On Dinophilus Gigas.

By

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With Plate X.

In the spring of last year Mr. Shipley brought to Cambridge a few specimens of a Dinophilus, which he had found in Mount's Bay, near Penzance. These he was kind enough to place at my disposal; and in April last I was able myself to procure a larger number of specimens from the same locality.

The animals were found in considerable numbers on red seaweeds, &c., in pools, near spring-tide low water mark, on the rocks to the west of St. Michael's Mount. The weeds were placed in shallow white basins, with plenty of sea-water, for from twelve to twenty-four hours, when the Dinophilus left the weed, and were easily seen against the white wall of the vessel, on the side turned towards the light.

The length of the body varied greatly, the smallest specimens found being about 0·75 mm., while the largest were nearly two millimetres in length. The colour was a brilliant orange, uniformly distributed in granules through the skin, and more intensely developed in the stomach.

The body consists of a head or præ-oral lobe, seven post-oral segments, and a ventral unsegmented tail.

The head is somewhat broader than the segment immediately behind it; its form is that of a truncated cone, and it is covered

with fine cilia, and with stiff sense hairs, the latter being especially prominent in a pair of patches at the anterior end (fig. 1, *s. h.*). On the dorsal aspect of the head are two bright red, kidney-shaped eyes. A small pair of ciliated pits, such as are described by Korschelt, M'Intosh, and Hallez was observed (fig. 1, *c. p.*).

The second segment bears on its ventral surface the mouth, which is an elongated slit, bounded by a number of slight folds, which are richly ciliated.

The six following segments are tolerably uniform in diameter, each in the extended condition being slightly dilated in the centre, and separated from its neighbour by an exceedingly shallow constriction.

Behind the last segment the body narrows suddenly, forming the tail.

The "segmentation" of the body is only conspicuous in the fully extended condition. By contraction the whole of the dorsal and ventral surfaces become uniform, and the very slightest indication on the sides alone remains to indicate the series of swellings and constrictions referred to. Fig. 2, drawn from a specimen which had contracted under the influence of corrosive sublimate, but which was not in any way otherwise distorted, shows this.[1]

The præ-oral lobe, the ventral surface of the body, and the tail are uniformly covered with short vibratile cilia, and in each segment the cilia are continued into a band which surrounds the animal, while behind the cilia of each segmental ring is a circlet of fine sense hairs (fig. 1, *s. h.*). Sensory hairs were also specially conspicuous on the tail.

The pigment granules and numerous oil-globules in the skin rendered the creature so opaque that little could be made out in the living state, except the outline of the highly-coloured stomach (fig. 1, *st.*) and the mouth (M.).

The three species of Dinophilus, possessing a brilliant yellow pigment, which have hitherto been described, are D. vorti-

[1] Only six post-oral ciliated rings are visible in this figure. I have noticed the absence of the seventh in one or two preserved specimens.

coides (= D. capitata), D. metameroides, and D. caudata. From each of these the Cornish species differs in some respect. From D. vorticoides it is distinguished by the absence of a general coating of cilia on the dorsal surface, and by the presence of definite "segmental" ciliated bands; from D. metameroides it differs in the entirely superficial nature of the apparent "segmentation," adjacent segments not being separated by infoldings of the body wall.

I have not been able to consult Levinsen's recent description of D. caudata,[1] but, so far as I can gather, it resembles D. vorticoides rather than the present form.

It will be seen from what follows that a further character is presented by the present species, which has not been recognised in others—the possession of a well-marked nervous system. In the absence of any detailed information as to the structure of other forms it would be premature to regard this as a specific character, but even without it there seems to be sufficient warrant for establishing a new species, which I propose to call D. gigas, from the large size of the sexually mature individuals.

II.—Anatomy.

In its general structure D. gigas agrees closely with the D. apatris of Korschelt, differing from it chiefly in the presence of a nervous system and in the histological structure of the ectoderm. The paper of Korschelt[2] is so complete, and contains so full an account of the previous observations on the genus, that it is unnecessary to do more than refer the reader to it before passing on to a detailed description of the present species.

