer (June to August), which may probably be regarded as the period at which the breeding season is at its height.

C. cornuta.—The ovicells appear to be commonest in April and May.

C. geniculata.—The only specimens in which I have found ovicells were obtained in the summer (June to August). I have not found this species at Plymouth.

TABLE OF MEASUREMENTS (IN MILLIMETRES).

		C. denticulata.		C. eburnea.				C. aculeata.			C. ramosa.			
A	Length of long terminal internodes	3·10	3·77	2·00	2·63			2·90	3·70	4·10	4·40	7·06		
	Number of zoœcia	15+*Ov.*	16+*Ov.*	10	12+*Ov.*			13+*Ov.*	19	18+*Ov.*	19	27+*Ov.*		
	Average length of zoœcia	·39	·44	·40	·40			·41	·39	·43	·46	·50		
B	Length of long internodes (not terminal)	2·80	2·87	1·83	2·26			1·80	2·10	2·23	5·90	6·46		
	Number of zoœcia	15	15	9	11			10	10	10	20	23+*Ov.*		
	Average length of zoœcia	·37	·38	·41	·41			·36	·42	·44	·59	·54		
C	Length of axial internodes with average number of zoœcia	1·87	2·13	1·43	1·00	1·13	·86	1·10	1·20		2·43	3·43	3·13	3·63
	Number of zoœcia	11	13	7	5	5	5	5	6		9	11	13	15
	Average length of zoœcia	·34	·33	·41	·40	·45	·34	·44	·40		·54	·62	·48	·48
D	Distance from aperture to aperture	·27—·40		·30—·41				·34—·40			·38— ·70			
E	Total length of zoœcium	·64—·83		·54—·73				·60—·80			·83—1·30			
		Average ·66		Average ·56				Average ·64			Average 1·00			
F	Breadth of zoœcium	·08—·11		·08—·10				·07—·09			·08— ·11			
		Average ·09—·10		Average ·09				Average ·08			Average ·09			
G	Breadth of branch	·22—·30		·19—·24				·16—·25			·20— ·33			
H	Length of "basis rami"	·19—·24		·18—·24				·14—·35			·30— ·56			
				Average ·22				Average ·19			Average ·38			
I	Length of ovicell	·63—·80		·40—·70				·47—·67			·70—1·23			
		Average ·73		Average ·67				Average ·63			Average 1·00			
				N.B.—The lower limit here given is unusually small				N.B.—In the case of this species the method of measuring exaggerates the apparent size						
J	Greatest breadth of ovicell	·40—·48		·32—·45				·33—·41			·40— ·61			

In **A**, **B**, and **C** of the above table the length of the internode is measured from joint to joint, or from joint to apex of branch if the internode is a terminal one. The "average length" of the zoœcia is obtained by multiplying the length of the internode by two, and dividing by the total number of zoœcia. It is obvious that this does not give the total length of the zoœcium, since the zoœcia overlap one another; but an approximation to the distance from mouth to mouth of the zoœcia is obtained. This gives a more accurate average than any single measurement of this distance would give, since the distance is variable in connection with the extent to which the tubular apertures of the zoœcia are developed, and with other circumstances. For the purposes of this calculation an ovicell is counted as an ordinary zoœcium. If the length of the internode of five zoœcia shown in fig. 6 (C. eburnea) be compared with that of a corresponding number of units, beginning at the the base, of the ovicell-bearing internode in the same figure, it will be seen that the presence of the ovicell does not affect the result so much as would be expected at first sight, and the error due to counting the ovicell as a zoœcium is further lessened by the fact that this structure is nearly always borne on an internode which consists of many zoœcia.

In **D** the length is measured from any point of an aperture to the corresponding point of the aperture of the next zoœcium on the same side of the internode, and in making this measurement two zoœcia whose tubular mouths were about equally developed were always chosen.

E gives the total length of zoœcia with well-developed tubular apertures from the point where their cavity disappears at their proximal end to the furthest point of their apertures, the measurements being made from transparent (Canada balsam) specimens.

G is measured immediately above the aperture of a zoœcium.

H gives the length of the base with which a lateral branch articulates.

I. The length of the ovicell is estimated by drawing an imaginary line joining the point where the zoœcium next

below the ovicell on the same side becomes free from the internode (if any tubular aperture is developed), with the corresponding point on the zoœcium next above that zoœcium on the other side of the internode. The "length" of the ovicell is the distance of the middle point of the line drawn as above to the uppermost point of the ovicell, exclusive of its tubular aperture, if any.

This measurement, on the whole, gives the most constant results. The relation of the zoœcia below the ovicell to the ovicell itself is very variable, and it is impossible to take one of these zoœcia as a fixed point, a more definite result being obtained by taking two as described above. In C. eburnea, if the ovicell is the second member of an internode the imaginary line is drawn from the base of the tubular aperture of the first member of the internode in a direction parallel to that connecting the apertures of the upper pairs of zoœcia in the internode (a method which usually gives more satisfactory results than might be supposed from fig. 6).

The numbers given in the table do not profess to give the total limits within which a given part may vary, but the limits given will probably be found to include nearly all the variations which are observed in the ordinary forms of colonies.

In cases where it seemed to me possible to define the normal size of any part, I have put this down as the "average" size.

An examination of this table shows that C. eburnea, C. aculeata, and C. ramosa form an almost continuous series, as Smitt indeed has stated. C. denticulata can hardly be confused with any of the other forms, amongst which C. eburnea is the one that resembles it the most.

It will be seen that in every single measurement given C. ramosa is the largest of the four species, although in the size of the entire colony C. denticulata surpasses it. In many of the measurements, however, the upper limit of C. aculeata overlaps the lower limit of C. ramosa. As these are the two species which most closely resemble one another, and which are probably very closely allied to one another, it seems to me that it is not possible, in all cases, to

distinguish between a colony of C. aculeata without spines and a small variety of C. ramosa unless ovicells are present.

C. ramosa further appears to me to be much the most variable of all the species I have examined, while C. eburnea, and, next to this, C. denticulata, are the least variable. The greater variability of C. ramosa comes out perfectly clearly by subtracting the minimum from the maximum measurements given in the table, and comparing together the results thus obtained for the different species. If this be done for **D—J**, it will be found that, in every case except **F** (in which the limits are the same for C. ramosa and C. denticulata), the greater variability of C. ramosa comes out, and usually with striking distinctness.

It will be noticed that the largest variations are in the length of the zoœcia, and, correlated with this, in the size of the ovicells. But though the ovicells are thus by no means exempt from variation, their principal specific character (the shape of their aperture) is retained throughout without material alteration.

The fact that a colony of C. eburnea, on which some unusually small ovicells were present, has been taken into account in the table, makes these structures appear much more variable than they are in normal cases.

EXPLANATION OF PLATE XI,

Illustrating Mr. Sidney F. Harmer's paper "On the British Species of Crisia."

(All the figures were drawn with a camera lucida under a Zeiss A objective, and were subsequently reduced 2½ diameters.)

Fig. 1.—C. denticulata.—Young internode, with growing-point, seen from the back (Canada balsam preparation).

Fig. 2.—C. denticulata.—Illustrating the relations of an even-numbered internode (pp. 129, 130).

Fig. 3.—C. denticulata.—Ovicell (p. 151, &c.).

Fig. 4.—C. aculeata.—Ovicell (p. 150, &c.).

Fig. 5.—C. eburnea.—Abnormality (p. 140).

Fig. 6.—C. eburnea.—Ovicell (p. 151, &c.). The internode which bears the ovicell has two branches, an unusual arrangement.

Fig. 7.—C. geniculata.—Internode with ovicell; back view (p. 154).

Fig. 8.—C. geniculata.—Another ovicell, seen from the front (p. 154). Greatest diameter of ovicell = ·208 mm.

Fig. 9.—C. cornuta.—Ovicell (p. 153).

Fig. 10.—C. ramosa.—Ovicell broken open to show the valve (p. 152).

Fig. 11.—C. ramosa.—Branch with ovicell (pp. 145, 150, &c.).

Fig. 12.—C. ramosa.—"Suppressed" ovicell (p. 147).

Fig. 13.—C. ramosa.—Internode which has abnormally developed four ovicells (p. 148).

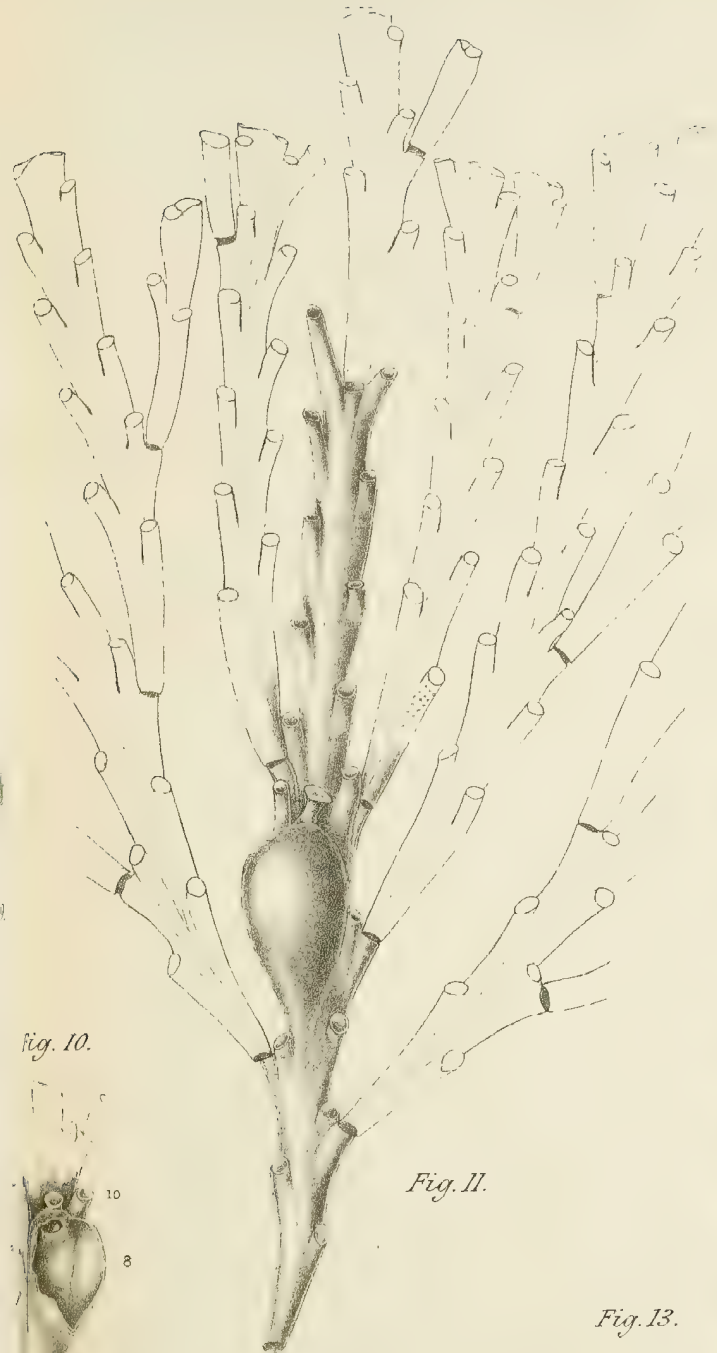


Fig. 11.

Fig. 12.

Fig. 13.

Fig. 10.

F Huth, Lith.r Edin.r

Fig. 1.

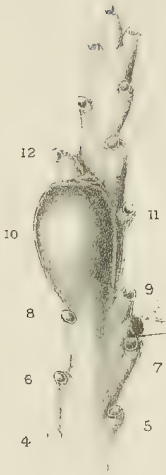


Fig. 3.

Fig. 4.

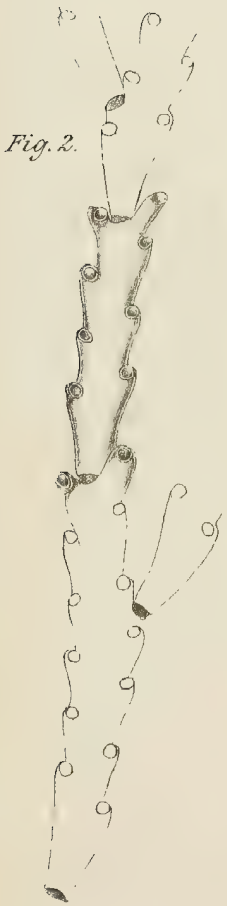


Fig. 2.

Fig. 5.

Fig. 7.

Fig. 8.

Fig. 9.

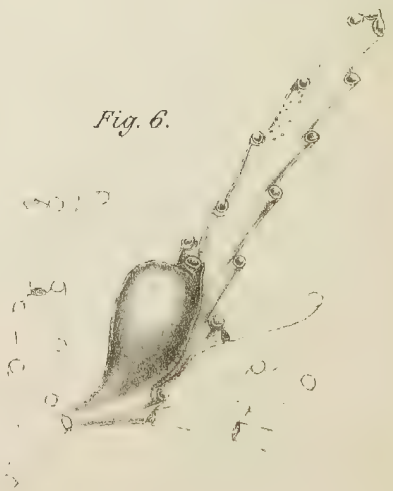


Fig. 6.

S. F. Harmer, del.

On a New Species of Phymosoma, with a Synopsis of the Genus and some Account of its Geographical Distribution.

By

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With Plate XII.

During a visit to the Bahama Islands in 1887, Professor Weldon made an excursion to the neighbouring island of Bimini. Whilst investigating the fauna of the lagoon in that island he came across a few specimens of what appeared to him to be a new species of Phymosoma. One or two of these he dissected on the spot; the remaining three he brought to England, and was good enough to give them to me for description at the time when he handed over to me his specimens of Phymosoma varians which form the subject of a previous memoir.

I have divided this paper into the following sections:

(i) A general description of the new species.

(ii) A detailed description of those organs which differ markedly from the similar organs in Ph. varians.

(iii) A synopsis of the genus.

(iv) A short account of the geographical distribution of the genus.

Part I.

Genus Phymosoma.

Phymosoma Weldonii, n. sp.

The length of the body is 3·5 cm. in the largest specimen, 3·25 cm. in the second, and 3 cm. in the smallest. The greatest width is 1 cm. At the base of the introvert, which was in each specimen retracted, the width is 2 mm. The body has a plump appearance and is slightly curved (fig. 1).

The ground colour of the preserved specimens is light buff, which is modified by the presence of dark brown papillæ; these are so numerous as to give the animal as a whole a dark brown colour. The papillæ are of two kinds (figs. 2 and 3).

No hooks or traces of hooks can be detected on the introvert.

The mouth is surrounded by a vascular lower lip, which in the dorsal middle line is continuous with the outer limbs of the lophophore. The latter structure is in the shape of a double horseshoe, the outer semicircle of tentacles corresponding to the lophophore of Ph. varians. In the ventral middle line this outer limb is bent dorsalwards, and thus the second horseshoe is produced (fig. 5). The lophophore bears a great number of long tentacles, seventy or eighty (figs. 5 and 8).

Behind the head is a well-developed collar, pigmented on the anterior surface (fig. 5).

The alimentary canal is tightly coiled, the number of twists being twelve or thirteen (fig. 4). It is supported by a well-developed spindle-muscle, which passes up the axis of the coil, and is attached at one end to the longitudinal muscles of the body-wall in the neighbourhood of the anus, and at the other to the posterior end of the body-wall. The anus is situated at the line of junction of the two kinds of papillæ.

The longitudinal muscles are arranged in ten or twelve bundles in the anterior half of the body; in the middle of the body there are about twice that number, as each bundle splits into two. These fuse together again at the posterior end of the body. At the base of the introvert the usual inversion of

layers occurs, the longitudinal muscles fusing into a continuous sheath, the circular muscles becoming broken up into bundles.

The retractor muscles are two in number, a right and a left; they arise about the level of the junction of the anterior two thirds with the posterior third of the body. They embrace the œsophagus, forming a semicircular band of muscle-fibres which are wanting only in the dorsal middle line where the heart lies.

The heart is provided with very numerous cæcal diverticula (figs. 4 and 7).

The external aperture of the kidneys lies on a level a little behind that of the anus.

Habitat: the lagoon, Bimini Island, the Bahamas.

Part II.

The Papillæ.

The papillæ of the skin are of two kinds, those on the body and those on the introvert. In the middle of the trunk the papillæ have an oblong outline, and are arranged in very regular rings (figs. 1 and 3); near the posterior end of the body, and also at the base of the introvert, the papillæ are so crowded together as to lose their rectangular outline. These papillæ are of a dark brown colour, and in those regions where they are crowded together the buff colour of the rest of the skin is completely obliterated. The trunk papillæ form only low elevations above the general level of the skin; each has a central pore, surrounded by a number of brown horny plates, which are modifications of the cuticle. These plates show a faintly laminated structure; they are represented in section in figs. 11 and 12.

Between these brown plates are placed a number of deeply pigmented granules of a dark brown, almost black colour. These give the dark brown colour to the papillæ (figs. 9 and 12). Neither the plates nor the pigment granules show any trace of being connected with any special cells; they seem to be modifications of the cuticle. The papillæ, like those of Ph. varians, are formed by the ectoderm-cells rising up and invaginating to form a double cup. The outer wall of the cup is formed by

ectodermal cells which have kept their ordinary character, and the inner wall is composed of a few cells of enormous size, which all but obliterate the cavity of the cup. These cells are wedge-shaped, and their broader ends are crowded with small spherical concretions, which do not dissolve in alcohol, chloroform, or benzine. Towards their outer, narrower ends these cells become free from these concretions and stain uniformly, or else they contain from two to five or six large star-shaped aggregations of crystals (fig. 9). Nothing like these were seen in the papillæ of Ph. varians.

The papillæ on the introvert stand out much farther from the level of the skin than those of the trunk (fig. 2). They are conical in shape, with a narrow basis. At their apex is a pore, and microscopic sections show that this is surrounded by a number of minute horny plates similar to those in the papillæ of the trunk, though much smaller, and not visible like the latter on the surface view. No crystals were found in the papillæ of the introvert, but the large wedge-shaped cells were in other respects similar to those described in the trunk papillæ.

The Head.

The head is represented diagrammatically in fig. 5. Part of the outer limb of the double horseshoe-shaped lophophore, involving eight or ten tentacles, has been cut out in order to show the pigmented region in the hollow of the original lophophore, and to display more clearly the arrangement of the tentacles. The thin transparent collar is extended over the head, a condition in which it is usually found when the introvert is retracted. The crescentiform mouth is shown surrounded by the lower lip, and at the base of the pigmented region on the dorsal side lies the brain, directly continuous at each side with the epidermis.

The tentacles are very numerous, seventy to ninety. Like those of Phymosoma varians, they are roughly triangular in section. One side, that directed towards the mouth, is grooved, and the groove is lined with cilia; the grooves of the various tentacles tend to fuse together near their lower ends,

and are directly continuous with the ciliated grooves on the wall of the œsophagus (fig. 8). A nerve runs along the base of the groove, and on each side of the nerve is a blood-vessel; the third blood-vessel occupies the angle opposite the side bearing the groove: all these three vessels anastomose occasionally, and communicate below with a large blood-sinus at their base.

In the diagram the plane of the tentacular crown is too flat; instead of being at right angles to the long axis of the body it should be raised up, and in a manner overhanging the mouth: in other respects the figure represents the disposition of the parts, although rather diagrammatically.

The sides of the tentacles which are directed away from the mouth are deeply pigmented, and the pigment is continued into a hollow at their base (figs. 5 and 8). This hollow lies partly between the two horseshoes of the tentacles, and is therefore itself horseshoe-shaped; at its dorsal end the depression becomes deeper, and lodges the brain.

The most important difference between the tentacles of Ph. Weldonii and Ph. varians lies in the absence of the rows of those skeletal cells which formed so interesting a feature of the latter species. Their place is occupied by a well-developed fibrous connective tissue, which passes down into the base of the lophophore, and is then continuous with the connective tissue which surrounds the œsophagus, and which serves as a point of attachment to the retractor muscles. The lower lip is also devoid of any skeletal structures; it is, however, very vascular; its inner surface is ciliated, the cilia being continued down the œsophagus; its outer surface is pigmented.

The area between the lower lip and the collar, as well as the inner surface of the latter, is also pigmented, although it has not been possible to represent this in the diagram. This continuous lining of pigment ceases at the edge of the collar; its outer surface is not pigmented. The collar is represented in fig. 5 completely expanded, and covering in the head; it is usually found in this condition when the introvert is retracted. It would be interesting to know whether it is ever expanded in this way when the head is extended during life. I have

never seen it in this condition in those specimens of the unarmed Gephyrea which I have been able to examine alive.

The absence of hooks on the introvert is a marked feature of this species of Phymosoma. Only five other species of the genus are devoid of these characteristic chitinous structures.

The Vascular System.

The vascular system of the unarmed Gephyrea consists of a closed space which has no capillaries in connection with it. The system is distributed in the various parts of the head, and its chief function would seem to be that of distending the tentacles and lower lip. In the tentacular blood-vessels the blood is separated from the surrounding water by a thin layer of tissue, and it is very probable that it becomes aërated during its passage through these organs. Its function as a carrier of oxygen cannot be of very great importance, since the system is entirely confined to one small part of the body. Probably those organs outside the head are dependent for their aëration on the corpuscles in the perivisceral fluid, though it is not easy to see where these can get their supply of oxygen and eliminate their waste matter.

The large vessel which lies on the dorsal surface of the œsophagus, and which is usually known as the heart, acts as a reservoir into which the blood retires when the tentacles are retracted (figs. 4 and 7). In Ph. varians, where there were few tentacles, the heart was a straight blind sac about ·5 cm. long, extending along the dorsal side of the œsophagus; but in Ph. Weldonii the number of tentacles is much greater, and the reservoir is correspondingly increased. The heart is much longer, being continued along the dorsal side of the œsophagus for a centimetre or two, and thus becoming involved in the twisting of the alimentary canal (fig. 4). Its capacity is also much increased by numerous small diverticula, which project as finger-like processes, and give the heart a very characteristic appearance. The walls of the heart and its diverticula are thin, with few muscle-fibres in its substance. Similar diverticula occur in the species Ph. antillarum, Ph. pelma, and

Ph. asser; and Ph. nigrescens has smaller diverticula of the same kind.

The corpuscles contained in this closed system are of two kinds—large clear cells with a well-developed outline, a well-stained nucleus which lies at one side of the cell, and apparently no cell-contents; the other corpuscles are smaller, with a protoplasmic body which stains well, and a nucleus in the centre.

In addition to the fluid of this closed system of spaces, the general fluid of the body-cavity contains corpuscles and the ova or sperm morulæ.

The Brain.

The nervous system has the same arrangement of nerve-fibres and ganglion-cells as that which I described in Ph. varians. The brain occupies the same relative position, situated at the dorsal side of the lophophore at the base of a slight depression. This depression is much smaller than the similar one in Ph. varians; its area being encroached upon by the bending back of the tentacular crown to form the inner horseshoe, the space is thus rendered rather slit-like and slightly curved (figs. 5 and 8). The depression is lined by a curiously crumpled and deeply pigmented epidermis, with which the brain is in direct continuity in two places. The shape of the brain is different from that of the other species, and this difference corresponds with the alteration in shape of the pigmented area in which it lies. It is bilobed, but the grooves between the lobes are very slight. Each lobe of the brain is smaller in transverse section than those of Ph. varians; on the other hand, their long axis is much longer, so that each lobe is slimmer and more elongated. The narrow outer end of the lobe bifurcates into two stout nerves, one of which passes round on each side in the connective tissue surrounding the walls of the œsophagus, and fuses with the similar one of the other side to form the ventral nerve-cord. The other passes up into the lophophore in the middle dorsal line, and then turns outwards and runs along the base of the tentacles, giving off a branch to each. There is a second lophophoral pair of nerves of small

size, which run into the outer end of the crown of tentacles where it fuses with the dorsal ends of the lower lip. I could not make out very satisfactorily whether these nerves supply branches to the tentacles of this region, but I am inclined to think that they do.

A pair of very minute nerves leave the brain close to the middle line; these run to the pigmented tissue of the depression at the bottom of which the brain lies. At about the point of the greatest circumference of each lobe the ganglion-cells of the brain are in continuity with this pigmented epithelium, and at one spot this epithelium is involuted into the substance of the brain, its cells become enlarged and crowded with pigment granules of dense black. The lumen of the involution is practically occluded; these pigmented involutions form the eyes.

The ganglion-cells form a cap which wraps round the fibres except for about a quarter of the circumference, where they come to the surface; this fibrous portion is ventral and posterior in position. The whole brain is half surrounded by the large blood-sinus into which the dorsal vessel opens anteriorly, and which gives off the vessels to the tentacles.

The arrangement of the fibres and ganglion-cells in the ventral cord is the same as that of Ph. varians (fig. 10).

The remaining organs of Ph. Weldonii resemble those of Ph. varians so closely as to render any detailed account superfluous. The nephridia are two in number (figs. 4 and 7). The relationship of their external and ciliated internal openings is shown in fig. 11. The outer wall of the nephridium is, as this figure shows, continuous with the body-wall, but this is for a short distance only. The organ soon becomes free, and stretches back to the end of the body, and then in its most extended condition may be bent back again.