The ectoderm, as has already been seen, varies in character in different parts of the body. In the head a transverse section (fig. 3) shows a well-marked difference between the dorsal and ventral portions. On the ventral side are seen cells

[1] 'Viddensk. Meddel. fra den naturh. Foren. in Kjöbenhavn,' 1879-80.

[2] 'Zeitschr. f. w. Zoologie,' Bd. xxxvii, Hft. 3.

of three kinds; the most numerous (fig. 3, *gr*) are columnar, staining moderately deeply, and crowded with granules; wedged in between these are certain cells, the peripheral extremities of which are conical (*m. ep.*), but which send inwards fine processes, some of which are probably muscular, while others are nervous. The cells of the third kind (fig. 3, *x*) are pale, with deeply staining nuclei. Immediately below the ectoderm, on the ventral side, is a delicate layer of transverse muscles (*r. m.*), the fibres of which are, I believe, continuous with many of the processes of the cells marked *m. ep.*, though this connection is not so easily seen in the head as it is in the trunk (cf. fig. 10).

The dorsal ectoderm of the head is composed of an indifferent epithelium several cells thick (cf. fig. 3, where, however, the curvature of the head has caused this portion to be cut tangentially, so that the thickness of the ectoderm appears too great).

Passing backwards, the dorsal and lateral surfaces of the body are uniformly covered, between the head and the anus, with a more or less cylindrical epithelium, one cell thick (cf. figs. 4, 5, 6, 8), which is ciliated only in the region of the transverse rings already referred to.

The ventral ectoderm, in the region of the mouth and lips, is a simple columnar epithelium with narrow, elongated cells (figs. 4—6), but behind the mouth, on the whole ventral surface of the trunk, it has much the same structure as on the corresponding side of the head. The myo-epithelial cells, with their processes, are, however, much better marked (figs. 8 and 10, *m. ep.*), and their connection with the circular muscles is more easily seen (fig. 10), while the cells lying between them are all of one kind—large, finely granular, and paler, with rounded nuclei (figs. 8 and 10, *gr.*). In the figures the whole of the conical ectoderm elements with processes are labelled *m. ep.*; it is, however, obviously probable that many are nervous in nature.

In the tail the ectoderm is throughout of the same character as that on the ventral side of the trunk, except that the

granular interstitial cells are replaced by elements secreting a more or less sticky mucus. By means of this secretion the animal can attach itself with some degree of firmness to foreign objects.

Closely attached to the ectoderm is the central nervous system, which consists of a brain and a pair of lateral ventral nerve-cords.

The brain (fig. 3, *n. f.* + *n. c.*) entirely fills the præ-oral lobe. It consists of a central mass of nerve-fibres (*n. f.*) surrounded by ganglion cells (*n. c.*). Embedded in its substance are the two eyes (E), each consisting of one or two cells loaded with granules of deep red pigment, surmounted by a small cuticular lens.

The lateral nerve-cords (figs. 4, 5, 6, 8) are everywhere in close contact with the skin. Large anteriorly, they grow gradually smaller in passing backwards (cf. figs. 4 and 8) till in the last segment they altogether disappear. Each cord consists of a mass of fibres (fig. 4, *n. f.*), which is in the anterior region more or less completely separated from the skin by nerve-cells (*n. c.*); in passing backwards, however, the nerve-cells almost entirely disappear, and it is to this that the diminution in size of the cord is chiefly due.

No trace of commissures between the cords, nor of any branches, could be found, though the presence of well-developed regions of sense hairs, already referred to, makes it certain that some kind of peripheral nervous plexus exists.

Just above the nerve-cords, throughout the whole length of the trunk, runs a small bundle of longitudinal muscle-fibres (*l. m.*). These, and the ventral circular fibres already mentioned, are the only traces of a muscular system which could be found. The walls of the alimentary canal, except a small part of the pharynx, and apparently the whole dorsal region of the body, are entirely destitute of muscles.

The space between the body wall and the alimentary canal is everywhere traversed by strands of connective tissue, which forms a network with large spaces between the meshes. There is no trace of an epithelial boundary to the spaces thus formed,

neither is there any sign of a division of the cavity by transverse septa.

In certain of the connective-tissue cells which thus traverse the body cavity are "flame cells" belonging to an excretory system of the ordinary platyelminth type. The granular and opaque character of the ectoderm made it extremely difficult to observe these organs in the living animal, and I did not succeed in finding them in sections. I can only say that there is certainly a group of "flame cells" at the points marked *ne.* in fig. 1.

The alimentary canal presents all the well-known characters distinctive of the genus. The mouth (fig. 1, M) is an elongated slit bounded by curved, ciliated lips. It leads into an upwardly-directed pharynx, which communicates anteriorly by a narrow opening with the œsophagus. The œsophagus itself passes horizontally backwards. The section represented in fig. 4 is taken immediately behind the point of communication between these two structures, so that the œsophagus (*œ.*) is here entirely shut off from the pharynx (*v.ph.*). The pharynx itself is seen to be a bounded vertical wall, composed of pale, columnar, ciliated cells; outside these lie masses of gland-cells (*m. g.*), which are in places closely attached to the pharyngeal epithelium; other similar gland-cells (*e. gl.*) lie at the base of the ectoderm of the lip.

A section or two further backwards (fig. 5) the pharynx is seen to be composed of two portions—a main vertical portion, the same as that seen in front, and a horizontal portion (*h.ph.*), in the form of a lateral pouch on each side. In this, as in the preceding section, groups of gland-cells are seen, attached both to the pharynx and to the œsophagus.

Passing on to the region behind the mouth, the epithelium of the vertical portion of the pharynx becomes darker and streaked with bands of mucus thrown into it by the glands, which still surround it (fig. 6). The ventral pouches have now united to form a horizontal limb below the main body of the organ, so that its lumen becomes ⊥-shaped. Finally, still further backwards, the vertical portion ends in a large muscular

bulb (fig. 7, *m. ph.*), lying ventral to the commencing stomach, while the horizontal portion closes and in section disappears.

From a consideration of these sections, and from the diagrammatic longitudinal section given in fig. 11, it is obvious that the pharynx of this Dinophilus has the same structure as that described by Korschelt, Hallez, and others, in the better known species of the genus.

I have, however, been unable to make the animal evert its pharynx, as some species are said to do. Irritation with fresh water, acetic acid, &c., or stimulation by pressing the cover-slip, were equally useless in this respect. Further, in no case did my preserved specimens evert the pharynx in dying.

The œsophagus has already been seen; it is a narrow tube lined by a ciliated epithelium (figs. 4—6), which opens, at about the beginning of the second segment, into the large, wide stomach (figs. 1, 2, and 8, *st.*), distinguished by its wide lumen and its granular, brilliantly pigmented epithelium. The cilia of the stomach are very long, and during life their action produces a most violent agitation of the contents of the organ.

In the sixth segment the stomach bears on its ventral side a small pyloric opening (fig. 9), leading into an intestine, which is also ciliated. The stomach is prolonged, as a kind of cæcum, for a short distance behind the pylorus. The intestine passes backwards through the seventh segment, diminishing gradually in diameter, till at last it narrows suddenly and opens to the exterior in the dorsal middle line.

The reproductive organs are in both sexes similar to those described by Korschelt[1] in the female of D. apatris; that is, they each consist of a Y-shaped mass of cells, the anterior limbs of which lie under the posterior half of the stomach (fig. 8, T_2), while the posterior unpaired limb lies under the intestine, or else, as is more generally the case (fig. 9, *me.*), pushes this latter organ to one side. The two sexes are similar externally, until the ripening of the reproductive cells renders the ova or spermatozoa distinguishable through the skin. At the time of sexual maturity the gonads enlarge, so as to com-

[1] Loc. cit.

pletely fill the body cavity, the alimentary canal becomes much reduced in size, and it and the ectoderm appear to undergo a kind of fatty degeneration. I could find no ducts of any kind for the generative products, and from the condition of the tissues of ripe individuals, I have no doubt that, when the generative products are mature, the animals rupture their body wall and die. If this be true, it explains the sudden disappearance of Dinophilus at the end of spring, which has been noticed by Hallez[1] and others. In the case of D. gigas, all the individuals collected at Mount's Bay on April 22nd had undergone so much degeneration that they were quite useless for histological purposes, while the absolute number of individuals collected between the 16th and 23rd of April was so small compared with the number obtained in the same time a fortnight earlier, as to show that the process of disappearance was beginning.