In its histological details the structure of the nephridium is similar to that which I described in my former paper. The inner surface is broken up into a series of crypts which are lined by large glandular cells. Outside these is a meshwork of muscle-fibres which I have endeavoured to depict in fig. 6,

and covering these again is the layer of flat peritoneal epithelium.

The very curious mode by which the glandular cells of the nephridium in Ph. varians excrete their waste products, by casting off vesicles into the lumen of the organ, is repeated in this species. These vesicles contain granules. Their method of formation and of breaking off from the free end of the secreting cell is paralleled by the secreting cells which line the mammary glands of Mammalia, or by the cells which give rise to the secretion of the liver in Astacus.

The generative organs consist of a band of modified peritoneal epithelium which lies at the base of the retractor muscles. The generative products split off into the peritoneal cavity.

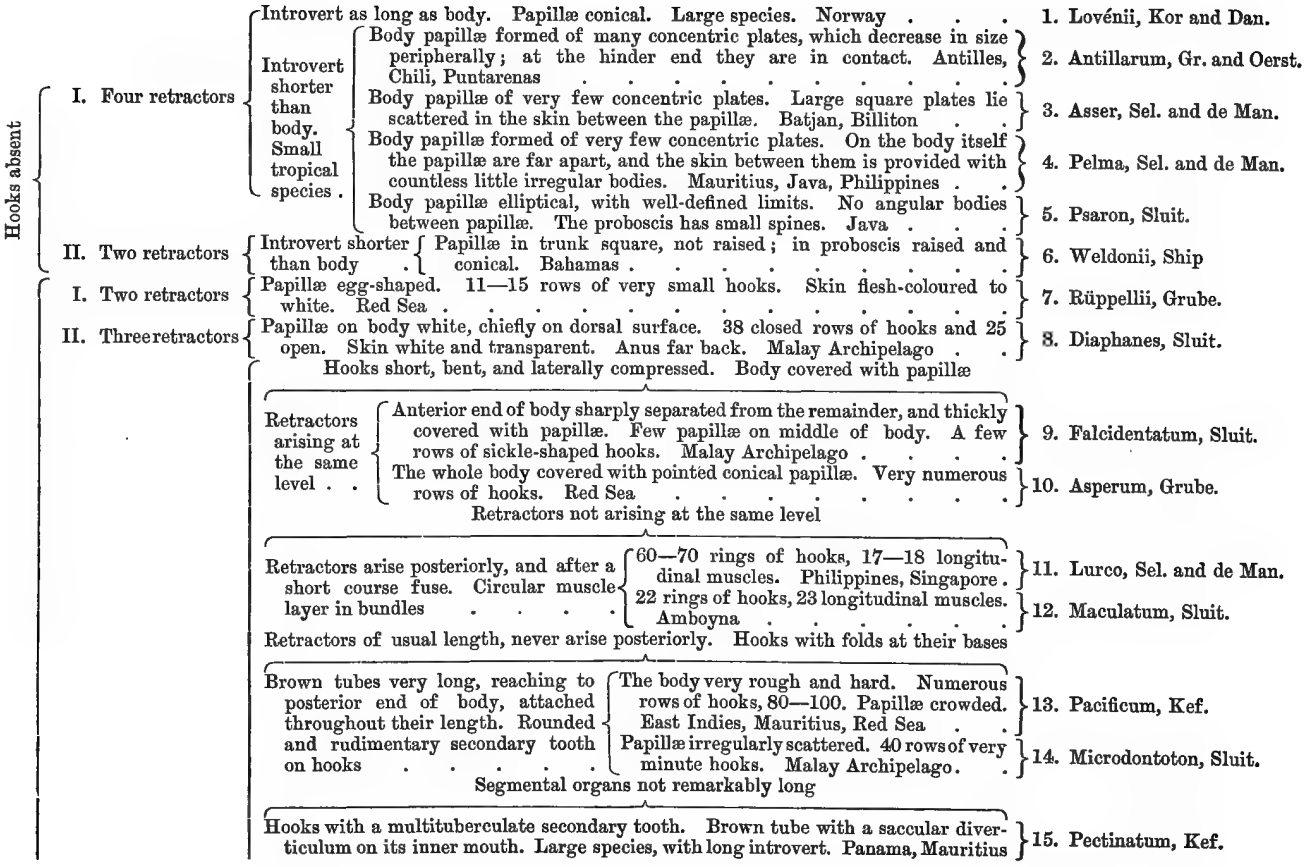
Part III.

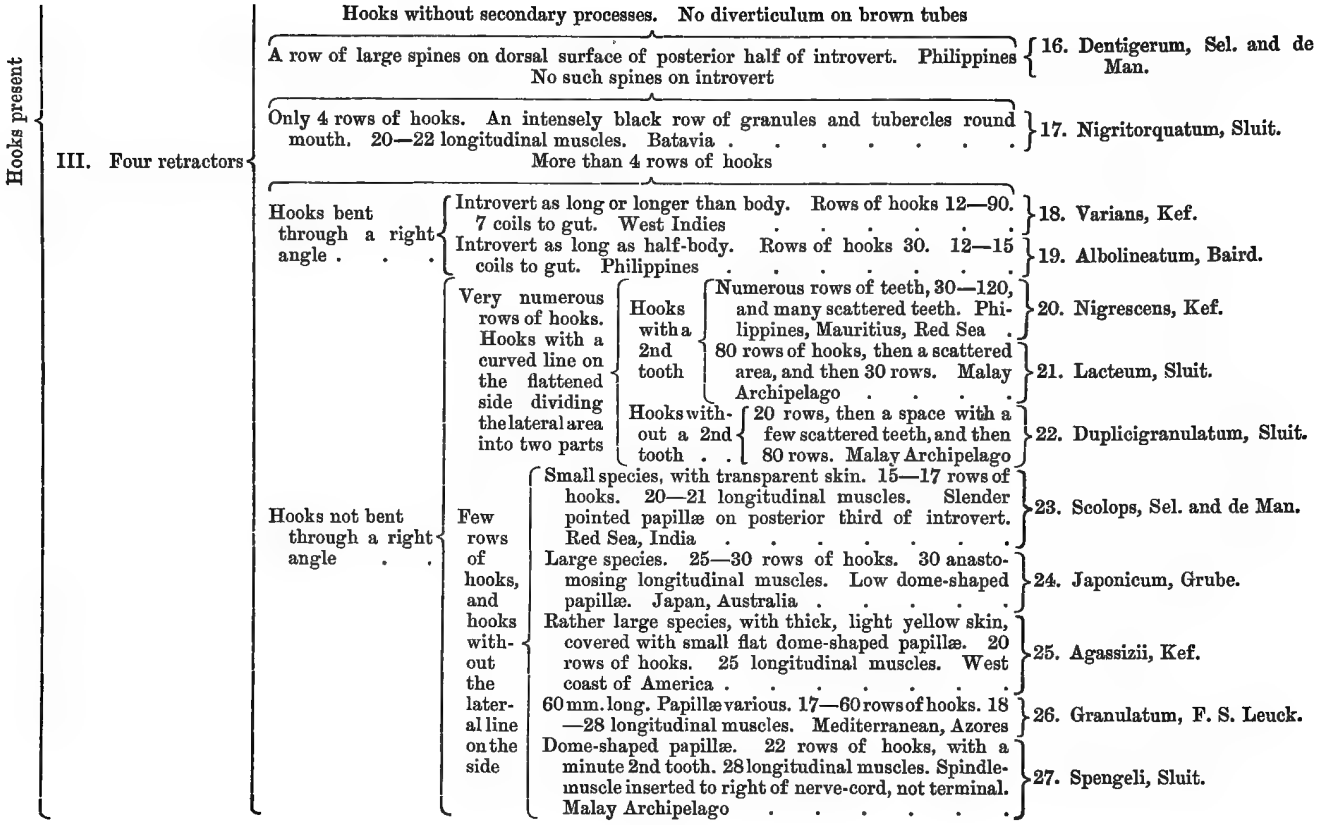
A Synopsis of the Genus Phymosoma.

In the admirable systematic monograph[1] on the Sipunculidæ, in which Prof. Selenka, with the assistance of Dr. de Man and Dr. Bülow, published the results of their work on the Gephyrea collected by Prof. Semper in the Philippine Archipelago, a synoptical table of the genus Phymosoma, which included at that time eighteen species, is published. Since 1883, the year of the publication of the above-mentioned work, nine new species have been added to the genus. Eight of these are due to the energy of Dr. Sluiter,[2] who has done so much to increase our knowledge of the marine fauna of the Malay Archipelago. The ninth was found by Prof. Weldon in the Bahamas. It will thus be seen that since the publication of Selenka's synopsis the number of described species of Phymosoma has increased by half the original. I have, therefore, prepared the following table, which is largely founded on Selenka's, but which includes those new species of the genus which have been described since the publication of his monograph.

[1] In a note in my previous paper on Ph. varians this work was inadvertently attributed to Prof. Spengel.

[2] 'Beiträge zu der Kenntniss der Gephyreën aus dem Malayischen Archipel,' von Dr. C. Ph. Sluiter.


Hooks absent
I. Four retractors
Introvert shorter than body. Small tropical species.
Introvert as long as body. Papillæ conical. Large species. Norway . . . 1. Lovénii, Kor and Dan.
Body papillæ formed of many concentric plates, which decrease in size peripherally; at the hinder end they are in contact. Antilles, Chili, Puntarenas . . . . . 2. Antillarum, Gr. and Oerst.
Body papillæ of very few concentric plates. Large square plates lie scattered in the skin between the papillæ. Batjan, Billiton . . 3. Asser, Sel. and de Man.
Body papillæ formed of very few concentric plates. On the body itself the papillæ are far apart, and the skin between them is provided with countless little irregular bodies. Mauritius, Java, Philippines . . 4. Pelma, Sel. and de Man.
Body papillæ elliptical, with well-defined limits. No angular bodies between papillæ. The proboscis has small spines. Java . . . 5. Psaron, Sluit.
II. Two retractors
Introvert shorter than body
Papillæ in trunk square, not raised; in proboscis raised and conical. Bahamas . . . . . 6. Weldonii, Ship
Hooks not absent
I. Two retractors
Papillæ egg-shaped. 11—15 rows of very small hooks. Skin flesh-coloured to white. Red Sea . . . . . 7. Rüppellii, Grube.
II. Three retractors
Papillæ on body white, chiefly on dorsal surface. 38 closed rows of hooks and 25 open. Skin white and transparent. Anus far back. Malay Archipelago . . 8. Diaphanes, Sluit.
Hooks short, bent, and laterally compressed. Body covered with papillæ
Retractors arising at the same level . .
Anterior end of body sharply separated from the remainder, and thickly covered with papillæ. Few papillæ on middle of body. A few rows of sickle-shaped hooks. Malay Archipelago . . . . 9. Falcidentatum, Sluit.
The whole body covered with pointed conical papillæ. Very numerous rows of hooks. Red Sea . . . . . 10. Asperum, Grube.
Retractors not arising at the same level
Retractors arise posteriorly, and after a short course fuse. Circular muscle layer in bundles . . . . .
60—70 rings of hooks, 17—18 longitudinal muscles. Philippines, Singapore. 11. Lurco, Sel. and de Man.
22 rings of hooks, 23 longitudinal muscles. Amboyna . . . . . 12. Maculatum, Sluit.
Retractors of usual length, never arise posteriorly. Hooks with folds at their bases
Brown tubes very long, reaching to posterior end of body, attached throughout their length. Rounded and rudimentary secondary tooth on hooks . . . . . .
The body very rough and hard. Numerous rows of hooks, 80—100. Papillæ crowded. East Indies, Mauritius, Red Sea . . 13. Pacificum, Kef.
Papillæ irregularly scattered. 40 rows of very minute hooks. Malay Archipelago. . 14. Microdontoton, Sluit.
Segmental organs not remarkably long
Hooks with a multituberculate secondary tooth. Brown tube with a saccular diverticulum on its inner mouth. Large species, with long introvert. Panama, Mauritius 15. Pectinatum, Kef.


Hooks present
III. Four retractors
Hooks without secondary processes. No diverticulum on brown tubes
A row of large spines on dorsal surface of posterior half of introvert. Philippines
16. Dentigerum, Sel. and de Man.
No such spines on introvert
Only 4 rows of hooks. An intensely black row of granules and tubercles round mouth. 20—22 longitudinal muscles. Batavia
17. Nigritorquatum, Sluit.
More than 4 rows of hooks
Hooks bent through a right angle
Introvert as long or longer than body. Rows of hooks 12—90. 7 coils to gut. West Indies
18. Varians, Kef.
Introvert as long as half-body. Rows of hooks 30. 12—15 coils to gut. Philippines
19. Albolineatum, Baird.
Hooks not bent through a right angle
Very numerous rows of hooks. Hooks with a curved line on the flattened side dividing the lateral area into two parts
Hooks with a 2nd tooth
Numerous rows of teeth, 30—120, and many scattered teeth. Philippines, Mauritius, Red Sea
20. Nigrescens, Kef.
80 rows of hooks, then a scattered area, and then 30 rows. Malay Archipelago
21. Lacteum, Sluit.
Hooks without a 2nd tooth
20 rows, then a space with a few scattered teeth, and then 80 rows. Malay Archipelago
22. Duplicigranulatum, Sluit.
Few rows of hooks, and hooks without the lateral line on the side
Small species, with transparent skin. 15—17 rows of hooks. 20—21 longitudinal muscles. Slender pointed papillæ on posterior third of introvert. Red Sea, India
23. Scolops, Sel. and de Man.
Large species. 25—30 rows of hooks. 30 anastomosing longitudinal muscles. Low dome-shaped papillæ. Japan, Australia
24. Japonicum, Grube.
Rather large species, with thick, light yellow skin, covered with small flat dome-shaped papillæ. 20 rows of hooks. 25 longitudinal muscles. West coast of America
25. Agassizii, Kef.
60 mm. long. Papillæ various. 17—60 rows of hooks. 18—28 longitudinal muscles. Mediterranean, Azores
26. Granulatum, F. S. Leuck.
Dome-shaped papillæ. 22 rows of hooks, with a minute 2nd tooth. 28 longitudinal muscles. Spindle-muscle inserted to right of nerve-cord, not terminal. Malay Archipelago
27. Spengeli, Sluit.

Part IV.

Geographical Distribution.

The genus Phymosoma contains considerably more species than any other genus of the unarmed Gephyreans with the exception of Phascolosoma. Including the new species described by Sluiter, and by Selenka in his report upon the Gephyrea collected by the "Challenger," the former genus comprises twenty-seven species, the latter twenty-five. Next to these comes Aspidosiphon with seventeen, and Sipunculus with sixteen.

Of the twenty-seven species of Phymosoma which have been described, seventeen are found in the Malay Archipelago; of these seventeen, thirteen have been found there alone, whilst four have a wider distribution. Three species are found in the West Indies, of which two are found nowhere else; five species in the Red Sea, of which two are peculiar; and four species in the Mauritius, all of which occur elsewhere.

It will thus be seen that the Malay Archipelago is the headquarters of the genus, nearly two thirds of the number of species composing the genus being found there, and nearly one half of the whole number being confined to that region. This is very possibly partly due to the fact that this region of the world is much visited by collectors, and its shore fauna is probably better known than that of any other considerable area within the tropics. On the other hand, the great predominance of the species in these seas is undoubtedly striking.

The following four species have a somewhat remarkable distribution:

(i) Ph. japonicum.—This extends along the Japanese coast, and is again met with in the Fiji Islands and off the coast of Australia. It was one of the two species brought home by the "Challenger," and was found by that expedition at Port Jackson. It thus has a considerable north and south distribution. On the other side of the Pacific we find another species,—

(ii) Ph. Agassizii, which, while it occurs as far north as the former species, reaches very much farther south. This species stretches from Vancouver's Island down the west coast of America as far as Puntarenas in the Straits of Magellan, and has been found at the intermediate points of San Francisco and Panama. The third species, with a somewhat unusual distribution, is—

(iii) Ph. Lovénii, which is found only in the Bergen Fiord. This is still further removed from the equator than the southernmost point reached by Ph. Agassizii, but it must be remembered that the Gulf Stream keeps the water on the west coast of Norway comparatively warm. Finally, we find one species,

(iv) Ph. granulatum, inhabiting the Mediterranean, and stretching out into the Atlantic as far as the Azores.

If we except the four species whose geographical distribution is described above, the whole genus is confined, with the exception of Ph. antillarum, which extends to Puntarenas, between the tropics, or only ventures just beyond them.

The species just mentioned has a somewhat curious distribution; it occurs all round the West Indian Islands, as well as at Surinam and Puerto Cabello; it then crosses over the Isthmus of Panama, and is found along the coast of Chili and Puntarenas. Another West Indian species, Ph. pectinatum, is found on the west coast of America, and turns up again at Mauritius, but has not been described from anywhere else. Finally, Ph. pacificum has a wide range, stretching from the Red Sea by the Mauritius and India to the Malay Archipelago, and thence to the Philippines and the Fiji Islands; and Ph. scolops has a very similar range, occurring in the Red Sea, at Singapore, at the Philippines, and also off the Mozambique coast.

With regard to the bathymetrical distribution of the members of this genus there is little to say; they all live in shallow water, and the greatest depth which I have seen mentioned in connection with them is fifty fathoms.

It is not possible to arrive at any very satisfactory results

from the scanty material at our disposal, with reference to the geographical distribution of this Gephyrean. Nevertheless, so little has been done with regard to the distribution of the lower marine invertebrates, that it seemed to me to be worth while to put together what is known about the occurrence in space of the genus I have been lately working at. The most striking deductions from the facts before us are—(i) the importance of the Malay Archipelago as the headquarters of the genus, but this is possibly more apparent than real; (ii) the restriction, with few exceptions, of the genus to tropical seas; and (iii) their preference for shallow waters. The last two generalisations are obviously connected with the fact that the animals only flourish in comparatively warm water.

In conclusion, attention may be drawn to the association of these animals with coral islands. This may be accidental, and due to conditions of temperature only; but, on the other hand, several species make their homes in tubular holes burrowed out in the soft coral rock.

The Morphological Laboratory;
Cambridge, July, 1890.

DESCRIPTION OF PLATE XII,

Illustrating Mr. Arthur E. Shipley's paper "On a New Species of Phymosoma, with a Synopsis of the Genus, and some Account of its Geographical Distribution."

Fig. 1.—A view of Phymosoma Weldonii, enlarged 3 diameters. The introvert with its conical papillæ is slightly protruded.

Fig. 2.—A conical papilla from the introvert, seen from the side and from above.

Fig. 3.—Some of the depressed oblong papillæ from the trunk, enlarged to show the pore and the cuticular plates.

Fig. 4.—A view of the animal cut open just to the right of the middle ventral line. The introvert is retracted. The ventral nerve-cord is seen running up the introvert and back close to the cut edge; the right and left retractor muscles and the two kidneys lie on each side of the coiled intestine. The kidneys are much elongated, and show irregular swellings. The heart with its diverticula is seen in places. The longitudinal muscles of the body-wall are not indicated. Enlarged $2\frac{1}{2}$ diameters.

Fig. 5.—A diagrammatic view of the head of Phymosoma Weldonii. The collar is completely expanded, and surrounds the head. Part of the outer limb of the lophophore involving about ten tentacles has been removed in order to show the pigmented area within the lophophore, and the inner circlet of tentacles. The lower lip surrounds the mouth, and at its dorsal end fuses with the end of the lophophore. The dorsal side of the tentacles, which are fully expanded, is pigmented. The lophophore is represented too flat; it should be oblique and overhanging the mouth.

Fig. 6.—A surface view of a piece of the wall of the kidney, showing the glandular areas—crypts—separated from one another by muscle-fibres.

Fig. 7.—An enlarged view of the end of the coiled intestine, with the heart partially dissected out. The spindle muscle running up the axis of the coil is shown near its termination by the anus. The anterior ends of the kidneys are seen right and left.

Fig. 8.—A transverse section through the base of the lophophore, showing the lower lip, the mouth, some isolated tentacles, the fused bases of others, and their blood-vessels and nerves. The fusion of the dorsal ends of the lower lip and of the lophophore, and the distribution of the pigmented and ciliated epithelia are seen.

Fig. 9.—A transverse section through a trunk papilla. This shows some circular muscle-fibres, the ectodermic epithelium passing into the gigantic

excretory cells. Some of the latter contain crystals, others large granules. Only that part of the cuticle which is modified to form the horny plates is shown. Between the plates and round the pore are pigment granules.

Fig. 10.—A transverse section through the skin of the introvert and the ventral nerve-cord. The introvert is retracted so that the outer surface is concave, the inner convex. The section shows the conical papillæ, the thick cuticle with pigment granules, the single layer of ectoderm-cells, the continuous layer of circular and longitudinal muscles, the latter broken only for the insertion of the mesentery supporting the ventral nerve-cord; and the peritoneal epithelium. The nerve-cord shows the dorsal disposition of the nerve-fibres and the ventral ganglion-cells. Some of the secondary nerves are cut as they leave the cord and traverse the mesentery.

Fig. 11.—A transverse section through both the external and internal openings of the nephridium. The structure of the skin is shown, and four of the circular nerves arising from the ventral nerve-cord are seen. The outer wall of the nephridium is fused with the integument, but becomes free posteriorly. The section does not show the whole of either opening, as they do not lie wholly in one plane.

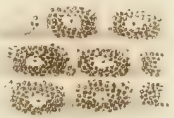
Fig. 12.—A section through the integument.

Mr. Wilson, of the Cambridge Scientific Instrument Company, has drawn Figs. 1 and 5, and Figs. 4 and 7 are drawn from sketches made by Prof. Weldon in Bimini.

Fig. 2.

SIDE VIEW. UPPER VIEW.

Fig. 3.



UPPER VIEW

Fig. 4.

Fig. 1.

Introvert

Fig. 6.

Fig. 8

Fig. 7

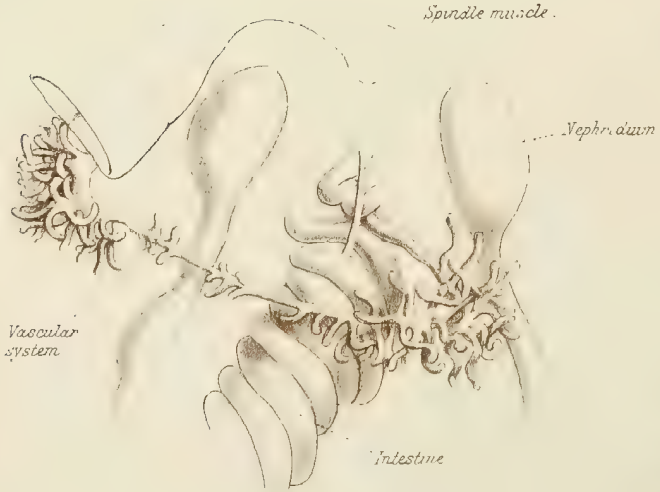


Fig. 9.

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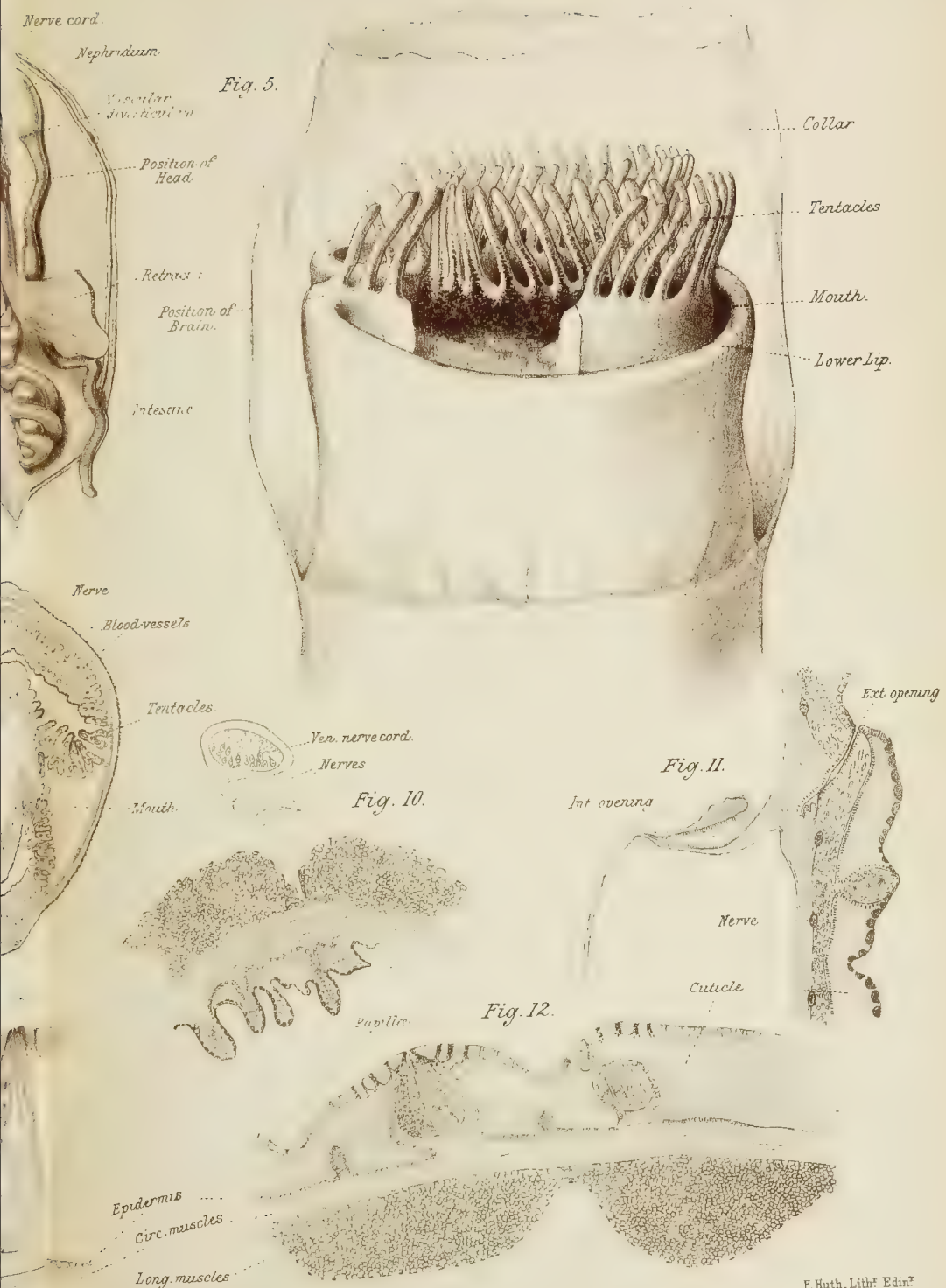

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THE MEDUSÆ OF MILLEPORA MURRAYI AND THE GONOPHORES OF ALLOPORA AND DISTICHOPORA

BY

SYDNEY J. HICKSON, M.A., D.Sc., &c.,
Fellow of Downing College, Cambridge.

With Plates XIII and XIV.

I. The Medusæ of Millepora murrayi.

In 1884, Quelch (**11**), while examining the structure of the hard parts of a new species of Millepora (M. murrayi), discovered a number of small cavities which he supposed to be the receptacles of the ova or embryos like the ampullæ of the Stylasteridæ.

Professor Haddon has recently placed in my hands some excellently preserved specimens of a species of Millepora that he collected on the reefs of one of the islands in Torres Straits. This species seems to be closely allied to Quelch's Millepora murrayi, but the identification is a matter of some difficulty, as the pieces at my disposal are small.

On making a series of sections through a portion of a decalcified branch I discovered a number of medusiform structures, each bearing a large saucer-shaped spermarium. They are situated immediately beneath the surface, and covered by an operculum of modified ectoderm cells.

Sections made by von Koch's method of grinding hard and soft parts together in solid Canada balsam show further that

these medusæ exactly fit into the ampullar cavities of the skeleton, and form the only explanation of their presence. The eggs of this species are, as in Millepora plicata (**6**), very small and contain no yolk, and I have seen no embryos and no parasites that could cause or fit into these cavities. Quelch's ampullæ, then, are the cavities that contain male medusæ.

The Structure of the Medusæ.—The medusæ may be found in all stages of development in the different parts of the same branch. They are very irregularly distributed, and it is difficult at present for me to give any hints to guide naturalists in the search for them. They are never found, so far as my experience goes, close to the free extremities of the branches. In my specimens they were found in greatest abundance at a distance of three-quarters of an inch to one inch from the free extremity, but a few specimens were found quite close to the attached base of the colony. Some branches appear to be devoid of them.

All the stages of development may be found with care and patience, but the stage represented in fig. 10 is the most frequent in my preparations.

A central MANUBRIUM (*Man.*) hangs in the sub-umbrella cavity bearing the large spermarium (*Sperm.*). It is composed of irregular endodermal cells, and contains a considerable cavity continuous with the cavity of the subjacent cœnosarcal canals.

The SPERMARIUM appears to be double in section, but is really saucer-shaped. It contains a large number of spherical spermoblasts lying in a homogeneous fluid (?). It is covered by a very thin coat of flattened ectoderm cells continuous with the inner ectodermic lining of the umbrella.

The UMBRELLA is composed of three layers: a median layer of solid endoderm continuous with the endoderm of the manubrium, and an inner and outer sheath of ectoderm continuous with one another at the free rim of the umbrella.

The inner sheath of ectoderm is, as mentioned above, continuous at its proximal side with the thin coat of ectoderm covering the spermarium. The outer sheath is continuous

with a sheath of ectoderm (*Gon.*) lining the cavity of the ampulla; and this again is continuous with the superficial ectoderm of the colony.

At the margin of the umbrella both ectoderm and endoderm are thicker than they are elsewhere, and the medusa presents in consequence a thickened rim at its free border. There are no radial or ring canals. In medusæ at this stage no cavity is apparent between the outer wall of the umbrella and the ectoderm lining the ampulla.

Above the codonostome (i.e. mouth of the umbrella) there is an operculum (*op.*) of flattened ectoderm cells continuous with the superficial ectoderm and the ectoderm lining the cavity of the ampulla, which completely closes the gonangium.

Different Forms of the Medusa.—The spermarium varies immensely in size. Sometimes it is simply a thickened ring round the manubrium, sometimes it nearly fills the cavity of the umbrella. In consequence perhaps of this variation in the size of the spermarium, the appearance of the manubrium varies. In fig. 10 the manubrium is a large well-developed structure with a considerable lumen. In fig. 9, which represents a younger stage, there is no manubrium at all apparent, but the spermarium simply rests on an irregular mass of vacuolated endoderm cells. Many intermediate conditions between these two extremes may be observed. Further, the condition of the endoderm of the manubrium presents many variations. In some cases the cell outlines are well marked, and the nuclei regular in position and spherical in shape. In other cases the endoderm is a loose vacuolated tissue in which no cell outlines can be distinguished, and the nuclei are irregular in shape and scattered through the spongy substance of the tissue.

It is not my purpose to offer in this place any explanation of these appearances. I wish merely to call attention to them before passing on to other matters.

Development of the Medusa. The medusa of Millepora is a transformed zooid. It is not a zooid specially modified from its first appearance to bear the spermarium, but an ordinary zooid of the colony changed into a medusa after the

migration of spermospheres into its ectoderm, and subsequent development there.

The evidence that supports this statement rests upon a number of observed facts, that for convenience' sake may be arranged under the following heads:

1. The various stages in the transformation of the zooids into medusæ that can be observed in sections of the decalcified corallum.

2. The absence of any structure that can be compared to the ectodermic invagination, called the entocodon or glockenkern, that characterises the early stages in the development of the medusa of the Hydroidea.

3. The position of the medusæ in the colony.

4. The presence of large nematocysts in the superficial ectoderm above the younger forms of medusæ.

1. The most important of these, and the only one upon which much stress can be laid, is the first. The others afford the necessary confirmation.

The earliest recognisable forms of the sperm mother-cells are found in the canals in the immediate neighbourhood of the zooids (*Sperm.* S_2., fig. 1). They migrate from this position into the ectoderm of the zooids, where they collect together to form a spermarium.

That the sperm mother-cells do actually migrate from the germinal epithelium into the zooids seems to me to admit of no doubt. The youngest stages of the germ-cells are never found in any part of the zooids, and the youngest stages of the zooids never bear either germ-cells or spermoblasts. These two observations prove, firstly, that the germ-cells do not arise in fully developed zooids; and secondly, that new zooids or medusæ are not formed at the localities in the canals where the germ-cells arise. They must, therefore, move from the position where they are first developed to the position they occupy in the zooid.

In a few cases I have seen two or three spermospheres (*Sperm.* S_2., fig. 1), or aggregations of spermospheres, lying separately in the ectoderm of the zooids, but in the majority

of cases there is but a single cluster or aggregation (figs. 2, 3, and 4). The largest and most fully developed of these lie at the apex of the zooids (figs. 5, 6, and 7).

The conclusions from these facts seem to be that the germ-cells developing in the canals until they reach the stage corresponding to the sperm-morula or spermosphere migrate towards the zooids, fusing into aggregations as they do so. Having reached the zooids they take up a position between the ectoderm and endoderm of their apices, and continue there the later stages of their development.

The spermospheres are most frequently found in the dactylozooids, but in a few cases I have found them in gastrozooids (fig. 3). They have probably no preference for either the one form or the other; but they are found more frequently in the dactylozooids, partly because these forms are more numerous, and partly because the gastrozooids are usually more remote from the larger cœnosarcal canals.

The spermarium having been formed at the apex of the zooid certain noticeable changes take place. In the first place by a thickening of the ectoderm the pore becomes narrowed (figs. 5, 6, and 7). The tentacles become flattened out, and the nematocysts disappear. The spermarium sinks into a cup-shaped receptacle on the summit of the zooid, and the endoderm of the edge of the cup grows out, pushing before it the ectoderm.

These changes are represented in the two figs. 6 and 7 In the next stage the cup-shaped receptacle of the spermarium has grown out into a bell-shaped structure (fig. 8). The spermarium is much larger in size, and the pore is completely closed by ectoderm. In the later stages (figs. 9, 10, and 11) the following changes may be noted. The operculum is formed, shutting off all access from the cavity of the gonangium to the exterior. The walls of the bell-shaped outgrowth become considerably attenuated, and lie close against the ectodermic wall of the ampulla. The manubrium is formed probably by a regeneration of the endodermic tissue and its growth into the centre of the spermarium.

In the last stage I have observed the medusa is completely separated from the canal system, and lies freely within the cavity of the ampulla. The walls of the umbrella, except at the margin, are extremely thin. The manubrial endoderm contains a closed cavity (fig. 11). This stage is probably the last that occurs before the embryo escapes from the corallum. There are no nematocysts developed on the thickened margin of the umbrella, there are no sensory bodies, there is no velum, and no mouth.

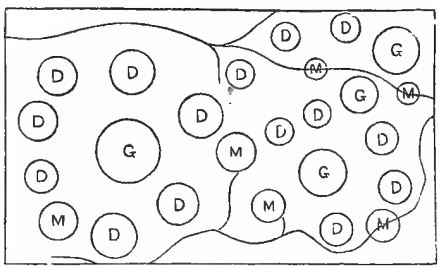
2. In the development of the medusæ of Millepora that has just been described there is no structure formed at any time that can be compared with the inner fold of ectoderm or "glockenkern" that forms the walls of the sub-umbrella cavity of the medusa of the Hydroidea. Had such a structure been found, there might have been some ground for supposing that this medusa is a bud that grows out of the degenerated tissues of a zooid. The medusæ of Millepora are, however, certainly not formed by budding from the zooid in the sense that the medusæ of such a form as Corymorpha are budded from the hydranth.

3. The diagrammatic figures that are frequently given of zooids of Millepora, representing a centrally placed gastrozooid in a complete circle of dactylozooids, is perfectly correct for some species of Millepora and the younger branches of others.

In M. murrayi the zooids are scattered over the older parts of the corallum in an irregular manner. The circular systems can be made out, but over and above the zooids in their regular circles there are both gastrozooids and dactylozooids scattered irregularly within and between the circles (cf. Quelch [**11**], p. 192).

The medusæ occur both in the regular circles and irregularly between them, as may be seen by reference to Woodcut 1. When a piece of Millepora is decalcified and cleared in oil of cloves or turpentine, and examined with a low power of the microscope, the arrangement of the zooids, medusæ, and cœnosarcal canals can be very readily observed. The figure I have

given was drawn, by the help of the camera, from such a preparation. The larger canals to which I have referred above form a wide-meshed network immediately below the surface. Each mesh is an irregular polygonal figure embracing the



WOODCUT 1. Diagram of the arrangement of the zooids and medusæ of Millepora murrayi. G. Gastrozooids. D. Dactylozooids. M. Medusæ. The larger canals are represented by irregular black lines.

whole of one circular system of zooids. The medusæ are always found either upon or quite close to these large canals, and thus they are sometimes without the circles, and sometimes in a position corresponding to that of a dactylozooid of the regular circle.

The position of the medusæ in the colony cannot be used as an argument against my statement of their origin; in fact, whatever bearing it may have is in its favour.

4. When a decalcified specimen of Millepora is examined from above, a cluster of large nematocysts may be seen at the mouths of the gastropores and dactylopores. They may also be seen in sections (figs. 1, 2, 6, 7, *Nemat.*). When the medusa is formed and the pore closed by the operculum these large nematocysts can be of little or no service, so they are shot and no new ones take their place. In the figures of the sections through the older medusæ (9, 10, 11) the reader will notice that none of these large nematocysts are to be seen. Where the operculum is not completely formed (fig. 8), although the zooid has to all appearance changed into a medusa, one or two of these large nematocysts remain.

II. The Male Gonophores of Alloporа and Distichopora.

1. Distichopora.—The male gonophores of Distichopora may be seen in clusters on the branches of the male stocks. They are small whitish bodies lying in the ampullæ of the cœnosteum, and covered by a very thin semi-transparent wall of lime and cœnosarcal canals.

An examination of a series of sections through one of these branches shows that the male gonophores are found only in these superficial clusters (fig. 12). They are never found deeply seated in the cœnosteum, nor in other places than those indicated by external appearances.

One, two, or even three gonophores, in different stages of development, springing from a diverticulum of the cœnosarcal canal system, may occupy each ampulla.

A ripe male gonophore (fig. 14_1) is a spherical, oval, or pear-shaped body, with an endodermal cell-mass, representing the trophodisc on the side turned towards the axis, and a short conical or tubular seminal duct on the side turned towards the periphery. The sheath of the gonophore seems to be a simple layer of flattened ectoderm; but I am persuaded, after the examination of a great many sections and the study of the development, that two layers are represented, the inner or endodermal layer being extremely attenuated and devoid of nuclei.

When a very young bud is examined with a high power (figs. 13_2, 14_3, 15), the rudiment of the spermarium may be seen to be a homogeneous mass of protoplasm, containing a number of large spherical nuclei. It occupies a position apparently between the ectoderm and endoderm of the bud. As the spermarium increases in size the endoderm becomes cup-shaped in the bud, and the margins of the cup are produced into a very thin sheath between the ectoderm and the spermarium (fig. 16). At the peripheral pole of buds that are about half-way developed there is a thickening of the two sheaths of the gonophores, cell outlines are well marked, and

the cells are nucleated (figs. 14 and 16). In this way the first rudiment of the seminal duct is formed. The two layers are from their first appearance quite distinct from one another, and there is never any indication that the two cell layers are formed by a splitting of the ectoderm. Just before the spermarium becomes mature the ectoderm, and subsequently the endoderm, are folded to form a conical cap, and this subsequently pushes through the superficial covering of the gonangium to form the seminal duct to the exterior (fig. 18).

Meanwhile, changes have taken place in the endoderm at the base, i.e. on the axial side of the bud. In the early stages of the bud there is a wide lumen in the endoderm, the cells are cubical in shape, and their outlines well marked; in the later stages the lumen becomes obliterated, the cells lose their distinct outline, and the endoderm degenerates into an irregular mass of tissue, with scattered nuclei (figs. 13, 14, 15, 16).

2. In Allopora (fig. 19) the male gonophores are scattered irregularly in the corallum, and lie at such a distance from the surface that there is no trace of their existence externally. I have been able to find them only in the old thick branches. I cannot say for certain whether Allopora is hermaphrodite or dicœcious. The specimens at my disposal consisted of a number of fragments in a bottle, and I found on the smaller and younger branches numerous female gonophores, and on the thicker and older branches numerous male gonophores; but I have not found both sexes on the same branches. I have no information whether the older and younger branches in the bottle are fragments of the same colony. If Allopora is not dicœcious, then it is probably protogynous, like Millepora, the female sexual cells being formed first in the younger parts of the colony, and the male sexual cells later in the older parts.

The male gonophores of Allopora resemble those of Distichopora in every detail of structure except one, and that is that the endoderm of the base is produced into the substance of the spermarium as a club-shaped spadix or manubrium (fig. 20, *Spa.*).

The spermarium is covered by a double sheath of very thin ectoderm and endoderm, and the seminal duct is produced in the same way that it is in Distichopora. When the spermarium is ripe the seminal duct perforates the superjacent structures, and serves as the duct for the spermatozoa to escape to the exterior. As the gonophores of Allopora are situated much more deeply than they are in Distichopora, the seminal ducts are considerably longer.

As a rule, only one gonophore is seen in each ampulla of Allopora, but occasionally two (fig. 19, gonophore 2), and very rarely three, in different stages of development may be seen.

Lastly, it must be observed that the fully developed male gonophores of Allopora are much larger than those of Distichopora.

From a large number of measurements I have obtained the following average measurements:

Longest diameter of male gonophores of Allopora . 0·38 mm.
" " " Distichopora 0·19 "

The male gonophores of a few species of Stylasteridæ have been described by Moseley (**10**).

In Sporadopora dichotoma the specimens were all males. "They are ovoid bodies with the long axes directed at right angles to the surface of the coral. Sometimes only one such body is present in an ampulla; sometimes two or three. The outer extremities of the gonophores are sometimes drawn out into a short tail-like prolongation." This structure probably corresponds with the seminal duct of Allopora and Distichopora. "There is a cylindrical spadix in the centre. The bases of the gonophores are continuous with large canals of the cœnosarcal meshwork, the endoderm of the spadix being continuous with that of these canals."

In Pliobothrus symmetricus the male gonophores are sacs containing a number of small ovoid bodies, which contain spermatozoa, or sperm-cells, in various stages of development. The exact structure of these smaller bodies and their relations to the endoderm were not determined.

Only male specimens of Stylaster densicaulis were obtained. Each male ampulla contains two or three ovoid gonophores, which are attached to large offsets of the cœnosarcal meshwork at one end of their longer axes. They have an internal spadix, and in finer structure seem to differ very little from the male gonophores of Sporadopora.

Moseley also describes the male gonophores of Allopora profunda, and remarks that they are very similar to those of Sporadopora. He does not figure the seminal duct of this genus.

Only one male specimen of Astylus subviridis was examined by Moseley. "The male gonophores appear as large rounded lobulated masses resting within the ampullar sacs, and springing from stout offsets of the cœnosarcal meshwork, which pass into the sacs to reach them..... The sac as it enlarges becomes gradually pedicellate, and, when mature, is attached to the central mass by a narrow pedicle of some length. The walls of the pedicle are continuous with the ectodermal wall of the sac, which wall contains well-developed nuclei in its substance. Within the sac of the lobule a second sac, composed of a finer membrane, encloses the mature or developing generative elements. The wall of this inner sac is not prolonged into the cavity of the pedicle, but, passing across its commencement, shuts off the main cavity of the lobule from this latter..... No rounded spadix, such as that occurring in Allopora, is present in the interior of the lobules." These gonophores seem, from the figures and the description given, to be very similar to those of Distichopora.

It is not at all probable that Moseley overlooked the spadix, for in his figure there are represented no fewer than seven gonophores; and he remarks that his material was in a good state of preservation. The "inner sac" of the gonophore that he mentions and figures is most probably the same as the inner endodermic lining that I have described in both Allopora and Distichopora. It would be certainly very remarkable if this membrane is not attached to the endoderm of the pedicle in Astylus, but this point can only be deter-

mined with accuracy by the examination of a continuous series of sections.

The male gonophores of Cryptohelia pudica seem to be similar to those of Astylus.

III. The Female Gonophores of Distichopora.

The position of the female gonophores of Distichopora can be readily seen on the female stocks by the prominent swellings on the surface of the corallum. They are usually situated on only one side of the thicker branches, but occasionally there may be found in addition a small cluster on the opposite side.

A section through one of these clusters shows the eggs and embryos in many stages of development, from the minute immature yolkless eggs in the cœnosarcal canals to well-advanced planulæ (fig. 21).

The mature ova (fig. 23, *ovum*) are 0·3 to 0·4 mm. in diameter, and contain a large number of spherical yolk-globules. The large germinal vesicle is situated close to the peripheral border of the egg, and is surrounded by a number of yolk-globules much smaller in size than those of the other part of the egg. The egg rests in the cup-shaped trophodisc (cf. Allopora, Hickson, 7), and is covered by a thin coat of ectoderm and endoderm. The trophodisc is similar to that of the female gonophores of Allopora, but not so complicated in its foldings. In transverse section it exhibits twelve pouches at its margin (fig. 24). In vertical section it is simple (fig. 23); the inner and outer pliets that I have described in Allopora are not found in this genus.

When fertilisation has taken place the germinal vesicle loses its sharp outline, and remarkable changes occur in the shape and arrangement of the yolk-globules. My observations are not yet complete of the early stages of the development, but I hope to be able to publish shortly a separate memoir, giving a full account of the development of this form up to the stage when the larva escapes from the ampulla.

During the early stages of development the trophodisc rapidly atrophies, and by the time a layer of columnar epiblast-cells has formed round the embryo no recognisable trace of it can be seen (figs. 22 and 25).

In the meantime young eggs are migrating from the subjacent canals to the base of the ampulla, and in many cases before the larva has escaped a new egg, borne by a new trophodisc, occupies a considerable space in the same ampulla (fig. 25).

The young eggs (fig. 22, *ov.*) are frequently seen quite deeply situated in the canal system; those that are nearer to the ampullæ are larger in size and amœboid in shape. As soon as they reach the ampulla they show very minute yolk-granules, which increase in size with the growth of the egg and the development of the trophodisc.

The female gonophores of a few species of Stylasteridæ have already been figured and described by Moseley (**10**).

In Pliobothrus symmetricus "the gonophores are contained in ampullæ which are often sunk deep in the cœnosteum. .... The ova are solitary, one only being developed in each growing ampulla. Each ovum is developed within the cup of a cup-shaped spadix," i.e. trophodisc. "As the ovum advances in development and increases in size the spadix enlarges with it. Subsequently, however, in later stages, the spadix appears not to increase further, and when in relation with a nearly fully developed planula appears proportionately small."

In Errina labiata "the female gonophores are closely similar in structure to those of Pliobothrus symmetricus; but there is this great difference, that whilst in Pliobothrus the ampullæ and their contained ova and planulæ remain until maturity immersed in the cœnosteum beneath its surface, in Errina the ampullæ project more and more above the surface as development proceeds.

"The spadix in Errina labiata is at first cup-shaped, the walls of the cup being composed of a very thick layer of endoderm. The cavity of the cup is directed towards the surface of the coral, and within it rests the single large ovum with its

distinct germinal vesicle and spot. Each ampulla contains invariably only one spadix and ovum."

Moseley gives a detailed account of the female gonophore of Cryptohelia pudica. In a late stage the trophodisc is "complicated at its margin by subdivision of its lobes, which form a network over one half of the surface of the ovum, terminating in a fringe of numerous tentacula-like lobes."

From these descriptions of Moseley and my own it seems probable that the female gonophores of the various genera of Stylasteridæ are very similar in general structure to one another. Moseley does not describe nor figure an inner endodermal membrane covering the egg, but in other respects his descriptions of the female gonophores of the three genera, Errina, Pliobothrus, and Cryptohelia, agree with mine of Allopora and Distichopora. The chief point of variation among the different genera is probably the lobulation or branching of the margins of the cup-shaped trophodisc.

I prefer to retain the word trophodisc that I introduced in a former paper to the word spadix used by Moseley for the cup-shaped receptacle of the ovum. This structure cannot be considered to be strictly homologous with the spadix or manubrium of the adelocodonic gonophore of the Hydromedusæ. It seems to me to be more probable that it is homologous with the umbrella.

IV. The Gonophores of the Hydrocorallinæ and Hydromedusæ compared.

In the absence of a knowledge of the minute anatomy of the gonophores of the Hydrocorallinæ, the true position of this group in the classification of the Hydrozoa has not yet been very satisfactorily made out.

The peculiar characteristics of the group, namely, the dimorphism of the polyps and the extensive skeleton of carbonate of lime, have not been considered by naturalists to be of sufficient

importance by themselves to justify the separation of the Hydrocorallinæ from the Hydromedusæ.

Lankester (9) places them in a separate order of the subclass Hydromedusæ.

In the classification used at Cambridge Balfour placed Millepora and the Stylasteridæ in the sub-order Hydroidea of the order Hydromedusæ.

Claus, in his 'Grundzuge der Zoologie,' makes the Hydrocorallinæ the first sub-order of the order Hydromedusæ.

In Jackson's edition of Rolleston's 'Forms of Animal Life' (8) the order Hydroidea is divided into the three sub-orders (1) Tubulariæ, (2) Hydrocorallinæ, and (3) Campanulariæ.

The opinion I have come to, based upon Moseley's researches and my own, is that the Hydrocorallinæ should be placed in an order apart from the Tubulariæ and Campanulariæ (i.e. Hydroidea of Balfour and Jackson).