III.—On the Systematic Position of Dinophilus.

It is hardly necessary to indicate the points of resemblance between Dinophilus and a fairly late Chætopod larva. The ciliated rings and the ventral plate of ciliated ectoderm, associated with a pair of unsegmented lateral nerve-cords; the ciliated alimentary canal, with its large stomach, its narrow œsophagus with a muscular pharynx, and its intestine; these are features in which all species agree with a late Polygordius larva, while in D. gyrociliatus Ed. Meyer finds that the excretory system is "almost identical with that of a Nereis larva."[2] The only point of difference between Dinophilus and the Archiannelids is the absence of an epithelial body cavity, and this character, in spite of the importance given to it by many observers, seems to be, in this case at least, of secondary importance. For in the first place the body cavity of Saccocirrus seems to be devoid of any definite epithelium;[3] while in the second place

[1] 'Histoire naturelle des Turbellariés,' Lille, 1879.

[2] Quoted by Lang, 'Monographie der Polycladen,' p. 679.

[3] Compare the figures given by Fraipont, 'Archives de Biologie,' Tome v, Pl. xiv, which are confirmed by sections in the Cambridge Laboratory.

the head cavity of Criodrilus and of many Polychœts is, at an early stage,[1] exactly in the condition which is permanent in Dinophilus; it is a cavity, not bounded by any definite "cœlomic" epithelium, but traversed by mesodermic fibres, which form a plexus running through it.

From these considerations it may plausibly be argued that we have in Dinophilus a form representing in its main features a stage in the evolution of Chætopods which is in the existing members of that group repeated only in the larval condition—a form in which the only archiannelid character which is not developed is the epithelial and segmented character of the body cavity.

That the epithelial character of the body cavity may be acquired within the limits of a group, Saccocirrus, as already pointed out, seems to prove; while the acquisition of segmentation is well seen in the various species of Dinophilus itself. Thus, in D. vorticoides[2] we find the whole body unsegmented, with a uniform covering of cilia; in D. apatris[3] we have an external segmentation which is not shared by the excretory system; while in D. gyrociliatus we find the nephridia composed of "simple, intracellular, segmental organs, terminating in flame cells;"[4] and lastly, in D. metameroides we have the appearance of a commencing segmentation of the body cavity.[5]

But the anatomy of Dinophilus seems to show that from its near connection with the Trochozoon[6] it is related to other forms besides Chætopods. The pharynx seems especially to show this. Comparing the longitudinal section (fig. 11) with a similar section through the pharynx of Histriobdella (fig. 13) we see that the pharyngeal apparatus is obviously

[1] Cf. Hatschek, "Stud. üb. Entw. d. Anneliden," 'Arb. a. d. Zool. Inst. Wien,' 1878, and others.

[2] E. van Beneden, 'Bull. Acad. Roy. Belg.,' Tome xviii.

[3] Korschelt, loc. cit.

[4] Ed. Meyer, quoted by Lang, loc. cit.

[5] Hallez, loc. cit.

[6] I use this term to imply simply the type, whatever that may have been, which is now ontogenetically represented by the trochospheres.

homologous in the two cases. But the pharyngeal appendix of Histriobdella carries three chitinous teeth, showing that this organ may in some cases develope skeletal structures; and when once this is ascertained the resemblance to the Molluscan odontophore becomes obvious. Further, in Terebella, and other Polychœts, the pharyngeal armature is developed from a ventral and posterior diverticulum of the stomodæum (fig. 14), which is apparently homologous with the corresponding diverticulum of the Archiannelid pharynx. The wide distribution which some organ of this kind had among the Trochozoa is evident from its persistence in the larvæ of such creatures as Sipunculus and many others.