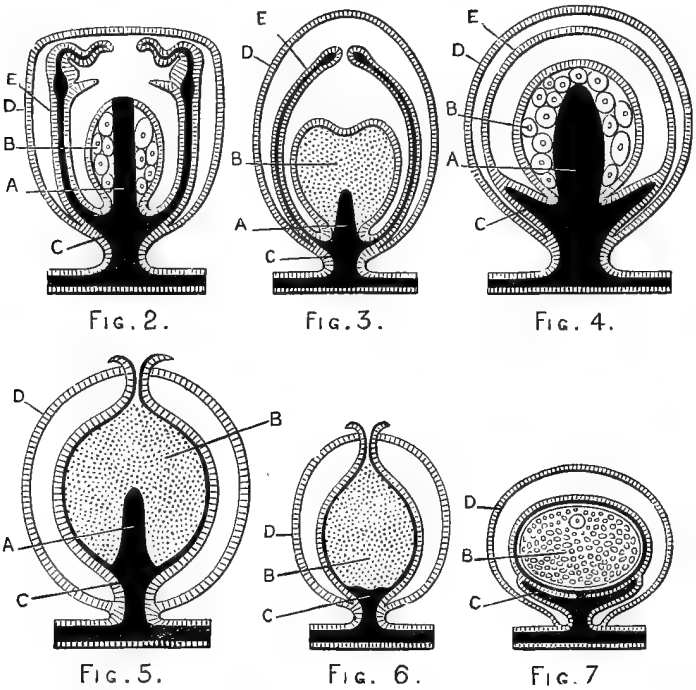
The classification of the Hydrocorallinæ with the Hydroidea was perfectly justified by the state of knowledge at the time. Both dimorphism and skeletal structures are, comparatively speaking, uncertain features for the purposes of classification, and the character and structure of the polyps and their connecting canal systems show undoubted affinities with many forms of Tubulariæ.

Unless, then, the organs that bear the sexual products can be shown to differ very widely from those of the Hydroidea, and present characteristics peculiarly their own, the Hydrocorallinæ must remain in the position that is assigned to them by some authorities in the order Hydroidea.

These considerations demand a careful and exhaustive comparison of the typical gonophores of the Tubulariæ, and of those Hydrocorallines that are at present known to us.

To aid in the discussion of the homologies I have given on p. 390 diagrammatic figures representing the structure of (Woodcut 2) a phanerocodonic medusa, (3) a medusa of Millepora, (4) an adelocodonic medusa, (5) the male gonophore of Allopora, (6) the male gonophore of Distichopora, (7) the female gonophore of Distichopora.

Figs. 2 and 4 are copied from Allman with this modification, that both endodermal tissue and endodermal cavity are



Woodcuts 2—7. The structures of the different gonophores compared. Diagrammatic sections of—2. A phanerocodonic gonophore. 3. The Medusa of Millepora. 4. An adelocodonic gonophore. 5. Male gonophore of Allopora. 6. Male gonophore of Distichopora. 7. Female gonophore of Distichopora. A. Manubrium. B. Gonad. C. Endoderm. D. Ectoderm. E. Umbrella.

represented in black. The diagrams are modified in this way, because no important morphological distinctions can be drawn between endodermal structures possessing a cavity and those that do not. For example, no one would think of drawing a fine morphological distinction between the dactylozooids of Millepora and those of Allopora because in the case of the

former there is a lumen and in the case of the latter the endoderm is solid.

In comparing the structure of the phanerocodonic medusa and the medusa of Millepora a very general similarity may be observed.

In both there is a centrally placed manubrium (A).

In both the generative elements (B) are developed between the ectoderm and endoderm of the manubrium.

In both there is a contractile bell umbrella, from the centre of whose concavity the manubrium is suspended; in both this umbrella is composed of a centrally placed sheath of endoderm covered by a sheath of ectoderm on both sides; and in both the gonophore lies in a gonangial cavity of ectoderm, which, before the medusa is set free, is continuous with the ectoderm of the outer wall of the umbrella.

The principal points in which these two forms differ from one another are these:

The manubrium of 2 possesses a mouth.

The manubrium of 3 does not.

There is a system of canals (longitudinal and ring) in the umbrella of 2.

There are no canals in the umbrella of 3.

There are tentacles and sensory epithelium at the margin of the umbrella in 2.

There are no tentacles or sensory epithelium at the margin of the umbrella of 3.

There is a velum in 2.

There is no velum in 3.

Too much stress should not be laid upon any of these points of difference, for it is quite possible that tentacles, eyes, or auditory organs, a velum and a system of gastro-vascular canals, may be subsequently developed in the medusa of Millepora after it is set free.

It is of importance to note, however, that these organs are not developed while the medusa is still attached to the parent stock, as they are in the typical phanerocodonic medusa of the Tubulariæ.

Comparing the medusa of Millepora with the adelocodonic gonophore (fig. 4) of Hydromedusæ, the following points of difference may be observed:

There is a codonostome in the former, there is none in the latter.

In the former the endoderm extends almost to the margin of the umbrella, in the latter the endoderm is reduced to a shallow cup surrounding the base of the manubrium.

In other respects the two gonophores are practically similar.

Comparing the adelocodonic gonophore (fig. 4) with the male gonophore of Allopora (fig. 5), two points of difference may be observed. In the first place the endoderm completely surrounds the gonad in the latter, excepting at a small aperture at the distal pole, where it forms the inner wall of a narrow seminal duct. Secondly, there is no layer of ectoderm between this endoderm and the gonad in Distichopora. In the adelocodonic gonophore there are two layers of ectoderm between the gonad and wall of the gonangium.

The male gonophore of Distichopora (fig. 6) resembles that of Allopora (fig. 5) in all respects except one, namely, that in the former there is no manubrium.

The female gonophores of the two genera of Stylasteridæ resemble the male gonophores in most respects, but in the former there is a more complicated plieting of the base to form a nourishing disc (trophodisc), and no structure corresponding to a manubrium can be observed.

Do these gonophores of the Hydrocorallinæ represent stages in the degeneration, or do they represent stages in the evolution of the free medusiform gonophore?

It would be more satisfactory, perhaps, to leave these questions to be answered at a time when we are better acquainted with the minute anatomy of the gonophores of other species of Millepora and the other genera of the Stylasteridæ.

The very convincing proofs that have been brought forward by Balfour, Weismann, and others, showing that the gonophores of the Hydroidea, however simple in structure, represent stages

in the degeneration of medusæ, may lead to the conclusion that these gonophores of the Hydrocorallines are also degenerate medusæ; and it is necessary to issue a warning that this is probably not the case.

That the medusa of Millepora is not degenerate but primitive in its simplicity must be apparent.

In the course of its development there is no abbreviation nor any trace of organs that were at one time functional and have since become rudimentary. Moreover, it cannot be considered at all probable that a free-swimming medusa, bearing immature spermatozoa, would have lost its mouth, tentacles, sensory organs, endoderm canals, and velum; or, if it is a degenerate medusa, that the development of these organs would be postponed until after its escape.

The only view that seems to me to be at all tenable is the one that considers the medusa of Millepora to be primitive in its simplicity.

As regards the male gonophores of Allopora and Distichopora, there is without doubt a close similarity in appearance between certain stages in the development of the male gonophores of both these genera and the younger stages of the medusæ of such forms as Pennaria and other Tubularians (cf. this paper, Pl. XIV, and Weismann (**12**), pl. xvii. fig. 3); and the manubrium of Allopora is undoubtedly closely similar in general appearance to the manubrium of the adelocodonic gonophore of many of the Tubulariæ. In fact, the gonophores of some of the Hydroidea, such as Clava (Allman) and Corydendrium (Weismann), are much less like adelocodonic medusæ, even when they reach their full development, than are these gonophores of Allopora and Distichopora.

If it could be shown that the inner membrane covering the spermarium is derived from the ectoderm and is not endodermic as I have described it, and that structures corresponding to the "glockenkern" do occur in the development of these gonophores, then my principal objections to the view that they are degenerate medusæ would fall to the ground. A very careful examination of my sections of gonophores in all stages of development

convinces me that there is in these forms no true "glockenkern," and that the two membranes covering the gonad are truly homologous with the two membranes covering the ova, namely, an outer ectodermic membrane and an inner endodermic membrane.

The manubrium of the gonophore of Allopora is, I believe, strictly homologous with the manubrium of the medusa of Millepora; that is to say, it is a subsequent endodermal ingrowth into the spermarium developed for the purpose of affording increased nourishment to the rapidly increasing spermoblasts.

These gonophores, then, do not represent, in my opinion, stages in the degeneration of medusæ. The Stylasteridæ never possessed free-swimming medusæ, I believe, although their gonophores may indicate to us some of the stages that the medusæ of Hydroidea passed through in the course of their phylogeny.

Before entering into a discussion of the meaning of the gonophores of the Hydrocorallines, it is necessary to consider briefly the principal views that have been put forward concerning the primitive or ancestral form of the Hydrozoan. Is it probable from the evidence at our command that the ancestral form was a fixed colonial hydroid, or was it like a scyphistoma larva (Hydra tuba); or, lastly, was it a floating Hydra or actinula?

Balfour says, "A condition like that of Hydra, in which the ovum directly gives rise to a form like its parent, is no doubt the primitive one, though it is not so certain that Hydra itself is a primitive form. The relation of Hydra to the Tubulariæ and Campanulariæ may best be conceived by supposing that in Hydra most ordinary buds did not become detached, so that a compound Hydra became formed; but that at certain periods particular buds retained their primitive capacity of becoming detached, and subsequently developed generative organs, while the ordinary buds lost their generative function."

Weismann's view is similar to that of Balfour. He says, "Die niedrigste d. h. einfachste Form der heute lebenden

Hydroiden ist wohl Hydra; es scheint mir wenigstens für jetzt kein Grund vorzuliegen, sie für eine rückgebildete Form, wohl aber manche Gründe sie für eine sehr alte Form zu halten, wie oben schon genauer begründet wurde, und wie es auch so von den meisten Forschern angenommen wird " (**12**).

Both of these authors considered that the primitive type of Hydrozoan was a simple sessile form more or less similar to our modern Hydra, and that the medusa originated by the modification of individuals bearing the sexual cells that were budded from, and set free from, the primitive simple sessile Hydra.

Lankester says, "The particular form which the proximate ancestor of the Hydrozoa took is most nearly exhibited at the present day in Lucernaria, and in the scyphistoma larva (Hydra tuba) of Discomedusæ. It was a hemispherical cup-like polype with tentacles in multiples of four, with four lobes to the wide enteric chamber. This polype, after passing a portion of its life fixed by the aboral pole, loosened itself and swam freely by the contractions of the circular muscular fibres of the hypostome (sub-umbrella), and developed its ovaria and spermaria on the inner walls of the enteric chamber. This ancestor possessed, like its descendants, a very marked power of multiplication, either by buds or by detached fragments of its body. Accordingly it acquired definitely the character of multiplying by bud formation during the earlier period of its life; each of the buds so formed completed in the course of time its growth into a free-swimming person. We must suppose that the peculiarities of the two phases of development became more and more distinctly developed, the earlier budding phase exhibiting a more elongated form and simple enteric cavity (Hydra form), which subsequently became changed in the course of ontogeny into the umbrella or disc-like form, with the coalesced enteric walls and radial and circular surviving spaces (medusa form). And now the ancestry took two distinct lines, which have given rise respectively to the two great groups into which the Hydrozoa are divided—the Scyphomedusæ and the Hydromedusæ."

Another view has been put forward by Brooks (**3**), who, from a consideration of the developments of the Trachomedusæ and Narcomedusæ, comes to the conclusion that the ancestral form was a simple solitary floating or swimming Hydra.

It does not seem to me to be at all clear that Claus previously expressed the same view in the 'Grundzüge der Zoologie,' for although he says that Hydra is certainly not a primitive form, that the medusa is a higher form than the polype, and that intermediate forms between the medusa and polype are represented by the actinula of Tubularia and Tetrapteron volitans, he does not commit himself to the view that the ancestral Hydrozoan was a free-swimming Hydra-like larva.

Böhm (**2**), on the other hand, expresses his views very clearly: "Eine der nächsten Nachkommen der uralten Gastraea muss als die Stammform der Zoophyten, eine nicht weit von ihr entfernte als die der Hydromedusen angesehen werden. Bei der hypothetischen Construction der letzteren hat man zwischen drei Möglichkeiten zu wählen.

"Entweder war diese schon entschieden polypoid, ihre nächsten Nachkommen waren Polypen, und die Medusen haben sich erst später aus diesen entwickelt.

"Oder sie war ganz medusoid, die Medusen die primären die Polypen die secundären Nachkommen.

"Oder schliesslich es war eine intermediäre zwischen Polypen und Medusen stehende Form, und Polypen wie Medusen haben sich von ihr aus nach zwei verschiedenen Richtungen hin entwickelt.

"Die letztere Annahme scheint mir manche Gründe für sich zu haben. Denn der lange Weg vom wenig differenzirten festsitzenden Polypen bis zur hochausgebildeten freischwimmenden Meduse wird wesentlich abgekürzt durch die Annahme einer Mittelform."

Notwithstanding the arguments of these authors, it is not easy to believe that the free-swimming actinula represents an ancestral type of Hydromedusan. The parasitic or semi-parasitic habits of the actinula of most of the Narcomedusæ suggest that it is an extremely modified form, and it seems to

me to be extremely hazardous on the part of Brooks to base his phylogenetic considerations upon such a weak and slender foundation. The views of the earlier writers that the sessile form is the more primitive, that in those cases in which the medusa develops directly from the egg the trophosome has disappeared from the developmental cycle, seem to be more probable.

It is not necessary to enter further into the discussion of these extreme speculative questions.

I have referred to them not in the hope of adding anything new, nor of throwing light upon them, but in order that I may place clearly before the reader the position I take with regard to them.

It seems to me to be more satisfactory to regard the sessile trophosome rather than the free-swimming actinula as the primitive type, and the medusa as a structure produced originally by a polypoid colony for the nourishment and distribution of the gonads.

Having thus stated my opinion as to the original form of Hydroid, it is necessary to go further and express an opinion as to the mode in which medusæ originated.

The views of Weismann and Balfour on this question are as nearly as possible identical. They supposed that the medusa originated by certain buds bearing the primitive sexual cells, retaining their primitive capacity of being detached from the parent, and that such buds became modified for a free-swimming existence. According to these views the medusa is homologous with a polype, it is simply a modified trophosome, or that trophosomes and gonophores are both modifications of some common type.

Huxley's original view that the gonophore is a peculiar sexual organ has in recent years been subject to a storm of criticism, and there are very few naturalists of the present day who would defend the position he took. "A medusoid, though it feeds and maintains itself, is in a morphological sense simply the detached generative organ of the hydrosoma on which it is developed."

The gonophores of the Hydrocorallinæ do not seem at first sight to throw much light upon these questions. If we arbitrarily assume that they are degenerate medusæ comparable to the adelocodonic gonophores of the Tubulariæ and Campanulariæ, we cannot expect to find in them any evidence to support either the one view or the other. But there is no reason to suppose that they are degenerate medusiform gonophores. Neither in Millepora, nor in Allopora and Distichopora, are there any features in development that suggest rudimentary structures of medusæ.

If they are not degenerate structures, then, but gonophores of a primitive type, how can we reconcile the medusa of Millepora, which is a metamorphosed polype, with the gonophores of Allopora and Distichopora, which show no trace of polypoid or medusoid structure?

The explanation I would suggest is briefly as follows: When the ova or sperm-mother cells reach a certain size and are too large to move freely in the canal system, they set up a local stimulus or irritation, which causes a cup-shaped folding of the adjacent canal or polype wall. This cup-shaped fold being of advantage to the sexual cells during their maturation, by affording increased facilities for nourishment and by increasing the size of the cavity by solution of its walls, has been modified into a definite form in each species by natural selection. When the sexual cells arrive at their maturity the nourishment afforded by these cells is no longer necessary, and consequently the stalk of connection with the canals becomes constricted until the gonophore is set free in the cavity of the ampulla. In the ancestral form of the Millepora a ready access to the exterior was opened to the separated gonophore by way of the dactylopore, and thus the detached gonophore was able to escape and lead a free-swimming existence.

It is reasonable to suppose that all the cells of the colony of a Millepora are capable of a certain amount of contractility, and that the slight power of contractile movement that the original free gonophore possessed being of advantage to the species—by enabling the gonophore to keep afloat longer and

thus spread the sexual products farther—was increased by natural selection. Similarly the rim of the gonophore cup was produced until it assumed the size and shape of a medusa.

The whole of this hypothesis of the origin of the medusæ rests upon the supposition that the sexual cells when they reach a certain size set up a local irritation or stimulus, causing a cup-shaped growth of the cœnosarc in its immediate neighbourhood.

Is it reasonable to suppose, in the first place, that the gonads when they reach a certain size do produce a local stimulus or irritation? In young immature stocks there is no trace of ampullæ or other receptacles in the cœnosteum of sufficient capacity for the mature gonads. Nor are there found in stocks that are bearing but few sexual organs any empty cavities in the cœnosteum. It is almost certain, then, that the gonads, when they reach a certain size, cause a stimulus to certain cells to secrete an acid (?) which dissolves the lime of the cœnosteum and causes an ampulla to be formed. There can be no doubt, then, that the sexual cells do cause one kind of stimulus to the tissues.

But is a local irritation or stimulus likely to cause any such modification as circumferential folding of the canals in its neighbourhood?

The only direction in which we can look for an answer to this question is to the effects caused by the irritation of foreign substances and parasites. The Hydrocorallines, like most of the corals, are subject to the attacks of many kinds of parasites. Worms, molluscs, barnacles, and other forms may be seen in every specimen that is examined.

When the colony is attacked by such a form as Tetraclita, for example, the cœnosarc at the immediate spot on which the parasites settles is killed, but this does not cause an atrophy of the surrounding canal system. On the contrary, a pronounced hypertrophy of the canal system immediately surrounding the parasite takes place, and in time it grows round and over the parasite until it is almost buried in its substance. An examination of other forms of coral will show similar examples of

parasites and other foreign bodies covered by an hypertrophied growth of the cœnosarc.

The formation of the corbula of Aglaophenia may be accounted for by a similar explanation. The stimulus of the growing blastostyles causes, not only an increased activity in the growth of the lateral branchlets, but a growth in such a manner as to enclose the blastostyles in a cup.

Similarly the various kinds of animal galls found in Hydroids and Alcyonarians are probably caused by a circumferential hypertrophy of the tissues surrounding the parasitic pycnogonid, crab, or mollusc.

From this evidence, then, it does seem probable that a local stimulus or local irritation of the cœnosarc of these forms causes a growth of the tissues which gradually folds over the seat of the irritation.

If this is the case, then, the production of a very rudimentary and imperfect umbrella-shaped structure is a physiological result of the stimulus caused by the growth of the sexual cells, and the medusa is simply a modification, produced by natural selection, of such a structure.

If this view is a reasonable one, we get over the principal difficulty in accepting the view that the ancestral Hydrozoan was a colonial Hydra form.

One of the chief features of the higher Protozoa and of the Cœlenterata is the power they possess of forming large colonial organizations by asexual reproduction. And it is reasonable to suppose that when the primitive Hydrozoan became differentiated off from its colonial Protozoan ancestry it retained the power of forming colonies by fission or gemmation.

It has seemed to me improbable that Hydra can be closely related to the ancestral type, because it does not possess this power.

If this view of the origin of medusæ is correct, there is no difficulty in believing that the ancestral form was a colonial trophosome, and that medusæ of different kinds may have originated quite independently of one another from the Hydroid stocks.

The original position of the gonads was the centre of the concavity of the umbrella. As they became larger and larger in phylogeny a conical growth of the endoderm, with respiratory and nutritive functions, penetrated them, and became the manubrium. All of these stages may be seen repeated in the ontogeny of the medusa of Millepora. When a mouth was formed at the end of the manubrium the gonads were in some forms (anthomedusæ) restricted to the sides of that organ; but in other forms (leptomedusæ) they were shifted to a more convenient place in the radial canals. According to my view, then, the manubrium of the male gonophore of Allopora does not prove that it is a degenerate medusa, but, rather, that it is one stage further than Distichopora on the road that all medusæ have travelled in the early history of their phylogeny; that is to say, a stage with a larger spermarium, and a special process of endoderm for its more perfect nourishment and respiration.

Another question arises in connection with the gonophores of the Hydrocorallinæ that at one time would have been considered one of vital importance.

In the description given above of the development of the medusa of Millepora, I have shown that it is formed by a metamorphosis of a dactylozooid. This would support the view, then, that the medusa is a modified trophosome.

In the description of the development of the gonophores of Allopora and Distichopora I do not mention the zooids at all. The gonophores are not developed in these genera (figs. 12, 19) in connection with either the gastrozooids or dactylozooids, they arise quite independently from the cœnosarcal canals. They have no particular relation to the systems in which the zooids are arranged, and there is every reason to suppose that they are quite independent of them. Further, these gonophores are not, according to my view, degenerate medusæ. They must, therefore, be special organs of the colony bearing the gonads.

To those naturalists who believe that there is a sharp distinction to be drawn between the idea of the "individual" and the "organ" in the animal kingdom, these apparently contradictory cases must be very puzzling. In the one case

they would say the gonophore is an "individual;" in the other, it is an "organ."

I am not inclined, however, to believe that it is possible to draw a sharp distinction between these two ideas. They are relative ideas, as Claus (5) maintains, just as "cell" and "tissue," "individual" and "colony," must be.

The stimulus of the sexual cells of a certain size would produce the same effect if they were formed in the cœnosarcal canals or the zooids; but natural selection has stepped in in the case of the Hydrocorallines, so that in the case of Millepora the gonads do not produce this effect until they reach the zooids, and, in the case of the Stylasteridæ, not until they reach certain parts of the canal system.

The two kinds of gonophores are, then, to my ideas really homologous, although in the one case they have reached such a stage of development as to justify us in considering them "individuals," while in the other case they cannot be considered more than sexual "organs."

General Conclusions.

1. In Millepora murrayi (*sp. ?*) the male gonads are borne by medusæ which escape from the ampullæ in which they are developed before the spermatozoa are matured.

2. The ova of this species are, like the ova of Millepora plicata, extremely small and alecithal. They move in an amœboid manner in the cœnosarcal canals, and do not ultimately rest in gonophores, nor in any specialized portion of the system.

3. The medusæ of Millepora murrayi have no radial nor ring canals in the endoderm of the umbrella, no velum, no sensory organs, and no mouth.

4. The medusæ are formed by a metamorphosis of an ordinary zooid; in the majority of cases dactylozooids, but in others gastrozooids.

5. The sperm-cells originate in the ectoderm of the cœno-

sarc and wander into the ectoderm of the zooids, where they fuse into aggregations to form a spermarium.

6. The young spermarium is formed at the distal extremity of the dactylozooid, and when it has reached a certain size it causes a retrograde metamorphosis of the tissues. The tentacles flatten out and disappear, and the zooid loses all its characteristic features.

7. A cup-shaped outgrowth next appears which forms the umbrella of the medusa, and subsequently a conical growth of the endoderm penetrates into the substance of the spermarium and forms the manubrium.

8. The male gonophores of Distichopora occur in groups of two or three in each ampulla in different stages of development. The gonad is supported by a small cup-shaped trophodisc, and enclosed in a double sac of ectoderm and endoderm. At the distal pole of the ripe gonophore there is a short seminal duct.

9. The male gonophore of Allopora differs from that of Distichopora, in the fact that it is provided with a club-shaped endodermal manubrium or spadix.

10. The female gonophore of Distichopora resembles that of Allopora described in a previous paper; but the folds of the trophodisc are not so complicated.

11. The gonophores of the Hydrocorallinæ are not degenerate medusæ.

BIBLIOGRAPHY.

1. F. M. Balfour.—'Comparative Embryology,' 1880.
2. R. Böhm.—"Helgolander Leptomedusæ," 'Jen. Zeits.,' xii. 1878.
3. W. K. Brooks.—"The Life History of the Hydromedusæ:" a discussion of the origin of Medusæ and the significance of Metagenesis, 'Mem. Bost. Soc. Nat. Hist.,' vol. iii. No. 12, 1886.
4. Claus.—"Ueber Halistemma tergestinum," &c., 'Arbeiten des Zool. Instit. zu Wien,' tom. i. 1878.
5. C. Claus.—"Zur Beurtheilung des Organismus der Siphonophoren und deren phylogenetischer Ableitung," 'Arbeiten Zool. Instit. zu Wien,' viii. Heft 2, p. 159; translated in the 'Annals and Magazine of Natural History,' vi. 21, pp. 185—198.
6. S. J. Hickson.—"The Sexual Cells and the Early Stages in the Development of Millepora plicata," 'Phil. Trans.,' vol. clxxix. 1888, B., pp. 193—204.
7. S. J. Hickson.—"On the Maturation of the Ovum and the Early Stages in the Development of Allopora," 'Quart. Journ. Micr. Sci.,' vol. xxix. p. 579.
8. W. H. Jackson.—'Rolleston's Forms of Animal Life,' 2nd edition, 1888.
9. E. Ray Lankester.—Article "Hydrozoa," 'Encyclopædia Britann.,' 9th edition.
10. H. N. Moseley.—"Report on Certain Hydroid, Alcyonarian, and Madreporarian Corals," '"Challenger" Reports,' vol. ii. 1881.
11. J. J. Quelch.—"On the Presence of Ampullæ in Millepora murrayi," 'Nature,' vol. xxx. 1884, p. 539; and in '"Challenger" Reports,' vol. xvi. "Reef Corals."
12. A. Weismann.—'Die Entstehung der Sexualzellen bei den Hydromedusen,' Jena, 1883.

DESCRIPTION OF PLATES XIII & XIV.

Illustrating Mr Sydney J. Hickson's paper "The Medusæ of Millepora murrayi and the Gonophores of Allopora and Distichopora."

Calc. The calcareous skeleton or cœnosteum. *Cœn.* The cœnosarcal canals. In the superficial regions the canals are crowded with zooxanthellæ. *Ect.* Ectoderm, coloured red. *End.* Endoderm, coloured blue. *Gon.* The ectodermal lining of the ampulla forming the wall of the gonangium. *Man.* Manubrium of the medusa. *Nemat.* Large nematocysts guarding the dactylopores. *op.* Operculum of modified ectoderm cells covering the pore of the ampulla. *Sperm.* Spermarium. *Sperm.* S_1 Spermospheres or aggregations of spermospheres in the ectoderm of the zooids. *Sperm.* S_2. Yóung spermospheres in the ectoderm of the canals. *Tent.* Retracted tentacles. *Umb.* Umbrella of the medusa, consisting of a solid endoderm covered on both sides by ectoderm.

PLATE XIII.

Millepora murrayi.

Fig. 1.—Section through a retracted dactylozooid of Millepora murrayi, showing a number of spermospheres (*Sperm.* S_2.) in the ectoderm of the cœnosarc, and in the ectoderm (*Sperm.* S_1.) at the base of the dactylozooid.

Fig. 2.—Section through a retracted dactylozooid, showing a single small aggregation of spermospheres (*Sperm.* S_1.) in the ectoderm at the base of the dactylozooid.

Fig. 3.—Section through a retracted gastrozooid, showing an aggregation of spermospheres in the ectoderm. The gastrozooids may be readily distinguished from the dactylozooids by the presence of a mouth and by the large endoderm cells, the peripheral portions of which are filled with mucus. Just below the gastrozooids may be seen a plate of vacuolated ectoderm cells in section, which forms the last tabula of the gastropore.

Fig. 4.—Section through a dactylozooid, showing a large aggregation of spermospheres on its side in a condition very similar to that I have described in Millepora plicata (6). The spermospheres have caused a very considerable depression in the dactylozooid, and are partially covered by the surrounding parts.

Fig. 5.—An aggregation of spermospheres at the peripheral extremity of a dactylozooid. The tentacles (*tent.*) are visible.

Fig. 6.—An aggregation of spermospheres (*Sperm.* S_1.) at the peripheral extremity of a dactylozooid, sunk in a cup-shaped receptacle. At *Umb.* may be seen the first trace of the formation of the umbrella by the growth of the endoderm. The position of the tentacles is still indicated by the rows of small nematocysts.

Fig. 7.—Section through another dactylozooid, showing a still further growth of the folds forming the umbrella. All trace of the tentacles has disappeared.

Fig. 8.—Section through a young medusa of Millepora. The form of the dactylozooid is completely lost. The endoderm of the umbrella is solid, and much thicker than it is in later stages. The opening of the dactylopore can still be traced, although it is blocked with the thickened ectoderm cells. The pore is guarded by nematocysts (*Nemat.*).

Fig. 9.—Section through another medusa. The umbrella is not completely developed, but the endoderm is much thinner than it is in Fig. 8. The spermarium is much larger, but there is no trace of a manubrium. The dactylopore is completely closed by an operculum (*op.*) formed by flattened strap-shaped ectoderm cells.

Fig. 10.—Section through another medusa, with a well-developed manubrium (*man.*), containing a cavity continuous with a large canal. The umbrella walls are much thinner than they are in the specimens drawn in Figs. 8 and 9, except at the margin.

Fig. 11.—Section through a medusa that lies freely in the gonangium. It is not connected organically with the colony at any point. It is probably ready to escape. The umbrella (*Umb.*) is extremely thin, except at the margins. There is a small cavity in the endoderm, but there is no mouth. There are no tentacles, velum, nor sensory bodies on the margin of the umbrella. Between the codonostome and the superficial ectoderm there is a layer of mucus.

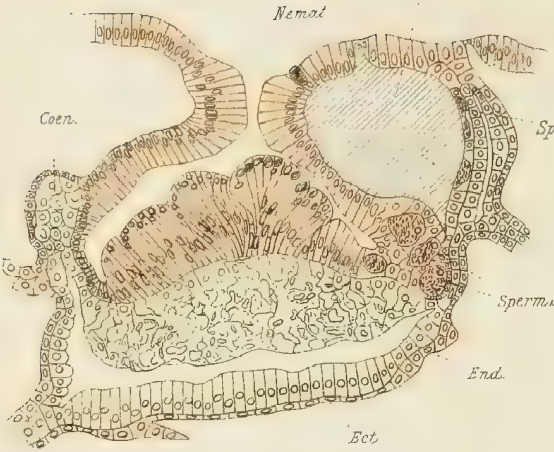
PLATE XIV.

Fig. 12.—Transverse section through a decalcified branch of Distichopora, showing the male gonophores lying in the ampullæ. One, two, or three gonophores occur in each ampulla. At the edges of the branch are situated the rows of dactylozooids (*Dact. Z.*) and gastrozooids (*Gast. Z.*).

Fig. 13.—Section through an ampulla of Distichopora, containing two young male gonophores. Each of these is supported by its own trophodisc containing a large lumen.

Fig. 14.—Section through an ampulla of Distichopora, containing three male gonophores in different stages of development. The largest of these (1) contains ripe spermatozoa, and shows on its distal pole a conical cap of

Fig. 1



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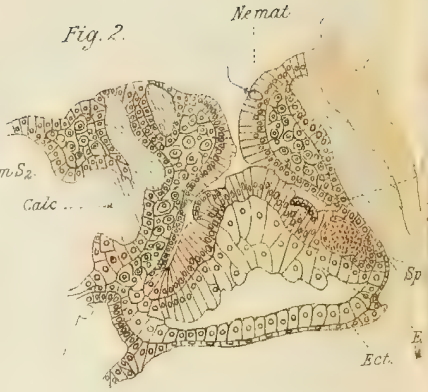
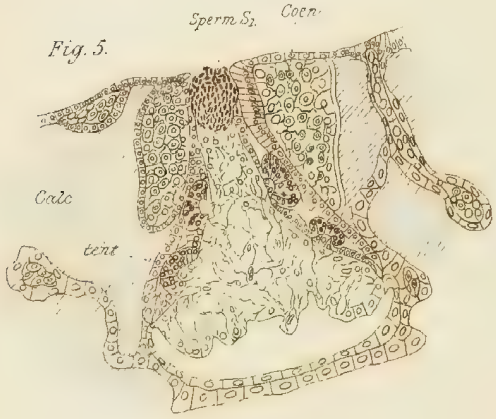


Fig. 5.



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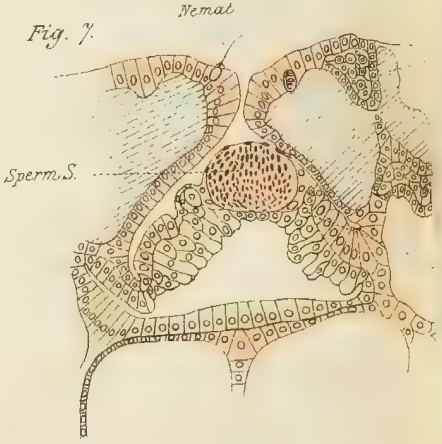

Fig. 8

Fig. 9.

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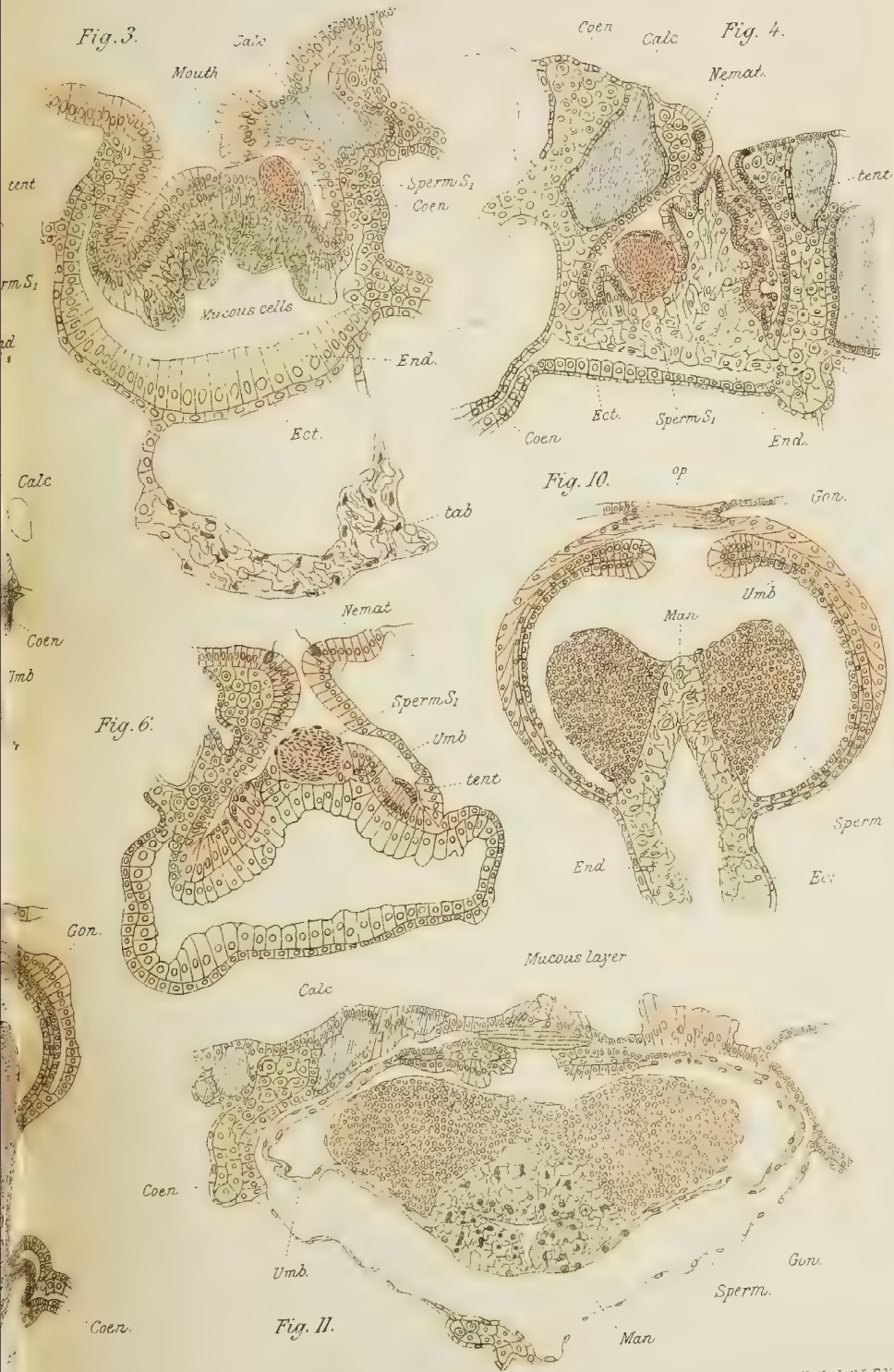

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Fig 12

Fig. 13.

Fig 14

Fig. 17

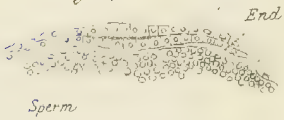


Fig. 18.

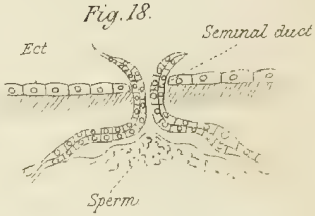
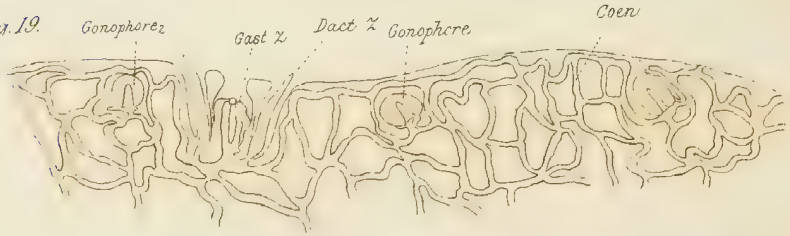


Fig. 19.



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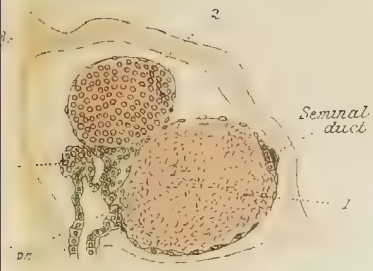


Fig. 15.

Fig. 16.

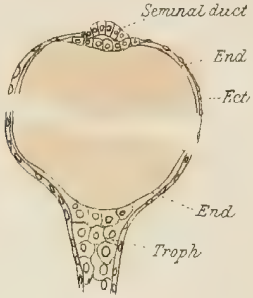


Fig. 21.

Fig. 20.

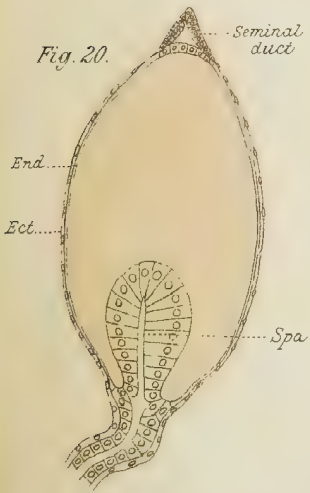


Fig. 23.

Fig. 24.

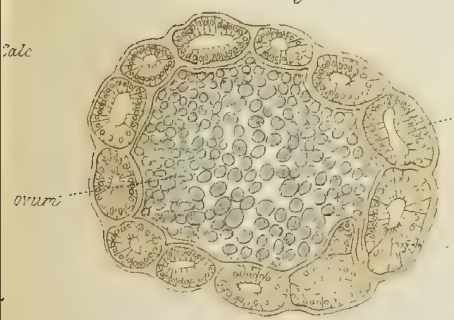
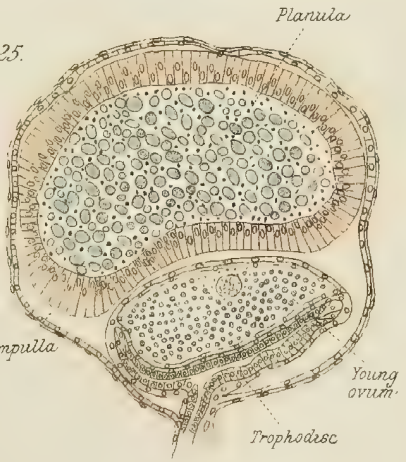


Fig. 25.



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cells, the undeveloped seminal duct. The trophodisc (*troph.*) is reduced to an irregular mass of endoderm cells.

FIG. 15.—Section through a very young male gonophore of Distichopora. The young spermarium (*sperm.*) lies apparently between the ectoderm and endoderm of the bud, but the endoderm is cup-shaped, and the margins of the cup project between the ectoderm and the proximal hemisphere of the spermarium.

FIG. 16.—Section through an older male gonophore of Distichopora, showing the spermarium covered by the two membranes, a thin nucleated ectoderm and a thinner non-nucleated endoderm, which is continuous with the endoderm of the trophodisc.

FIG. 17.—Section through the earliest stage I have found of the formation of the seminal duct. The ectodermic and endodermic elements are from the very first quite distinct from one another.

FIG. 18.—Section through a seminal duct of a ripe male gonophore, open to the exterior.

FIG. 19.—Section through a portion of a decalcified branch of Allopora, showing three male gonophores lying in their ampullæ. As a rule, only one gonophore is found in each ampulla; but one case is figured (gonophore 2) in which a large gonophore and a very young bud occur in the same ampulla.

FIG. 20.—Section through a nearly ripe male gonophore of Allopora, showing the club-shaped endodermal spadix, and the two membranes (*Ect.* and *End.*) surrounding the spermarium.

FIG. 21.—Section through a portion of a decalcified branch of a female stock of Distichopora, showing a number of ova and planulæ in various stages of development lying in their ampullæ.

FIG. 22.—A portion of the same as Fig. 21, more highly magnified. The ampullæ are occupied by planulæ. Below the ampullæ there may be seen in the endoderm of the canals some very young eggs, containing no yolk-granules and showing blunt amœboid processes.

FIG. 23.—An ovum of Distichopora that is nearly mature, as seen in section. The germinal vesicle (*Germ. Ves.*) lies near the superficial side of the egg, and is surrounded by small yolk-granules. The trophodisc is simple, in vertical section, and contains a pronounced lumen.

FIG. 24.—Transverse section through an ovum and trophodisc of Distichopora in the plane represented by the line *xx'* in Fig. 23, showing the twelve pouches of its margin.

FIG. 25.—Section through an ampulla of Distichopora, containing a planula, and below it a young ovum in a young trophodisc.

SUPPLEMENTARY LIST OF SPIDERS TAKEN IN THE NEIGHBOURHOOD OF CAMBRIDGE.

BY

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In Part I. Vol. v. of these *Studies* a list was given of some hundred species of local Araneæ. To these must now be added the following, some of which have been taken since the former publication, while others are inserted on the authority of the Rev. O. Pickard-Cambridge, who has kindly furnished a list of Spiders sent to him some years ago by the late Mr Farren.

Unfortunately Mr Farren did not record the exact locality nor the frequency of his captures, but he is known to have carefully searched Wicken Fen, which is probably the habitat of most of his species.

DYSDERIDAE.

Dysdera
crocota, C. L. Koch, rare, Castle Hill.

Segestria
senoculata, Linn.

DRASSIDAE.

Drassus
troglodytes, C. L. Koch, rare, Wicken Fen.
blackwallii, Thor.

Clubiona
corticalis, Walck., rare, University bathing enclosure.
reclusa, Cambr.

Anyphaena
accentuata, Walck.

Phrurolithus
festivus, C. L. Koch, Fleam Dyke.

DICTYNIDAE.

Dictyna
latens, Fabr.

AGELENIDAE.

HAHNIA
nava, Bl., rare, Wicken Fen.

LETHIA
humilis, Bl.

THERIDIIDAE.

THERIDION
simile, C. L. Koch.
tinctum, Walck., common, on shrubs and bushes.
rufolineatum, Luc.

NERIENE
cornuta, Bl., rare, in the "Backs."
nigra, Bl., rare, Turf Fen, Chatteris.
fuscipalpis, C. L. Koch. In the bathing enclosure.
apicata, Bl.
bicolor, Bl. Castle Hill.
bituberculata, Wid.

WALCKENAERA
bifrons, Bl.
unicornis, Bl.
cristata, Bl., rare, Christ's Coll. Garden.

PACHYGNATHA
listeri, Sund.

EURYOPIS
blackwallii, Cambr.

LINYPHIA
nigrina, Westr.
setosa, Cambr., Wicken Fen.
clathrata, Sund.,, Wicken Fen.
circumspecta, Bl. rare.

EPEIRIDAE.

EPEIRA
acalypha, Walck.
solers, Walck.
quadrata, Clrk., occasional, Fens.

ERRATA.

In the previous list, *Amaurobius fenestralis* should have been recorded as *rare* instead of *common*, and the habitat of *Theridion varians* as being "boathouses and out-buildings" rather than "bushes."

On Onchnesoma Steenstrupii.

By

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With Plate XV.

The genus Onchnesoma was established in the year 1877 by Koren and Danielssen,[1] its name being derived from ὄγχνη = a pear, and σῶμα = body. The genus is characterised as follows:

"The body small, pear-shaped. The proboscis long. The anal aperture a little in front of the base of the proboscis. No tentacles; no vascular system. One retractor."

The genus consisted of two species: O. Steenstrupii, which the authors regard as synonymous with Sipunculus pyriformis of Danielssen[2] and Phascolosoma pusillum of Sars;[3] and O. Sarsii, synonymous with the Phascolosoma lævissimum of Sars.[3] These two species, with their characteristics, are mentioned in Selenka's monograph of the Sipunculidæ. In 1881 a third species, O. glaciale, was described by the Norwegian authors[4] from amongst the material collected by the Norwegian North Atlantic Expedition, so that

[1] "Contribution to the Natural History of the Norwegian Gephyrea," by J. Koren and D. C. Danielssen, 'Fauna Littoralis Norvegiæ,' Bergen, 1877.

[2] Danielssen, 'Videnskabsselskabet Forhandlinger i. Christiania,' Aaret, 1859.

[3] Sars, 'Videnskabsselskabet Forhandlinger i. Christiania,' Aaret, 1868.

[4] 'The Norwegian North Atlantic Expedition, 1876—1878, Gephyrea,' by D. C. Danielssen and Johan Koren, Christiania, 1881.

the genus at present comprises three species, all found on the north-west coast of the Scandinavian peninsula.

The species differ considerably in size. O. Steenstrupii, whose body measures but 3 mm. in length, is the smallest Gephyrean hitherto described, and, corresponding with its minute size, the structure of the body is very much simplified. O. Sarsii attains a body length of 8 mm., whilst the body of O. glaciale is 35 mm. long. I have hitherto been unable to obtain specimens of the two last-mentioned species; but, thanks to the kindness of Professor E. Ray Lankester and Canon Norman, I have been enabled to investigate the structure of the smallest species, of the minute anatomy of which the following is an account.

The External Appearance.

In the better preserved specimens the body was about 3 mm. long, pointed behind, and in front passing abruptly into the introvert (figs. 1 and 2); some, however, which were not well preserved, and which did not appear to be normal, had a longer and more slender body, which passed gradually into the introvert. The length of the latter structure varied in accordance with the amount of its protrusion: it was, when fully extended, almost invariably coiled up, and consequently difficult to measure, but in no specimen was it 34 mm. long, the length described by Koren and Danielssen.

The skin is of a French grey, almost greenish colour, and is divided into small areas by numerous crinkles, which at the posterior end of the body cross one another almost at right angles; in some cases such folds of the skin occurred at more or less regular intervals round the proboscis, giving it a superficial appearance of being segmented (fig. 1).

The introvert is covered with papillæ, which, according to Koren and Danielssen, are disposed in regular rows. The nature of these organs, which correspond with the papillæ of the larger Sipunculids, will be described below; they open to the exterior, but the opening is not always situated on an eminence, but may be found anywhere on the wrinkled surface of

the body. The skin of the introvert, when extended, is transparent, so that the œsophagus and nervous system may be seen through it.

There is a marked thickening of the skin where the introvert joins the body; the anus is situated a little anterior to this. The external opening of the kidney is a little behind, just to the side of the ventral nerve-cord.

The Structure of the Skin.

The layers which compose the skin of Onchnesoma have been described by the Norwegian writers; there are, however, one or two details which may be added to their account. As in the skin of other Sipunculids, we meet with six layers. The state of preservation of my specimens did not allow the epidermal cells to be made out. But this outermost layer of cells probably forms part of the deeply stained external layer seen in fig. 6.

In section this layer appears ridged, the ridges corresponding with the wrinkles on the surface of the animal. It is obscured by a number of granules, which stain very deeply with hæmatoxylin; these granules are apparently produced by certain structures which correspond with the epidermal glands of other forms. Between the darkly stained external layer and the circular muscles is a thick gelatinous connective-tissue layer, or cutis, in which hardly any trace of cells could be detected. At the base of this the skin glands are situated.

The state of the preservation of my material did not allow me to see this point very clearly, but I have no doubt that the epidermal glands are composed of specialised epidermal cells. Each gland is of a spherical shape; from the outer edge of this a duct with sharply defined outline leads through the cutis to the surface of the body. Within the glands lie numerous darkly stained granules, similar to those which cover the outside of the body; and there is little doubt that the latter have their origin in these structures, and pass out with the mucus which

has in some cases been seen to exude from the pores of the glands.

The external circular layer of muscles is well developed in the introvert, and in the anterior half of the body; but about the middle of the body it fades away, so that the posterior end is provided only with longitudinal muscles (fig. 7). The circular muscles are arranged in bundles, but the longitudinal are in a continuous sheet.

Both the cutis and the external and internal layers of muscles take part in the thickening of the skin which exists at the junction of the proboscis and the body.

The body-wall is lined by an endothelium, which extends over the internal organs. In the living specimens, according to Koren and Danielssen, it can be distinctly seen that this endothelium is ciliated, and that the cilia, by their action, keep the perivisceral fluid in motion.

The General Anatomy.

If a longitudinal incision be made in the body-wall of Onchnesoma, and the sides reflected, the arrangement of the internal organs and their relation to one another become at once evident without further dissecting. These relations are clearly shown in fig. 3, which I have borrowed from Koren and Danielssen's 'Fauna Littoralis Norvegiæ.' It will be seen that the œsophagus is very long and loosely coiled, in order to allow for the extension of the introvert. The intestine, whose diameter is larger than the œsophagus or rectum, is also much coiled. The anus is situated rather too far forward to the right of the ventral nerve-cord.

There is only a single retractor muscle, which has its origin at the extreme posterior end of the body, where the skin is thickened and produced into a blunt point (fig. 7). The other end of this muscle is inserted into the wall of the œsophagus immediately below the brain. The muscle-fibres which compose this retractor muscle are bigger than those of the muscular sheaths in the skin. They are fusiform, with a rather flattened transverse section and a faint longitudinal striation.

There is no closed vascular system such as exists in the larger Sipunculids. The perivisceral fluid which bathes the internal organs is crowded with nucleated corpuscles and generative cells.