It sems, therefore, legitimate to conclude that in the pharyngeal appendix of Dinophilus and the Archiannelids we have a persistent record of some ancestral organ from which developed the stomodæal armature of least the Molluscs and Chætopods, and probably also of Rotifers and Crustacea.

As for the derivation of Dinophilus and the forms which it represents from simpler types, there are, as Korschelt has already pointed out, many features which connect it with the Rhabdocœl Turbellarians. The body cavity and excretory system especially are in exactly the same condition as those of a Rhabdocœl with well developed cœlomic spaces, such, for example, as Mesostoma.

It is commonly stated that myo-epithelial cells are absent from the ectoderm of Rhabdocœls, and that the muscle-fibres are in this group devoid of nuclei. I hope, however, shortly to show that, in Convoluta at least, certain of the ectoderm cells have a structure practically identical with that just described in Dinophilus.

The only characters of importance which separate Dinophilus from the Rhabdocœls are, the possession of an anus, and the metameric repetition of ciliated bands. Of these, the second may very possibly have arisen within the limits of the genus, since D. vorticoides is uniformly ciliated; but in any case we have in Allostoma[1] a precisely similar formation

[1] Graff, 'Monographie der Turbellarien,' Bd. i, Taf. 19.

of a single ciliated ring in an undoubted Rhabdocœl. The assumption of a pelagic life might easily cause in any Rhabdocœl a hypertrophy of the cilia in certain definite regions and the consequent appearance of ciliated bands; and it seems safe to predict that a more thorough investigation of the pelagic inhabitants of those warm seas which are most favorable to the development of surface faunas will reveal the existence of genera in which this character has been developed.

The researches of Lang on Oligocladus and Cyclo-porus[1] have shown that at least in Polyclads there is no difficulty in the temporary establishment of an anus in any region of the body, and when this is once recognised the passage from a temporary to a permanent condition is easy.

The pharynx of Dinophilus and of the lower Chætopods offers another strong proof of Turbellarian affinities. On comparing the diagrams given in figs. 11 to 16 we see that the stomodæum of Dinophilus, Polygordius, and Histriobdella possesses a posterior muscular thickening lying in the wall of a lateral outgrowth from the pharynx, which is in all cases conceivably, and in Dinophilus certainly, eversible. In the embryo Terebella (fig. 14) a similar posterior outgrowth from the stomodæum exists, which subsequently[2] envelopes the whole circumference of the pharynx, and constitutes the rudiment of the pharyngeal armature. In Nais (fig. 15) we have a similar muscular thickening on the anterior wall of the stomodæum.

These facts receive at least a plausible explanation, if we suppose that the various forms of pharyngeal apparatus just mentioned are derived from a structure which primitively surrounded the whole organ, persistence in the posterior region only being in such forms as Polygordius, perhaps associated with the filling up of the præ-oral lobe by the brain, while the existence of an elongated proboscidiform prostomium in Nais renders it most convenient to preserve the musculature in front. But such a circumœsophageal apparatus as is here in-

[1] Lang, op. cit., pp. 155, et seq.

[2] Salensky, 'Archives de Biologie,' t. iv.

dicated is exactly furnished by the Rhabdocœl pharynx (fig. 16).

We seem, therefore, to have in Dinophilus a form which, related on the one hand to the Archiannelids, retains on the other many features characteristic of the ancestor common to those groups (especially Chætopods, Gephyreans, Mollusca, Rotifers, and Crustacea) which possess a more or less modified trochosphere larva; and of these the relations of the body cavity, of the excretory system, and of the pharynx, seem to point unmistakeably to a Turbellarian origin.

EXPLANATION OF PLATE X,

Illustrating Mr. W. F. R. Weldon's Paper on a "Species of Dinophilus Gigas."