The single kidney varies in position; in some of my specimens it was situated to the left of the ventral nerve-cord, in others to the right. Both its internal and external openings are too small to be made out except by section. The ventral nerve-cord may be seen as a very fine strand running just inside the skin (fig. 8).

The Head.

The head of Onchnesoma is of a remarkably simplified nature compared with that of the larger Gephyrea, but whether the simplification is primitive or the result of degeneration is not an easy matter to decide. The hooks which are so common in the group, arranged in rings round the proboscis, are entirely absent in this genus. This is a point of some interest taken in connection with the absence of several other structures which are usually met with in the group, but too much stress must not be laid on it, as with one exception, S. australis, the whole genus Sipunculus is devoid of these structures, and in other genera several species are without hooks; they are also apt to drop off as the animal grows old.

A more important feature is the entire absence of any tentacles. There is no trace whatever of the lophophoral ring of tentacles such as occurs in Phymosoma, and the crumpled pigmented tissue which occupied the hollow of the horseshoe is also entirely absent. The place of these structures, in the dorsal side of the mouth, is occupied by a slight elevation or blunt process which contains the brain. This process has a slight resemblance to a Doge's cap, but it is really nothing more than an extension of the body-wall on the dorsal side of the thickened lip which surrounds the mouth. The skin covering this process is not pigmented, but the whole of it is uniformly ciliated, the cilia being continuous with those which

line the œsophagus. The cilia also cover the ventral lip. The lobe is more or less solid (fig. 12), and contains the brain, the rest of the space being filled up with connective tissue. The brain gives off a median nerve (figs. 10 and 11), which passes into the lobe, and is distributed, I believe, to the epidermal cells, so that doubtless the lobe has a tactile and sensory function.

Just beneath the brain, on the dorsal surface of the œsophagus, the retractor muscle is inserted; it wraps round about two thirds of the circumference of that tube (fig. 12).

Corresponding with the absence of the tentacular crown there is a total absence of any vascular system, a peculiarity which Onchnesoma shares with Petalostoma and Tylosoma. There can be no doubt that in those forms which possess tentacles they have both a tactile and sensory function, and that they serve, by the currents their cilia give rise to, to bring food to the mouth. It is also believed that they have a respiratory function; and though this is probably the case, it must not be overlooked that the above-mentioned genera manage to respire without tentacles. Where the exchange of gases takes place is not so easy to state. The skin of Onchnesoma is relatively to the size of the animal at least as thick as that of the larger Sipunculids, and is covered by a thick cuticle. It has occurred to me that the cœlomic fluid may possibly obtain the oxygen it requires from the water which passes through the intestine of the animal. The coiled nature of this tube exposes a very considerable area to the fluid in the cœlom, and the extreme thinness and delicacy of its walls would favour a ready exchange of gas. If such a function were exercised by the alimentary canal, it would possibly explain the thinness of the digestive walls, which in other respects seems ill adapted to a diet of sand.

In Onchnesoma there is only one kind of corpuscle in the cœlomic fluid; this is spherical or nearly so, with granular protoplasm and a well-defined nucleus (figs. 7 and 8). The cœlomic fluid must be kept in very constant motion, both by the ciliated cells of the peritoneal epithe-

lium, and by the alternate protrusion and retraction of the introvert.

In the two species of Phymosoma which I have described[1] there is a very extensile fold of skin or collar which surrounds the base of the head, and which, when the introvert is retracted, usually completely encloses the head. The function of this collar is perhaps to shield and protect the delicate ciliated tentacles and lips from contact with the indurated surface of the introvert, provided as it often is with horny hooks. No such collar is found in Onchnesoma.

The Nervous System.

The brain is an elongated mass situated dorsal to the mouth, at the base of the median dorsal ciliated lobe (fig. 11). It shows no trace of being bilobed. Like that of Phymosoma, the brain of Onchnesoma consists of a cap of ganglion-cells which cover in a fibrous portion on all sides except that nearest the œsophagus, the ventral (fig. 12). There are no giant ganglion-cells to be seen. The nerve-cells are all of one size, with nuclei which stain deeply. On the dorsal surface the brain is continuous with the epidermis; but in this region, just at the base of the median dorsal process, the epidermal cells are not in any way modified. The pigment which accumulates in similarly placed cells in other Sipunculids is absent. There are also no eyes.

The brain gives off three nerves; a median nerve to the median dorsal lobe, and one on each side, which pass round the œsophagus and fuse together to form the ventral nerve-cord (figs. 9, 10, and 11). The median nerve is doubtless the equivalent of the pair of nerves which supply the pigmented pre-oral lobe in Phymosoma. The median lobe is probably sensory and tactile, and is therefore supplied with a stout nerve. The second pair of nerves in Phymosoma, which supply

[1] "On Phymosoma varians," 'Quart. Journ. Micr. Sci.,' April, 1890. "On a New Species of Phymosoma, with a Synopsis of the Genus," 'Quart. Journ. Micr. Sci.,' March, 1891.

the tentacular lophophore, is naturally not represented in Onchnesoma, as the tentacles are absent.

At the sides the brain is continued into two nerves which pass round the mouth embedded in the tissue, just where the retractor muscle is attached to the œsophagus (fig. 9); they fuse together on the ventral surface, and form the ventral nerve-cord, which shows no sign of its double origin (fig. 8). The portion of this cord which lies in the introvert is oval in cross section; that which lies in the body is round. In Phymosoma and in Sipunculus the ventral nerve-cord is supported by numerous strands of muscle continuous with the skin, which permitted the introvert to be extended or withdrawn without any strain being placed on the cord; but in Onchnesoma the cord is closely attached to the skin, and in the region of the introvert is almost embedded in the muscular layer.

As is the case in other Sipunculids, the ganglion-cells are arranged on the ventral surface, the fibres on the dorsal. The nerve-cord gives off numerous branches into the body-wall, whose course I was not able to follow; but Koren and Danielssen have traced them into a fine ganglionated network amongst the muscles, &c.

The nerve-cord extends to the posterior end of the body.

The Nephridium.

There is only a single nephridium in Onchnesoma, and its position is not very constant; it may lie either to the right or to the left of the nerve-cord, but its external orifice is always a little below the ring-like thickening which marks the junction of the proboscis and the body.

In its main features the nephridium resembles the same organ in Phymosoma varians, with the exception that there is no distinction between glandular and non-glandular regions. The external orifice leads straight into the lumen of the gland, which is as a rule somewhat pear-shaped. The internal opening is close to the external; it has a flattened, funnel-shaped border, and is ciliated.

The walls of the nephridium are lined throughout, with the exception of the small area between the external and internal opening, with glandular cells of a considerable size; with the exception of the ova they are the largest cells in the body (fig. 4). The lumen of the kidney in Onchnesoma is not split up into a series of crypts communicating with a central cavity, as was the case in Phymosoma; and the cells do not get rid of the product of their secretion by breaking off a bubble from their free end. Each of the large columnar cells has a very definite outline; their protoplasm is very clear and does not stain well, but scattered through it are a great number of granules which stain deeply. These concretions differ in size; they are always spherical, and the larger ones have a double contour. These latter are often found in the lumen of the nephridium, having doubtless passed out of the glandular cells, and being on their way out of the body.

I have never seen ova or spermatozoa in the lumen of the kidney, though I have no doubt that they leave the body through this channel.

The muscular layer is not so well developed in the nephridium of Onchnesoma as in that of some other Sipunculids, and the size of the kidney was more constant. Covering the outside of the organ is a layer of peritoneal epithelium.

With regard to the number of nephridia, two is undoubtedly the normal number in the Sipunculids; the genera Phascolion, Tylosoma, and Onchnesoma being singular in having but one. There are, however, exceptions to this rule: thus Phascolosoma squamatum has but one, and Aspidosiphon tortus also retains but one; and in both these cases it is the left that persists. Some species of Phascolion, on the other hand, retain the kidney of the right side only; and in Onchnesoma sometimes the left and sometimes the right persists, but never both together.

The Alimentary Canal.

The cilia which cover the dome-shaped dorsal process of the head and the lower lip are continued without break into the

alimentary canal (fig. 12). When the introvert is extended, the first part of the digestive tube or the œsophagus forms a straight tube with smooth walls; when, however, the introvert is retracted, the walls of the œsophagus are thrown into a number of circular folds with intervening depressions. The cells lining this part of the alimentary canal are cubical, and thickly beset with cilia.

Throughout the intestine the lining epithelium is surrounded by a layer of connective tissue, which is in its turn covered by the peritoneal epithelium; the connective tissue varies in thickness in different parts of the tube, but it is especially thick on the dorsal surface of the anterior end of the œsophagus: it is just here that the single retractor muscle is inserted.

The œsophagus passes into the descending intestine, whose walls are lined by large glandular cells: these have, when the intestine is comparatively empty, a columnar shape; but if the intestine is full of food its walls are stretched, and the lining cells become cubical, or even depressed. Owing to the small size of the animal it is not possible to wash the food out of the alimentary canal, and the nature of the food rendered it very difficult to cut satisfactory sections of the walls of the alimentary canal. These were in most cases torn; hence I have not been able to settle quite definitely whether the cells lining the descending intestine are ciliated or not, but I am inclined to think they are.

The ascending intestine is certainly lined with ciliated cells. It is distinguished by the possession of a longitudinal groove, which is lined by cells bearing especially long and large cilia. A similar groove is described by Mr. E. A. Andrews in Sipunculus Gouldii.[1] He states that "in it a current of liquid passes from the action of cilia, and possibly also of the radiating fibres, towards the anus during life." The absence of this groove is the only thing which distinguishes the short rectum from the descending intestine.

[1] "Notes on the Anatomy of Sipunculus Gouldii, Pourtalès," E. A. Andrews, 'Studies from the Biological Laboratory,' Johns Hopkins University, Oct., 1890.

The whole alimentary canal is attached to the body-wall by a few fibrous strands, but there appears to be no spindle muscle running up the axis of the spirally coiled intestine.

The food of Onchnesoma, judging by the contents of the intestine, consists of vegetable débris; mixed with this is a considerable amount of sand and a number of spicules, whose precise nature I was not able to make out.

The enormous amount of sand and mud which passes through the body of the Sipunculids shows that these animals must take a considerable share in the reducing action to which the mineral substances at the bottom of the sea are subjected. Mr. J. Y. Buchanan has recently published an interesting paper "On the Occurrence of Sulphur in Marine Muds,"[1] in which he has drawn attention to the fact that most silicates are to some extent soluble when pulverised under water, and the sand is to some extent crusted in passing through the body of most mud-eating animals, and this solubility is increased by the sulphates in the sea water which passes through the intestine of the animals. The sulphates are reduced by the organic products of the body to sulphides, and these unite with the iron or manganese of the silicates, and leave the body as sulphides of iron or manganese. These sulphides are then oxidised by the oxygen which exists in sea water, and form the red clays and chocolate muds which cover a considerable extent of the bottom of the sea. Thus the constitution of the mud at the bottom of the sea is to a very large extent artificial, and the Sipunculids play a considerable rôle in bringing this about.

These processes must be mainly effected by Holothurians, Echinids, Polychætes, and Sipunculids; and to arrive at some sort of an estimate of the amount of sand taken into the body of the latter animals, I recently weighed five specimens, chosen at random, of S. nudus from Naples, and then weighed the sand in their intestines. The average weight of their body

[1] "On the Occurrence of Sulphur in Marine Muds and Nodules, and its Bearing on their Mode of Formation," J. Y. Buchanan, 'Proc. of the Royal Soc. of Edinburgh,' Dec., 1890.

was 19·08 grms., that of the sand 10·03 grms. In two of them the sand weighed more than one half the total weight, the body being in one case 24·4 grms. and the sand 13·72, and in the other 15·05 grms. and 9·45. The contents of the intestine consisted of blackish sand with a few Foraminifera mixed with it. In spite of the considerable amount of sand which these figures show to be contained in the intestine, the wall of this tube in all the Sipunculids with which I am acquainted is excessively thin, and apparently but poorly adapted to retain the sharp and jagged pieces of sand which lie within it. A similar tenuity of the wall of the alimentary canal also occurs in Echinids and Holothurians. Although this wall is so thin I have never found a Sipunculid with its intestine ruptured, so that in spite of appearances it seems to serve its purpose well.

I have mentioned above that I am of opinion that the respiration of Onchnesoma is carried on through the walls of the intestine. The seat of the process of respiration is still a debatable point in the anatomy of the unarmed Gephyrea. Of the two recent authors who have written on the anatomy of Sipunculus, Mr. Andrews[1] is convinced that the tentacles act as branchiæ, whilst Mr. Ward[2] is of opinion that they do not. In Onchnesoma, at any rate, there cannot be any question as to the respiratory action of the tentacles, as the latter are entirely absent. In other Sipunculids the tentacles may to a slight extent serve as the organs of respiration, but the closed vascular system which supplies them with blood is of such a very limited extent that it would only suffice for a small portion of the body; on the other hand, it seems to me quite possible that the brain, which is almost entirely surrounded by this system, may obtain its oxygen from it.

The chief circulating medium in the body of the unarmed Gephyrea is undoubtedly the corpusculated cœlomic fluid, and

[1] Loc cit., p. 419.

[2] "On some Points in the Anatomy of Sipunculus nudus, L.," Henry B. Ward, 'Bull. of the Museum of Comp. Anat., Harvard College,' vol. xxi, No. 3, May, 1891.

in the case of Onchnesoma this forms the only circulating fluid. All the organs of the body, the alimentary canal, the nerve-cord, the nephridia, the chief muscles, and the generative organs, are suspended in this fluid, and bathed by it on all sides. The cœlomic fluid is kept in constant movement by the protrusion and retraction of the introvert, and by the action of the ciliated peritoneal epithelium which lines the body-wall and covers the internal organs. Thus the corpusculated cœlomic fluid is continually flowing over and circulating around all the organs suspended in it, and there is not much doubt that it acts as a carrier of oxygen to them.

The problem next arises, where does it effect the exchange of gas which constitutes respiration? This seems capable of two solutions: the cœlomic fluid takes its oxygen either from the corpusculated fluid of the closed vascular space, or through the walls of the alimentary canal. I am inclined to think that the latter alternative is responsible for the chief supply of oxygen to the body.

The walls of the vascular system are not very thin, and they do not present a very large surface to the cœlomic fluid; and although I think it possible that this fluid acts to a certain extent as a carrier of oxygen, more particularly to the brain, which, except where it is continuous with the epidermis, is surrounded on all sides by it, I still think that the primary function of the closed vascular system is to extend the tentacles by the contraction of its muscular walls forcing fluid into them, and that the primary function of the tentacles is to bring food to the mouth by the action of their cilia. For these reasons I think it, both on morphological and physiological grounds, inexpedient to speak of the tentacles as branchiæ.

The alimentary canal, on the other hand, has very thin walls, and owing to its looped and coiled disposition presents a very large surface to the cœlomic fluid. A considerable amount of water must be continually passing through the alimentary canal, since the food of the animal is brought into the œsophagus in a current of water set up by the cilia. This current is set up by the cilia lining the lips and œsophagus,

and is, I believe, maintained as a constant flow by the action of the cilia lining the ciliated groove which runs along one side of the ascending intestine. This groove is lined by cells bearing strong cilia. I have never seen any trace of food in it; and its chief function is, I think, to maintain the current of water which passes through the alimentary canal.

Professor Semper, in his 'Animal Life,' has drawn attention to those animals which breathe through their intestine. He has described certain foliated processes on the stomach of a Holothurian—Stichopus variegatus—which function as gills; he also mentions the common loach, Cobitis fossilis, which breathes through its stomach, but in this case it swallows air from the surface of the water. This air "is deprived of a portion of its oxygen in the intestine." Certain Brazilian fish, of the genera Calichthys, Doras, and Hypostomus, which also swallow air, have curious processes or folds of the lining of the intestine, which have been regarded as especially adapted for respiration. The anal respiration, which Professor Hartog has described in so many Crustacea and insect larvæ, is but another example of the alimentary canal being used as a respiratory organ. These instances are sufficient to show that in ascribing a respiratory function to the alimentary canal of Sipunculids one is supported by numerous analogous cases.

The Generative Organs.

Onchnesoma, like other Sipunculids, is dicœcious. The testes are formed by the growth of a small clump of cells lining the cœlomic cavity in the neighbourhood of the point of origin of the single retractor muscle (fig. 7). I have not been able to find any ovary, though I suspect that when mature it is to be found in the same situation. Numerous ova were found floating in the cœlomic fluid of the females; but, as Koren and Danielssen have remarked, "while the ova continue their development in the perivisceral cavity, the last vestiges of the ovary disappear entirely, so that no trace of it remains."

Like the ova, the spermatozoa undergo a considerable de-

velopment whilst floating in the cœlomic fluid. They leave the testis in the condition of the mother-cells of the spermatozoa; these segment, and the sperm morulæ result. The spermatozoa keep together in sperm morulæ till they have passed through the nephridium and out of the body.

Conclusions.

Onchnesoma is the smallest Sipunculid with which we are acquainted, and its anatomy is to a considerable extent more simple than that of other members of the group.

The head is much simplified; the lip which surrounds the mouth bears no tentacles, but is produced dorsally into a blunt process covered with cilia. The simplicity of structure is shown by the absence of any tentacles, hooks, collar, pigmented skin, and eyes; there is also no vascular system, no spindle muscle, and no giant-cells are found in the brain. The retractor muscle is single and arises from the extreme posterior end of the body, and is, therefore, symmetrical; the nephridium is also single, and may lie to the right or left of the body. The brain is not bilobed.

Until we know something of the development of Onchnesoma it would be hazardous to express an opinion as to whether the absence of the above-mentioned organs is due to degeneration, or whether they are primitive. On the one hand, the small size of the animal and the presence of one nephridium, which occurs on either side of the median line, points to degeneration; whilst, on the other, the structure of the head indicates a primitive condition, which might admit of modification in various directions.

The absence of any closed vascular system, correlated with the absence of tentacles, may throw some light upon the vexed question of the seat of the respiratory processes in Sipunculids. Since there are no tentacles, there is one Sipunculid at least which does not breathe by them; and although I think, when they are present, some respiration may be carried on by them and the closed vascular system, especially in reference to the

brain, I am disposed to think that the main function of the tentacles is to create a current, and thus bring food to the mouth; and the chief use of the vascular system is to extend the tentacles.

I am inclined to look for the chief respiratory organ in the intestine; this has very thin and extensive walls, and exposes a large surface to the cœlomic fluid, which in its turn bathes all the organs of the body except the brain. A considerable volume of water passes through the alimentary canal, enough to supply the oxygen required, and this current is maintained by the ciliated cells of the groove in the ascending intestine.

THE MORPHOLOGICAL LABORATORY,
CAMBRIDGE; August, 1891.

EXPLANATION OF PLATE XV,

Illustrating Mr. Arthur E. Shipley's paper on "Onchnesoma Steenstrupii."

FIG. 1.—An enlarged view of O. Steenstrupii, with the introvert partially retracted.

FIG. 2.—The same, life size.

FIG. 3.—A view of the arrangement of the internal organs, shown by opening the body-wall along the right side and reflecting the sides. Copied from Koren and Danielssen.

FIG. 4.—Section through a portion of the glandular wall of the nephridium, showing the glandular cells and their concretions.

FIG. 5.—Section through the ascending intestine to show the ciliated groove.

FIG. 6.—Section through the skin, parallel with the long axis of the body, showing cutis, epidermal glands and their secretions, circular and longitudinal muscle layers, and lining peritoneal cells.

FIG. 7.—Longitudinal section through the posterior end of the body, showing origin of single retractor, and the group of peritoneal cells which form the testis.

Fig. 1.

Fig. 2.

Fig. 3.

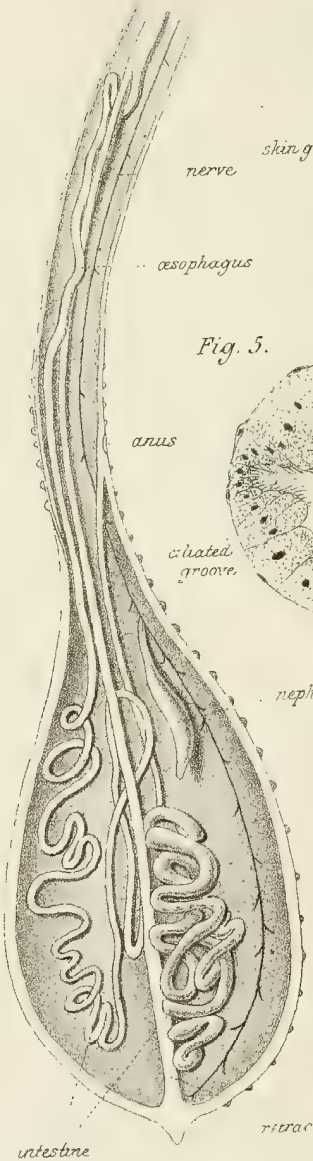

Fig. 4.

Fig. 6

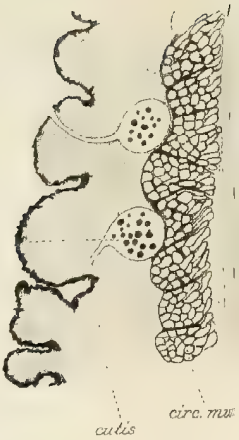

Fig. 5.

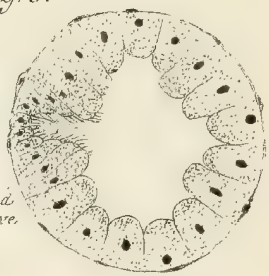

Fig. 8.

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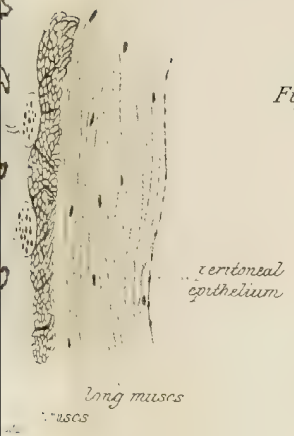


Fig. 9.

Fig. 11.

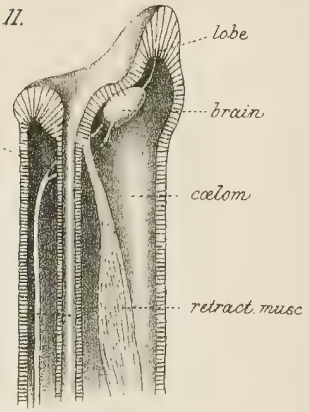
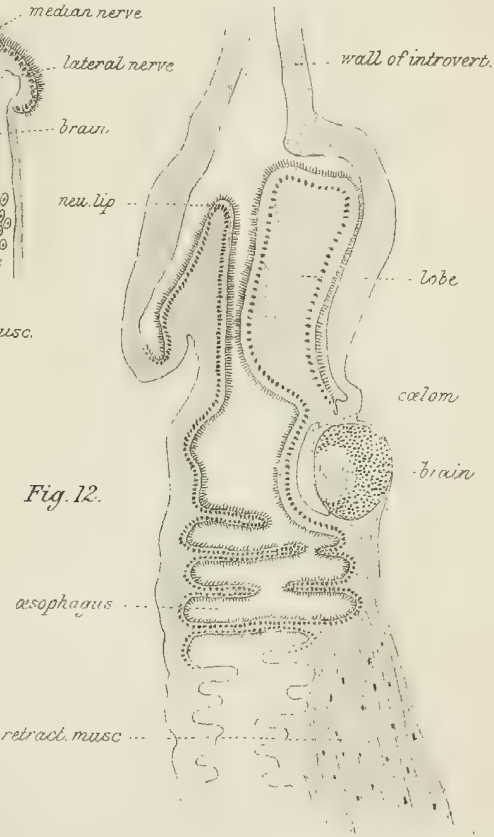


Fig. 10.

Fig. 7.

Fig. 12.



F Huth. Lith^r Edin^r

Fig. 8.—Transverse section through the introvert, showing the layers of the skin, the œsophagus, retractor muscle, and ventral nerve-cord. The body-cavity contains corpuscles and sperm morulæ.

Fig. 9.—Longitudinal lateral section of the extended introvert, showing mouth, œsophagus, and thickened ciliated lip, with the circum-œsophageal nerve of each side.

Fig. 10.—A section of the brain, parallel to the preceding (fig. 9), but more dorsal. It shows the distribution of the ganglion-cells and fibres in the brain, and the three main nerves given off from it; also the insertion of the retractor muscle, and one of the recesses formed by the crumpled nature of the œsophagus.

Fig. 11.—Diagram representing the arrangement of parts in the head, which is supposed to be divided medianly. The right half only is shown.

Fig. 12.—Section through the head and brain. The introvert is retracted. The section is not quite in the middle line, and does not show the connection of the brain with the epidermis.

Notes on Elasmobranch Development.

By

Adam Sedgwick, M.A., F.R.S.,
Fellow and Lecturer of Trinity College, Cambridge.

With Plate XVI.

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1. On the Formation and Growth of the Elasmobranch Embryo.

My observations on this subject, which were made upon the genera Scyllium and Raia, have led me to conclusions which differ in some respects from those of previous observers. In some of the points with regard to the tail I have been anticipated by Schwarz ('Zeit. f. wiss. Zool.,' Bd. xlviii, p. 191), Kowalevsky, and Kastschenko ('Anat. Anzeiger,' 3); but as Schwarz's account—excellent though it is—does not go over the whole ground, and Kastschenko's is without figures, while Kowalevsky's is inaccessible, being published in Russian, I have thought it worth while to treat the matter fully.

As is well known, the blastoderm attains a certain size before any trace of the embryo is visible, spreading by a uniform growth at all points of its circumference over the yolk. At Balfour's Stage A, however, the first trace of the embryo appears as a slight thickening at one point of the circumference of the blastoderm. This point is usually regarded as the hind end of the blastoderm. This is not quite correct, for it

really becomes the front end of the future embryo. After the appearance of the embryonic rim the blastoderm still continues to spread over the yolk by a uniform growth of all parts of its circumference, but in the centre of the embryonic rim a slight indentation appears. This indentation shares in the uniform growth of the blastoderm edge, and advances over the yolk equally with the rest of the embryonic rim and general edge of the blastoderm. As the embryonic rim travels away from the point of its first appearance, the surface of the blastoderm so formed—that is to say, the surface of the part of the blastoderm extending between the point of first appearance of the embryonic rim and the embryonic rim at any given moment of its growth—is slightly elevated from the rest of the blastoderm, and traversed by an inconspicuous longitudinal median groove. This raised part of the blastoderm soon becomes marked off by two ridges, which in front, *i. e.* at the point which marks the site of the first appearance of the embryonic rim, are continuous with one another, while behind they are continuous with the parts of the embryonic rim which bound the indentation. These portions of the embryonic rim are more markedly swollen than the rest, and form the "tail swellings" of Balfour. This elevated part of the blastoderm is the medullary plate, and the shallow groove traversing it marks the line of growth of the indentation above referred to. These points are all illustrated by my fig. 1, which represents the embryo at a stage where the indented embryonic rim has grown back a considerable distance from the point of its first appearance. Various stages in the process may be seen in Balfour's figures[1] of Stages B, C, D, and in Schwarz's figs. 1 and 2. The indentation of the embryonic rim is always placed at the hind end of the groove which marks the centre of the medullary plate. This groove is a transitory structure, and soon disappears; its importance consists in the fact that it indicates the line of growth of the indentation of the embryonic rim. (It is conterminous in

[1] 'Monograph of Development of Elasmobranch Fishes,' pl. vii; pl. viii of the Memorial Edition.

extent with the notochord, though the notochord beneath the front part of it is not at first developed.)

It must be clearly understood that the growth of the whole edge of the blastoderm has so far been a uniform one. The indentation in the embryonic rim advances equally (after its first establishment) with the more prominent parts of the embryonic rim called the caudal swellings. There is no reason to suppose that this advance of the indented part of the embryonic rim is due to the fusion of the divergent caudal swellings. On the contrary, there is every reason to suppose that the indented part of the embryonic rim advances by growth of its own substance, just as do the other parts of the edge of the blastoderm.

After a certain time the caudal swellings and the part between them begin to grow more rapidly than the adjacent portions of the edge of the blastoderm, and come to project beyond the latter like a kind of tongue overhanging the yolk (fig. 2). This appears to happen at about the time when the medullary groove is closing in its anterior part to form the medullary canal.

At the same time the edge of the blastoderm remote from the embryo has continued its rapid growth. It is only the edge of the blastoderm next the embryo in which the growth is retarded. The result of this is that the posterior projecting part of the embryo lies in a kind of bay of the edge of the blastoderm. Fig. 2 is drawn from an embryo at a stage when this bay was but little marked.

I now wish the reader to concentrate his attention upon the projecting tongue which will form the under part of the embryo. Its sides, which are part of the edge of the blastoderm, bend ventralwards and towards each other.[1] It consists on its dorsal face of the medullary plate ectoderm, which has become folded so as to form the neural canal (in fig. 2 the neural canal is established in the front part of the embryo, but widely open at the hinder end of this projecting tongue). At

[1] A good figure of this is given by His in the 'Zeitschrift f. Anatomie u. Entwick. Gesch.,' 1877, pl. vii, fig. 6.

its edge, which is part of the general edge of the blastoderm, the ectoderm is continuous with the endoderm which forms the under side of the tongue. A good idea of the appearance of a transverse section through this tongue is given by fig. 1 *b*, pl. x,[1] of the 'Elasmobranch Fishes' (Mem. Ed.). The hinder end of the tongue is of course notched, and the notch is continued forwards along the line of the groove above mentioned as occupying the centre of the medullary plate, as a slit which actually completely perforates the blastoderm, so as to lead into the space between the endoderm of the tongue and the yolk. This is shown clearly in fig. 3, and at a later stage in fig. 4. Whether this slit is due to a bilobed backward growth of the notched portion of the embryonic rim, the growth at the middle point, *i. e.* at the bottom of the notch, ceasing—in other words, to an emphasising of the notch already present—or whether it arises as a secondary perforation of the medullary plate and endoderm along the line of the groove before mentioned, I am unable to say; but I think it is due to the former.

While these changes have been taking place—and I must now refer back to fig. 2—the sides of the projecting tongue become bent ventralwards and towards each other until they meet or nearly meet in the ventral middle line. Now two important structural results, which should be noted and understood, follow from this bending: (i) the two angles formed by the junction of the edge of the blastoderm in the embryonic region with the edge of the blastoderm in the non-embryonic region—the angles, one of which is marked *a* in fig. 2, become closely approximated ventrally beneath the embryo; and (ii) a space is enclosed on the ventral side of the embryo, which space is lined by endoderm, and opens ventrally to the exterior through a slit formed by the contact of the ventrally bent edges of the tongue, and dorsally into the neural canal by the slit in the medullary plate. This space[2] is the hind

[1] Old edition, pl. ix, fig. 1 *b*.

[2] A section of the tongue in this stage in front of the neurenteric slit is shown in Schwarz's fig. 16.

gut, and the two slits which are continuous with one another round the hind end of the embryo are portions of the blastopore. By the time that the two angles marked *a* and the edges of the embryonic part of the blastoderm have come into contact ventrally, the non-embryonic edges of the blastoderm adjacent to the embryo have grown backwards over the yolk to form the bay mentioned by Balfour. The two sides of this bay, which it will be remembered are portions of the edges of the blastoderm, come to lie close together on the yolk beneath the tail of the embryo. For a little time they remain unfused, and the yolk is still freely exposed between them in a linear streak.[1] This slit, which is bounded by the edges of the non-embryonic part of the blastoderm of the two sides, is a part of the blastopore, and is continuous, passing along the hinder side of what will be called the umbilical stalk, with the portion of the blastopore leading into the hind gut and extending along the ventral side of the tail. This last portion is, as we have seen, continuous with a dorsal portion which leads through the medullary plate into the medullary canal.

The last part of the blastopore to be mentioned is the so-called yolk-blastopore, described by Balfour in the 'Elasmobranch Fishes,' p. 81 (Mem. Edition, vol. iii, p. 296), and in the 'Comparative Embryology,' 1st ed., ch. iii, p. 52.[2] The lips of this portion are continuous with the lips last mentioned as running back on the yolk parallel to one another, and ventral to the tail of the embryo.

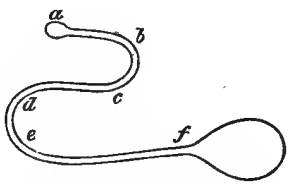
To recapitulate: the blastopore of Elasmobranchii is at the present stage—i. e. the stage immediately before closing—an elongated narrow slit, slightly dilated in front, where it lies on the floor of the medullary canal (fig. 3) and more dilated behind (Balfour's yolk-blastopore, 'Comparative Embryology,' vol. ii, ch. iii, fig. 30 *b*). Between these two limits it takes the course of a reversed letter S, as shown in the adjoining woodcut, where its lips are represented unfused.

The anterior part, *a b*, perforates the floor of the medullary

[1] Again see Schwarz's fig. 16, *d.o.*

[2] Mem. Ed., vol. iii, p. 63.

canal, and is dorsal; this is continuous round the end of the tail, *b c*, with a ventral part, which extends forwards along the ventral side of the tail, *c d*, as far as the yolk-stalk, along which it passes, *d e*, to continue backwards along the yolk, *e f*, as the slit-like non-embryonic part of the blastopore, which passes behind into the more dilated and posterior part of the so-called yolk-blastopore.



Shortly after this stage the blastopore completely closes, excepting one point in its dorsal portion, which persists for some time as the neurenteric canal.

Balfour, as is well known, was the first to compare the primitive streak of the Amniota to "the linear streak in Elasmobranchii, formed by the coalesced edges of the blastoderm which connect the hinder end of the embryo with the still open yolk-blastopore" ('Comparative Embryology,'[1] 1st ed., vol. ii, ch. xi, p. 240); and he also says, in the same place, that "the passage at the front end of the primitive streak [the neurenteric canal] is the dorsal part of the blastopore, which in Elasmobranchii becomes converted into the neurenteric canal." But he never, either in the chapter quoted or in his account of the actual development of Elasmobranchs in ch. iii, p. 52, describes the ventral embryonic part of the blastopore (woodcut, *c d*) which connects together the linear streak on the yolk, *e f*, with the dorsal part of the blastopore, *a b*.[2] In fact, he says (ch. iii, p. 52), "It is interesting to notice that, owing to the large size of the yolk in Elasmobranchs, the posterior part of the primitive blastopore becomes encircled by the medullary folds and tail swellings, and is so closed long

[1] Mem. Ed., p. 288.

[2] This part of the blastopore is clearly recognised and figured by Schwarz.

before the anterior [what I have called posterior] and more ventral part, which is represented by the uncovered portion of the yolk."

I have dwelt at some length upon this point because Balfour's description of the Elasmobranch blastopore has always bothered me, in that it does not show the connection between the yolk part of the blastopore—the linear streak—with the dorsal part; and also because I wish to present a slight modification of the comparison which Balfour made between the primitive streak of the Amniota and the linear streak on the Elasmobranch yolk. Balfour does not say that the two structures are homologous; he expressly guards himself from this. He says ('Comparative Embryology,' 1st ed., vol. ii, ch. iii, p. 51), "A linear streak [my woodcut, *ef*] formed by the coalesced edges of the blastoderm is left connecting the embryo with the edge of the blastoderm. This streak is probably analogous to (though not genetically related with) the primitive streak in the Amniota" (the italics are mine). But he undoubtedly does compare the primitive streak with this linear part of the yolk-blastopore of Elasmobranchs; and he says ('Comparative Embryology,' vol. ii, 1st ed., ch. xi, p. 240), "That it (primitive streak) is in later stages not continued to the edge of the blastoderm, as in Elasmobranchii, is due to its being a rudimentary organ."

The modification which I would propose to suggest in the comparison is as follows. The primitive streak of the Amniota is, as is well known, partly involved in the tail fold, and tucked under on to the ventral surface of the embryo. It thus becomes divided into a dorsal part, at the front end of which is the neurenteric canal or its rudiment, and a ventral part. The dorsal part is in birds for some time placed in a dilated posterior part of the still open medullary groove called the sinus rhomboidalis. This part I would compare to the dorsal part of the blastopore shown in the same position and relations in my figs. 3 and 4. The ventral part, on the other hand, I would compare to the part of the blastopore which in Elasmobranchs runs along the ventral side of the tail

:o the yolk-stalk (my woodcut, *c d*); while the linear part of the yolk-blastopore in Elasmobranchii (my woodcut, *e f*) is unrepresented or rudimentary in Aves and Amniota gene-:ally—is, in fact, the rudimentary part referred to by Balfour n the above quotation from the 'Comparative Embryology.'

The comparison has the advantage of bringing together the growing points of the embryos in the two cases. In Amniota the primitive streak is the growing point where the :ells are proliferated, out of which the greater part of the embryo is formed. In Elasmobranchii the tail swellings which form the sides of the dorsal and ventral parts of the embryonic blastopore (my woodcut, *a b c d*) are the points where the active growth takes place, as a result of which the hinder part of the embryo is formed. Indeed, the prominence of the tail swelling is due to the mass of mesoderm-cells produced by this proliferation at the edge of this part of the blastopore.

The proliferation of mesoderm takes place in a rudimentary fashion in Elasmobranchii, at all points of the circumference of the blastoderm; which circumference, gradually creeping over the yolk and enclosing it, constitutes the lips of the widely open blastopore; but the proliferation is very feeble except at the notched embryonic rim, the growth of which forms, as above described, the tail end of the embryo.

It is interesting to notice the different manner in which the tails of Elasmobranchii and Amniota are formed. There is in the former no tail fold as in the latter, but simply a bilateral bending round of the posterior tongue-like projection formed by the growth backwards of the notched part of the embryonic rim.

The above account of the Elasmobranch blastopore is not given for the first time, although when I did my work—now some years ago—I was unaware that a correct account of the process had been published by Schwarz in 1889 ('Zeit. f. wiss. Zool.,' Bd. xlviii).

Kastschenko, in the previous year, published an excellent paper on Selachian development in the 'Anatomischer An-

zeiger,' vol. iii, p. 445, in which he calls attention to the fact that Kowalevsky, in a paper published in Russian in about 1870, was the first to describe it correctly. That Kowalevsky's description, if correct, as maintained by Kastschenko, should have been overlooked, is of course attributable to the fact of its being written in Russian, and not reproduced in any of the more commonly known European languages. It seems a great pity that an observer of the eminence of Kowalevsky should thus secrete his work and render it unavailable to science.

Kastschenko's account of the matter is as follows:

"The closure of the medullary tube presents in the dog-fishes interesting peculiarities, which were first discovered and correctly described by A. Kowalevsky. . . . . The medullary folds are continuous at their hinder ends with the caudal lobes, and by means of the latter with the general edge of the blastoderm. Each caudal lobe presents a marked knee-shaped bend, the point of which is directed backwards. The lateral limbs of the paired caudal lobes approach one another on the ventral side of the embryo; and when the medullary folds fuse on the dorsal surface the adjacent caudal lobes also fuse. By the fusion of the former the medullary tube is formed, and by the fusion of the latter the neurenteric canal and the hind gut. The hind gut, therefore, is the immediate continuation of the medullary tube, and the neurenteric canal must be regarded as nothing else than a portion of the blastopore. Further forwards the hind gut remains for some time open ventralwards, but eventually this opening also fuses, the anus appearing considerably later in the same place."

This account, however, as will be gathered from my description, does not give the whole gist of the matter. It fails to notice the slit-like form of the dorsal part of the blastopore which perforates the floor of the medullary canal, and the author does not appear to understand, or at any rate fails to draw attention to the fact that the ventral opening leading into the hind gut is part of the blastopore, and is continuous with the slit-like non-embryonic part of the blastopore running along the yolk. The only point in which it supplements

Balfour's description is in the account given of the formation and of the at first open condition of the hind gut.

I quite agree with Kastschenko's remarks on the view that the embryo is formed by the fusion of two separate halves. It must, however, be admitted that the embryo is formed by a bilateral growth; that there are two growing points—one in each caudal lobe, which contributes to its development. With regard to the growth of the blastoderm, I agree essentially with Balfour, but I differ from him as to the growth of the embryo. His views are expressed in the following passage ('Comp. Emb.,' 1st ed., ch. iii, p. 35; Mem. Ed., vol. iii, p. 43):—"This rim [the embryonic rim] is a very important structure, since it represents the dorsal portion of the lip of the blastopore of Amphioxus. The space between it and the yolk represents the commencing mesenteron, of which the hypoblast on the under side of the lip is the dorsal wall. The ventral wall of the mesenteron is at first formed solely of yolk, held together by a protoplasmic network with numerous nuclei. The cavity under the lip becomes rapidly larger, owing to the continuous conversion of lower layer cells into columnar hypoblast along an axial line passing from the middle of the embryonic rim towards the centre of the blastoderm." The italics are mine, and are used to bring out the point in which my view is divergent from Balfour's. He regards the embryonic rim, at its first appearance, as marking the hind end of the future embryo, which is formed by a differentiation forwards of the blastoderm, as already established. I, on the other hand, regard the same point as marking the extreme front end of the future animal, and consider that the notched embryonic rim grows over the yolk uniformly with the rest of the blastoderm edge. It certainly does so extend itself, at any rate until the stage of my fig. 1, and of fig. 2 also, allowing for the shoot back of the caudal tongue. And it appears to me that this view—which is, to a certain extent, in accordance with the view of Roux on the growth of the Amphibian embryo ('Anat. Anzeiger,' vol. iii, p. 705)—must be looked upon as being nearer the

truth than Balfour's; for if Balfour's view is correct, the embryonic rim being stationary in growth backwards—all the differentiation being forward—ought, from the first, to be placed in a bay of the edge of the blastoderm.

According to my view, then, the blastoderm grows uniformly over the yolk at all points of its circumference. Indeed, its edge is everywhere raised into a marked ridge, which is continuous with the embryonic rim. The difference between the growth at the embryonic rim and elsewhere consists in the fact that, as the former extends over the yolk, a trail of columnar epithelial cells is left separated from the yolk by a space, whereas elsewhere the raised edge of the blastoderm simply slides over the yolk, leaving, as far as one can see, little (possibly a few mesoderm-cells) or no trail.

Further, it is clear, from what I have said above, that the notch of the embryonic rim represents the anterior end of the blastopore, and that on the view of embryonic growth above stated the blastopore does at one time or another perforate the whole length of the medullary plate. Posteriorly it does actually form for a short time a slit through the medullary plate, but anteriorly it keeps closing up as the embryonic rim grows backwards, so that it is never present in this region as more than a notch.

It will be maintained by some that this view of the growth of the embryo, and of the relation of the blastopore to the medullary plate, is incompatible with the objection to the concrescence theory above formulated. To this the reply would be that the body of the Elasmobranch embryo is no more formed by the fusion of two lateral halves than is the body of the Peripatus embryo, in which nearly the whole of the ventral surface is at one time traversed by the long blastopore.

The phenomenon we are in both these cases dealing with is the closure of the blastopore; and to talk about concrescence and fusion of two halves is merely obscuring the real question, and seeking to explain a process of growth by a phrase which has no satisfactory meaning.

Before leaving this part of my subject I may point out that

while the anus is formed within the area of the blastopore, and is in some Vertebrates actually a persistent part of the blastopore, in no Vertebrate has the mouth been traced into connection with the blastopore. The fact that no such connection has been established is not surprising when one remembers how early the anterior part of the blastopore closes in Elasmobranchs and Amphibia, and must not be taken as proving that the blastopore never extended in front of the present medullary plate on to the ventral surface of the head. I shall return to this question in the part of this paper which deals with the Vertebrate head.

It will be seen from the above account that the behaviour of the blastopore of Elasmobranchs—in its relation to the anus, neurenteric canal, and growing point—resembles very closely that of the frog as described in the admirable paper by Assheton and Robinson in vol. xxxii of the 'Quarterly Journal of Microscopical Science.'

2. On the Formation of the Mouth and Gill-clefts in Elasmobranchs.

I have had a number of drawings made of the head of embryos of Scyllium canicula to illustrate certain points in the formation of the mouth and clefts. Some of the points have been known before, and some are, I believe, recorded for the first time.

The mouth makes its first appearance in Stage I as a row of dots lying in the middle line between the two mandibular arches (fig. 5), and connected by a kind of shallow groove in the ectoderm, along which the ectoderm and endoderm are fused. These pores soon become connected (fig. 6) to form a long slit, which extends from the ventral point of junction of the mandibular arches forward along the depression between the latter as far as the pocket of ectoderm which is destined to give rise to the pituitary body. The first rudiment of the mouth actually extends into the rudiment of the pituitary body. At the front end of the buccal slit the fore-gut, the notochord, the ectoderm, and the mesoderm are all con-

tinuous with each other. The mouth soon widens and shortens (figs. 8, 10, 12) until it attains its adult form.

The **mandibular arch** is at first directed almost from before backwards (figs. 5, 6, 7), and its anterior end is under the mid-brain.

The **hyoid arch** is also directed very much backwards, though not so much as the mandibular; and its anterior (dorsal) end is well in front of the auditory sac (fig. 7).

The branchial arches are also directed backwards, but the inclination is less in the posterior arches than in the anterior (fig. 9).

The question now arises, what is the meaning of this backward direction of the visceral arches? The only answer that I can suggest to this question is that the same cause which has produced the flexure of the brain, and of the front end of the notochord, has affected the arches. If this is so the cranial flexure should really be called cephalic flexure, for it affects not merely the brain, but all the organs of the head.

To account for this flexure we must either suppose that there has been a great forward extension of the dorsal anterior end of the head, which would carry the dorsal ends of the arches forward, and, if the anterior end of the notochord and the infundibulum, i. e. the anterior end of the cranial axis, remained fixed at the front end of the mouth, would also cause the flexure of the brain and anterior part of the notochord; or that there has been a great shrinking of the ventral parts of the head just behind the mouth. If either of these views is correct, it necessarily follows that the mouth was originally a nearly vertically directed slit looking straight forward. It may even have extended on to the dorsal surface.

The early slit-like form of the mouth is very remarkable, and may be regarded as being in favour of the view that the mouth is derived from the anterior part of the slit-like blastopore, though I admit that this does dot constitute a very powerful argument.

The extension forward of the first rudiment of the mouth into the pituitary pocket is also very remarkable.

In Scyllium and Raja the hyobranchial cleft is formed before the spiracular cleft.

It is interesting to notice in this series of heads the manner in which the at first straight mandibular arch is bent upon itself at the point which will become the point of articulation of the upper and lower jaws. The part anterior to the angle develops a forward projection and forms the upper jaw—the part behind is bent ventralwards and outwards and forms the lower jaw. The widening and shortening of the mouth seems largely due to this bending of the mandibular arch (cf. series of figures of heads in ventral and side view).

The view that the mouth is derived from the anterior end of the blastopore was originally put forward in my paper on "The Origin of Metameric Segmentation" ('Quart. Journ. Micr. Sci.,' 1884, and these 'Studies,' vol. ii). Considering the early stage at which the anterior end of the blastopore closes in Vertebrates, and the relatively late appearance of the mouth, one would not expect to find any direct embryological evidence in support of this view. For the argument and indirect evidence in favour of it I refer the reader to pp. 73 et seq. of my paper above mentioned. To that evidence I now add the long slit-like form of the primitive Elasmobranch mouth.

3. Segmentation of the Mesoderm and Development of Nerves.

v. Wyhe[1] describes the cranial mesoderm in Scyllium as segmenting from behind forwards, and he says that in Stage I —and not before—the whole of the cephalic mesoderm is broken up into somites, and that all these somites contain a cavity except the first.

Kastschenko[2] says that the first somite is formed at what appears to be the junction of the head and trunk, and that the segmentation of the mesoderm extends backwards and forwards from this point. Anteriorly it becomes more and more

[1] 'Ueber die Mesodermsegmente u. d. Entwick. d. Nerven d. Selachierkoppes,' Amsterdam, 1882.

[2] 'Anat. Anzeiger,' vol. iii, p. 462.

indistinct as the front end of the embryo is approached, so that the anterior part of the cephalic mesoderm is at no stage of development broken up into somites. This unsegmented part of the cephalic mesoderm, which corresponds, according to Kastschenko, to several somites, is comprised in the second somite of Wyhe. The first somite of Wyhe occupies, in Kastschenko's opinion, a special position. Kastschenko's observations were made on the genera Scyllium and Pristiurus, but he does not state precisely the ages of the embryos to which his observations refer, nor distinguish between the genera in describing his observations. As the different genera of Elasmobranchs differ, as I hope to show, very remarkably in the condition of the mesoderm during these early stages, this latter point is one of considerable importance.

It is perfectly obvious to anyone who examines Elasmobranch development that the work of these two observers has been exceptionally thoroughly and carefully done; and if the results and views which I have arrived at differ from theirs, I would wish my work to be considered alongside of theirs, not as contradicting, but as supplementing it, by the future workers who succeed in obtaining a fuller and more accurate knowledge of the development of the different genera of this interesting group.

Balfour ('Elasmobranch Fishes,' Mem. Ed., p. 302), in describing Pristiurus, says that "coincidently with the appearance of a differentiation into a somatic and splanchnic layer the mesoblast plates become partially split by a series of transverse lines into protovertebræ." This statement I can entirely confirm for Pristiurus and Scyllium; its importance has not been fully appreciated or understood. What it means is this, that the body-cavity at the very first sign of its appearance (differentiation of mesoderm into somatic and splanchnic layers) is segmented.

Balfour goes on to say, "In the head, so far as I have yet been able to observe, the mesoblastic plates do not at this stage (D) become divided into protovertebræ." The term head

here must be regarded as meaning the anterior end of the body, for it is not possible in these young embryos to distinguish the head from the trunk. I am, however, in entire agreement with the statement that there is a stage in which there is a considerable tract of mesoderm in front of the first formed somite, which is entirely unsegmented, and with no signs of differentiation into somatic and splanchnic layers. But in Pristiurus this stage is of very short duration, for, according to Balfour, even in Stage D there is a cavity in the anterior part of the mesoderm. I can entirely confirm Balfour as to the presence of this cavity at this early age in Pristiurus; but it is not, as he seems to imply, ever continuons with the general body-cavity. It is, indeed, a somite—the second or mandibular somite of v. Wyhe,—and its appearance is followed by the breaking up of the mesoderm between it and the first so-called trunk somite into successive and contiguous but indistinct somites. I am not able to say in what order these somites are formed, whether from behind forwards, as Kastschenko maintains, or in the reverse direction. All I can say on this subject is that in Pristiurus the mandibular somite is formed before those behind it, and that in Scyllium I have an embryo a little older than Stage F, but younger considerably than Stage G, in which the whole of the mesoderm in front of the first so-called trunk somite is broken up into somites successively traceable in a series of transverse sections. The first of these somites (the second of Wyhe) is the most distinct and, I expect, the first formed, as in Pristiurus.

This early segmentation of the anterior part of the mesoderm into somites almost exactly like those in the hinder part of the body is a morphological point of great interest. It is very transitory in the genera mentioned, and disappears before any trace of the pharyngeal pouches are formed, except in the case of the mandibular somite, and possibly also of the one next it. In Stage I, where, according to v. Wyhe, the segmentation of the anterior part of the mesoderm is complete, I cannot find in either Scyllium or Pristiurus or Raja any of the somites described by him as the fourth, fifth, and sixth;

moreover the posterior limits of the third cannot be made out in Stage I.

Dohrn,[1] however, in his fifteenth study describes a complete mesodermal segmentation as occurring in Torpedo marmorata at a stage in which the mandibular and hyobranchial pouches could be made out. The embryos in question were considerably younger than the embryos in which v. Wyhe first observed the segmentation of the cranial mesoderm, and Dohrn ascribes them to Stage F; but the above-named pouches being present, he was able to compare his cephalic myotomes with those of Wyhe. He makes out ten myotomes in front of the hyoid pouch, arranged as follows:

4	myotomes	in the place	of Wyhe's	first.
3	„	„	„	second or mandibular.
3	„	„	„	hyoid.
2 or 3	„	„	„	fourth.

He admits that they are very transitory structures, and that they have lost their distinctness (by fusion with one another) in Stage G, i. e. before the stage at which v. Wyhe first saw them. Having a very practical acquaintance with the great variation of the mesoderm in embryos of different genera of Elasmobranchs I do not venture to impugn the accuracy of Dohrn's observations on a genus which I have not examined; but knowing the extreme difficulty of satisfactorily observing these rudimentary cranial somites, even when they are undoubtedly present, I cannot help feeling that it is desirable that Dohrn's statements should receive some confirmation. This confirmation is, to a certain extent, supplied by Herr Killian's[2] recently published work on Torpedo ocellata. I say "to a certain extent," because Killian's list of somites does differ slightly from that of Dohrn. I think that it is possible, and I trust that Dr. Dohrn (and Herr Killian) will forgive me for making the suggestion, that he has been misled by deceptive appearances afforded by the somites at the time of their disappearance. I know very well that in looking

[1] 'Mittheil. a. d. Zool. Station zu Neapel,' Bd. ix.

[2] 'Anat. Anzeiger,' Ergänzungsheft, 1891.

through any one series of sections it is very easy to make out what appears to be a great number of somites, but on carefully comparing the two sides of the embryo, and on estimating the intervals which the somites occupy, it is in my experience always found (after Stage F in the head region) that, with the exception of the first three head segments and the three posterior segments, these supposed somites are in embryos, in which the rudiments of the spiracle and hyoid cleft are apparent, quite irregular, and are either simply spaces in the mesoderm or remains of broken-down somites. This result comes out still more forcibly if one attempts to confirm one's observations on one embryo by similar observations on another embryo of the same size.

But even if Dohrn is right in his enumeration of the anterior somites, it is clear that Torpedo differs much from Scyllium, Raja, and Pristiurus, whether my account or Wyhe's be taken as correct. For in Torpedo there are four somites where in the other genera there is most unquestionably one, e. g. the somite of Wyhe.[1]

It would appear, then, if the number of primitive cranial somites in any given region of the head does really differ in closely allied genera in the manner indicated by the divergent observations of Wyhe, Dohrn, Killian, and myself, that the supposed indications of segmentation, which are found in the adult and are constant throughout the Vertebrata, can have very little value as real tests of the primitive metameric segmentation—i. e. of the segmentation which obviously persists in the trunk region, and which begins with the segmentation of the mesoderm, and is moulded upon it in the manner characteristic of all metamerically segmented animals.

We may, I think, even go further, and say that the adult arrangements of nerves and branchial arches, &c., characteristic of the Vertebrate head, must have arisen subsequently to

[1] I leave out of consideration the supposed somite anterior to the premandibular somite (first of Wyhe), which has been described by some observers in Acanthias, Torpedo, &c. I have seen traces of it in Scyllium, but it is in that genus merely a diverticulum of the premandibular somite.

the disappearance of the primitive segmentation. This position will be still further strengthened if my contention turns out to be correct, viz. that in embryonic development the mesodermal cranial segments do largely become indistinguishable before the adult landmarks have appeared.

If my arguments and facts are sound, it follows that any attempt to elucidate the adult structure of the head from the point of view of its being composed of a series of segments comparable to those of the trunk is foredoomed to failure; and the result of the whole inquiry shows up most thoroughly the weakness of the position of those who hold embryological research to be of small importance in comparison with the study of adult structure.

To a student of the multitudinous changes of structure which an organism passes through in the course of its existence it seems strange even now, and in the future will ever seem stranger to the philosophical morphologist, that one condition of structure only, and that the most complex and inexplicable, should have been regarded by anyone as holding the key to the solution of even a simple anatomical problem.

To sum up the matter, v. Wyhe holds that there are nine cranial segments which can be traced into the adult. Dohrn holds that there is a much greater number of cranial somites, some of which can be traced into the adult, and some of which disappear. I agree with Dohrn in asserting that the anterior mesoderm is completely segmented in Stage F, but maintain, in opposition to him, that it is not possible to say how these segments are related to adult structures, because they have for the most part vanished before any of the adult landmarks have appeared.

The premandibular somite of Balfour (the first somite of Wyhe).—There can be no doubt this is not, as Balfour supposed, separated off from the mandibular.

Kastschenko says that it develops from what he calls the prechordal portion of the gut, which becomes solid when the medullary plate is formed, and then subsequently again acquires a cavity. I find myself unable to accept this account

of the origin of the first somite. It is true that at the time of the formation of the medullary plate the notochord stops some little distance short of the front end of the body, and there is a portion of the gut in front of it; but this is only a temporary state of affairs, and is due to the fact that the front end of the notochord, which is developed from behind forwards, is not yet formed: moreover the solid mass of endoderm referred to by Kastschenko is present at the front end of the gut even at this stage. When the notochord has acquired its furthest anterior extension in Scyllium, just before Stage G, it terminates in a solid mass of cells, which is continuous also with the front end of the gut. The notochord has hitherto during the whole of its growth been continuous in front with the endoderm, and its condition at the period referred to is merely a persistence of that continuity. Wyhe's account of the anterior end of the notochord appears to me to be quite correct.

When the notochord has acquired its utmost anterior extension there is no portion of the gut in front of it, but merely this solid mass of cells, with which both it and the gut, and afterwards the ectoderm of the buccal slit and pituitary body, are continuous, and which underlies the very front end of the medullary tube. If this mass of cells be regarded as partly consisting of the anterior end of the notochord still undifferentiated, it may be said that the notochord reaches in Scyllium, at any rate, to the very front end of the neural tube; in other words, that Scyllium at this stage is truly cephalochordate in the sense that Amphioxus is cephalochordate.

The solid mass of cells in which the notochord and gut terminate becomes in Scyllium and Pristiurus very early, before Stage G, connected with the ventral ectoderm. Wyhe, who connects this fusion with the formation of the mouth, puts it down as taking place later in Stage H; but I can positively assert that in Scyllium and Pristiurus it is present before Stage G—before any trace of the cranial flexure has appeared.

There can be no question that the first or preoral somite develops in connection with this solid mass of cells, but whether entirely from it, as Wyhe appears to maintain, or only partly from it, is difficult to say. In Scyllium there are very clear indications that a part of the tissue from which the somite develops is derived from a paired ingrowth from the ectoderm. In Stage G the cell mass is continued forwards on each side in continuity with the ectoderm, and these paired tracts present the appearance of ingrowths.

The mass of cells of which I am speaking presents very remarkable differences in its relation to adjacent organs in the different genera that I have examined. In Scyllium and Pristiurus it is continuous with the ventral ectoderm throughout its whole extent from the earliest stage at which I have seen it, i. e. Stage F, or the earliest stage at which the ventral ectoderm is folded in.

In Scyllium it is for the most part not continuous with the medullary ectoderm, unless there is such a continuity, of which I am not certain, at its very front end. In Pristiurus and Raja it is markedly continuous with the medullary ectoderm throughout its entire extent, while in Raja the dorsal lateral outgrowths, which are soon formed from it, are also continuous with the medullary ectoderm. Further, Raja differs from the other two genera in that this cell-mass is not continuous with the ventral ectoderm at all (excepting through the endoderm and buccal slits).

As Wyhe has correctly stated, the first or premandibular somite of Balfour is formed by the hollowing out of this mass of cells and its lateral prolongations, and Kastschenko seems to be justified in placing it in a different category from the other somites. It differs from the other somites in two respects: (1) in its connection at origin with the ectoderm, either of the body-wall or of the neural tube (Raja, Pristiurus); (2) in its continuity with its fellow across the middle line.

Before leaving this cell mass which gives rise to the first somite, and which eventually breaks off from the various

organs with which it is at first continuous, i. e. notochord, ectoderm, and gut, I should like to point out a resemblance in its early condition to the primitive streak of the Amniota. Like the primitive streak, it is a densely packed mass of nuclei in continuity with all the layers and organs of the body. The ectoderm, endoderm, notochord, and mesoderm, all are continuous with it; and as the primitive streak is the growing point for the hind end of the embryo, so it appears to contribute in a similar manner to the front end.

The Anterior Somites in Raja.—In Raja the segmentation of the anterior mesoderm and the prominence of the first two somites are not nearly so conspicuous as in the other genera. The condition of the anterior mesoderm after its separation from the endoderm is quite different from that in Scyllium and Pristiurus. It does not assume the condition of an "epithelium" arranged round the cavities or the incipient cavities of somites. On the contrary, it at once assumes the form of "embryonic connective tissue," i. e. of a mass of stellate cells all connected together by their processes. In other words, it at once takes on the form which is only secondarily attained by the same mesoderm of the two other genera after passing through the epithelial condition. This difference in the early structure of the cephalic mesoderm of Raja and Scyllium is another proof, if such were needed, that the distinction between "mesenchyme" and epithelial mesoderm to which the Hertwigs have so prominently called attention has not the importance which they attribute to it. The cavities of the first two somites make their appearance in this stellate mesoderm at about Stages G, H. But they are at first inconspicuous, having the appearance of blood-vessels, and are without the conspicuous epithelial lining. In fact, the cells lining them have at first simply the characters of the reticulate mesoderm tissue, of which, indeed, they are merely a part.

Continuity of Cells and Layers.

The continuity between the different layers and organs of the embryo to which I first called attention in Peripatus is found in all Vertebrate embryos that I have examined. In fact, there is a network of pale protoplasmic fibres extending inwards from the nucleated protoplasm of the various surfaces. When this network has nuclei at the nodes, we get the reticulated tissue, or embryonic mesoderm, or mesenchyme. In Scyllium it is at first sparse and without nuclei. In Raja, on the other hand, it is very richly developed, and rich in nuclei. In Raja, in other words, the protoplasmic connections passing between the various organs and layers are very conspicuous and well marked. In Scyllium this tissue is at first without nuclei, as I have said. But soon it acquires nuclei and becomes denser. Where do the nuclei come from? In my opinion they are derived partly from the epithelial walls of the somites, partly from the anterior mass of mesoderm in which the notochord, gut, &c., ends, and partly from the growing tissue of the caudal swellings, and perhaps also from the neural crest.

We now pass on to speak of the neural crest in those Elasmobranchs which I have studied.

The nerve crest was first discovered by Balfour in the trunk region of Elasmobranch embryos. Marshall[1] has observed it in the chick, and describes it as occurring in the anterior part of the spinal cord region and extending continuously forward into the fore-brain.

Van Wyhe and Kastschenko also both describe the nerve crest in the Elasmobranch embryos they examined as reaching from the region of the fore-brain continuously backwards. The cranial nerves and the posterior roots of the spinal nerves grow out from the nerve crest, and the nerve crest persists itself in part as the longitudinal commissure. Both Balfour and Marshall state that this longitudinal commissure extends

[1] 'Quart. Journ. Micr. Sci.,' vol. xviii.

back continuously from the root of the glossopharyngeal to the spinal cord, connecting together the posterior spinal roots and the roots of the vagus and glossopharyngeal. It is not, however, developed in front of the glossopharyngeal, the nerve crest atrophying between the ninth and seventh, and between the seventh and fifth nerves.

My observations agree with this account except in one point, and that relates to the nerve crest. In Scyllium and Pristiurus the nerve crest is not a continuous structure, as Wyhe and Kastschenko assert (Balfour and Marshall have no observations on the cranial part of the nerve crest in Elasmobranchs). It is in three separate pieces. The first of these is found in the anterior part of the brain; the fifth nerve and presumably the ophthalmicus profundus grow out from it. The second is found a little further back, and gives origin to the seventh and eighth nerves. The third piece occurs a little further back, and reaches from the hind brain continuously back the whole length of the spinal cord. The ninth and tenth cranial nerves and the posterior roots of all the spinal nerves grow out from it. It is this latter part of the nerve crest which gives rise to the longitudinal commissure of Balfour.

There are three views as to the origin of the peripheral nerves.

1. According to Hensen's[1] view, the rudiments of the nerve-fibres are present from the beginning as persistent remains of the primitive connections between the incompletely separated cells of the segmented ovum.

2. Balfour[2] regarded them as cellular outgrowths from the central nervous system extending to the periphery. The original continuity between the central and peripheral organs, which must have existed, has, it was supposed, been lost in ontogeny by rupture, and reacquired by means of these outgrowths.

[1] 'Virchow's Archiv,' vol. xxxi, 1864.

[2] 'Development of Elasmobranch Fishes,' Mem. Ed., p. 384, vol. i.

3. The view of His,[1] which was previously held by Bidder. According to this view the nerve-fibres are the elongated processes of cells. The anterior roots are derived from non-cellular outgrowths of the spinal cord, consisting of the elongated processes of the nerve-cells of the central organ. The fibres of the posterior roots, on the other hand, are the elongated processes of the ganglion-cells of the ganglion on the posterior roots. Processes of these cells grow out to the periphery and inwards to the centre.

Balfour expressed on a priori grounds a strong preference for the view of Hensen, but rejected it on the ground that there was no evidence for the connection which it demanded. Now, however, we know that in many types the segmentation of the ovum does not bring about a complete separation of the cells of the ovum.[2]

There is no such separation in Peripatus; and in many Arthropoda—if not in all—it is known not to take place. It does not take place in Elasmobranchs, as I can certify from my own observations; but for a summary of the facts and a discussion of the whole question I must refer the reader to my monograph already quoted.[3]

If the segmentation of the ovum does not bring about a complete separation of the cells of the germ, as it was formerly supposed to do, then the connections required by Hensen's theory exist.

Turning to the special case before us of the Vertebrata, I have in the present paper dwelt upon the fact (see above, p. 256) that the cells of the young embryo (subsequent to cleavage) are connected by delicate processes, and that these processes are often extremely fine, and unite together into networks below the epithelial arrangement of the protoplasm which is characteristic of the surfaces. This network is sometimes of a very

[1] 'Anatomischer Anzeiger,' vol. iii, p. 500.

[2] See Self, "Monograph on the Development of Peripatus capensis," in 'Studies from the Morphological Laboratory of the University of Cambridge,' 1889, pp. 47—50, and pp. 130, 131.

[3] Loc. cit., pp. 99—106.

loose mesh, and its fibres are always delicate; and it is no doubt often torn and destroyed by the preserving processes to which the embryo has to be subjected. But delicate as it is, there can be no doubt of its existence in Vertebrate embryos; and there can be no reasonable doubt that it is derived from the processes and strands left between the cells as a result of the incomplete cleavage of the ovum. There can be no doubt, I say, that the network exists; but that the peripheral nerve-fibres and the central nerve-fibres are derived from it has not yet been shown. That is the point which now needs investigation, and I hope myself to treat of it in a future paper.

Meanwhile I may say that there is in my opinion evidence to show that the whole of the nervous connections (by nerve-fibres and otherwise), both in the central organ and at the periphery, are developments of this pre-existing network, which connects together at all times the whole of the cells derived from the fertilised ovum.

I do not dispute for one moment the description given by Dohrn[1] of the structure of particular stages in the development of a nerve-fibre; but in saying that it consists of a row of ecto-derm-cells laid on end to end he is, I think, going beyond his facts, being led to such an interpretation of the appearances not so much by observation of previous stages as by a process of reasoning based upon the cell theory of structure, which theory implies that the animal body at one stage of its ontogeny consisted of cells which are separate from one another and only secondarily fuse to form the adult tissues and combinations.

[1] 'Studien z. Urg. d. Wirbelthierkörpers,' No. 17.

EXPLANATION OF PLATE XVI,

Illustrating Mr. Sedgwick's "Notes on Elasmobranch Development."

Fig. 1.—Embryo of Scyllium canicula, 2½ mm. in length. The hinder end of the embryo is notched. The medullary groove is just beginning. The tail swellings of Balfour are well marked.

Fig. 2.—Embryo of Raja ? sp., 4 mm. in length. The medullary groove is closed except at the hind end. The notched embryonic part of the edge of the blastoderm has grown faster than the rest, and come to project over the surface of the yolk. The sides of this projection are already slightly bent ventralwards. They will eventually meet and form the ventral part of the caudal region of the body.

Fig. 3.—Raja ? sp. Embryo of Stage E or F, 4½—5 mm. in length. The medullary canal is still open, but the medullary folds are almost touching except behind, where the medullary canal widens out in a wide medullary groove, in the floor of which is placed the dorsal part of the blastopore. The blastopore is slit-like, but dilated in front; posteriorly it is continued round the hind end of the body into the ventral portion.

Fig. 4.—Raja ? sp. Stage E or F, 5—5½ mm. in length, a little older than Fig. 3. Medullary canal closed except behind, where it widens out and encloses the blastopore. The blastopore is slit-like, but the hinder end of the dorsal portion is faintly marked.

Figs. 3 and 4 are somewhat diagrammatic, but they show correctly the relations of the medullary groove and dorsal part of the blastopore. I hope to publish figures of the sections through them shortly.

Fig. 5.—Ventral view of head of Scyllium canicula between Stage I and K. Total length 7—8 mm. The two first pharyngeal clefts are open. The mouth rudiment is present as a longitudinal groove in the ectoderm of the buccal depression, which is fused with the endoderm. At intervals there are perforations along this groove. The groove reaches into the rudiment of the pituitary body. The mandibular arch is present as a backwardly directed longitudinal ridge, and bounds the buccal depression externally.

Fig. 6.—Ventral view of head of Scyllium canicula a little older than the preceding. The buccal groove has become a longitudinal slit.

Fig. 7.—Side view of head of Scyllium canicula a little younger than Stage K. Total length about 9 mm. I could not distinguish any trace of

the limbs. I do not think the fourth slit is open. The posterior end of the mandibular arch is slightly bent ventralwards.

FIG. 8.—Ventral view of head of same embryo drawn to a slightly smaller scale. The anterior part of the buccal slit has become much wider.

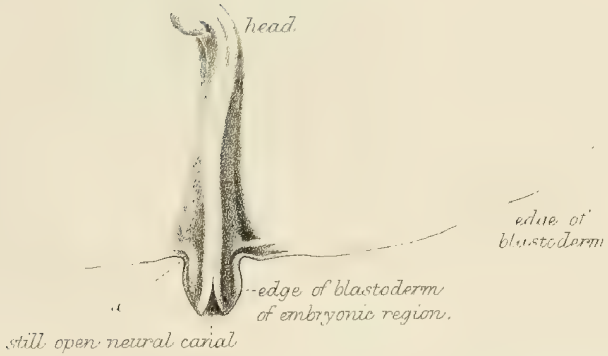
FIG. 9.—Side view of head of Scyllium canicula about Balfour's Stage K. Total length about 11—12 mm. External gills have appeared on the first and second branchial arches. The ventral bend of the hind end of the mandibular arch is more marked.

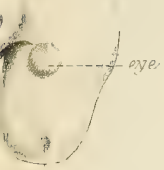
FIG. 10.—Ventral view of the same head drawn to a slightly smaller scale. The future angle of the jaw can be distinguished, the mouth being widest at that point. The posterior slit-like part of the mouth is still present.

FIG. 11.—Side view of head of Scyllium canicula about Balfour's Stage L. Total length about 16 mm. The external gills have increased in number, and are present on the mandibular arch. The angle of the jaw where the lower part of the mandibular arch bends ventralwards is very marked.

FIG. 12.—Ventral view of same head drawn to a smaller scale. The mouth has much widened, and the posterior slit-like part has almost entirely disappeared. The anterior part of the mandibular arch has a process towards the middle line. The hinder end of the body has been tilted upwards so as to bring the fronto-nasal process into view.

Fig. 2.





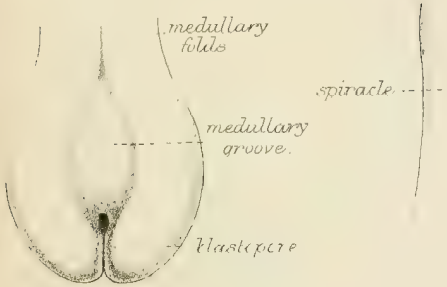
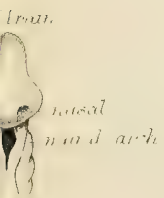
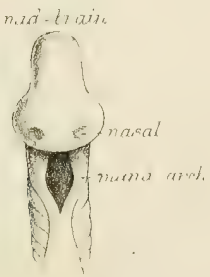


Fig. 3.

Fig. 11.





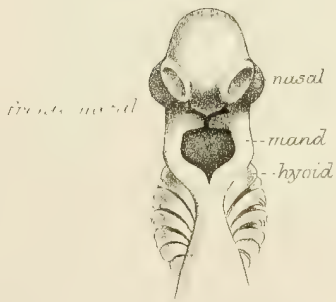


Fig. 8.

Fig. 10.

Fig. 12.

Mintern Bros., lith., London.

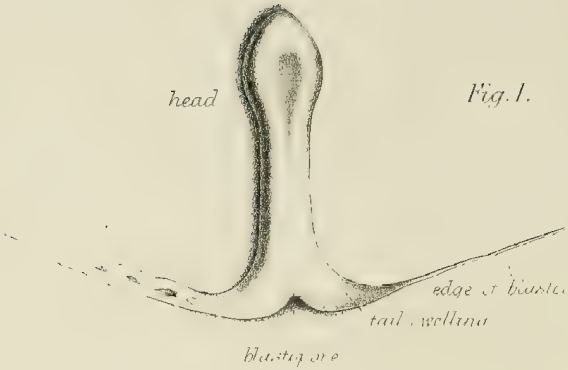
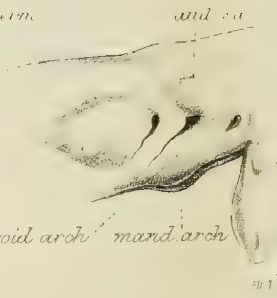


Fig. 1.

Fig. 7.



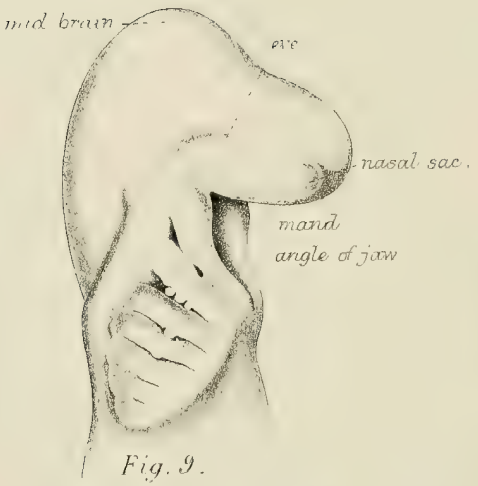


Fig. 9.

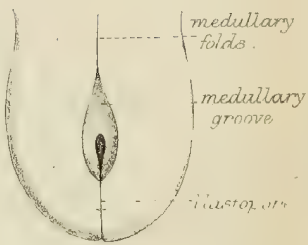


Fig. 4.

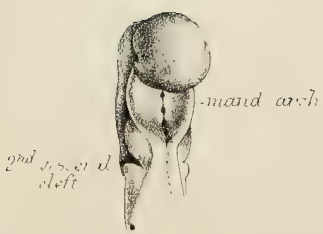


Fig. 5.

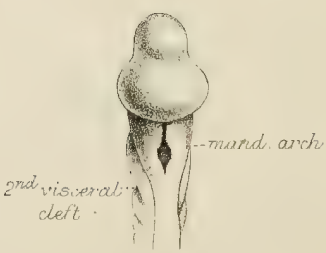


Fig. 6.

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