List of Reference Letters.

an. Anus. *c. p.* Cephalic ciliated pits. *ci.* Transverse ciliated bands. *E.* Eye. *e. gl.* Gland cells of lips. *gr.* Granular cells of ectoderm. *h. ph.* Horizontal diverticulum of pharynx. *In.* Intestine. *l. m.* Longitudinal muscle-fibres. *M.* Mouth. *m. ph.* Muscular appendix of pharynx. *m. ep.* Myo-epithelial cells of ectoderm. *Me.* Median lobe of gonad. *ne.* Position of observed nephridia. *n. f.* Nerve-fibres. *n. g.* Nerve-cells. *n. l.* Lateral nerve-cord. *œ.* Œsophagus. *r. m.* Circular muscles. *st.* Stomach. *s. h.* Cephalic sense hairs. *sh*^{1}. Post-cephalic rings of sense hairs. *x.* Deep cells of cephalic ectoderm. *Br.* Brain. *St.* Stomodæal musculature.

FIGS. 1—10.—Dinophilus gigas.

Fig. 1. The live animul extended, seen by transmitted light.

Fig. 2. A specimen contracted by treatment with corrosive sublimate solution, but not otherwise distorted. This figure shows fairly well the shape assumed on irritation by the live creature.

Fig. 3. A transverse section through the præ-oral lobe.

Figs. 4—6. Transverse sections through the pharyngeal region.

Fig. 7. The muscular bulb of the pharynx, in transverse section.
Fig. 8. Section through the middle of the trunk.
Fig. 9. Section through junction of stomach and intestine.
Fig. 10. Section of ventral ectoderm. Zeiss's im., oc. 2.

Figs. 11—16.—Diagrams of various forms of pharyngeal apparatus, as seen in longitudinal sections of the head.

Fig. 11. Dinophilus (original).
Fig. 12. Polygordius (schematised from Uhljanin).
Fig. 13. Histriobdella (schematised from Foettinger).
Fig. 14. Terebella larva (schematised from Saleusky).
Fig. 15. Navis (schematised from Vejdovsky).
Fig. 16. Vortex (schematised from von Graff).

Fig. 1.

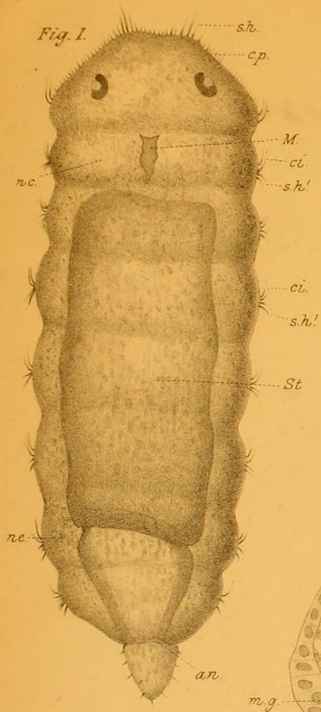


Fig. 2.

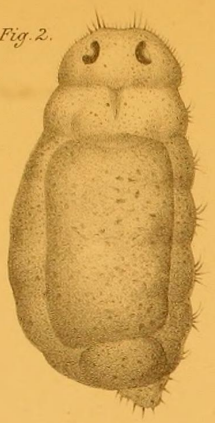


Fig. 3.

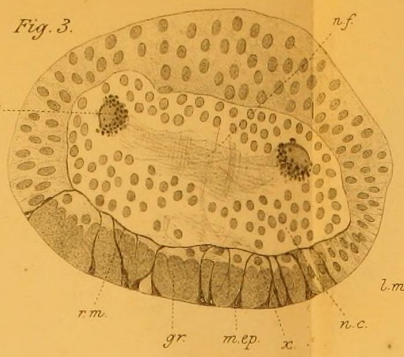


Fig. 4.

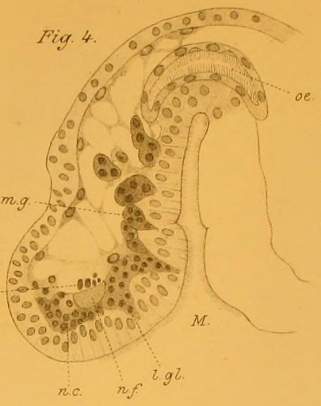


Fig. 5.

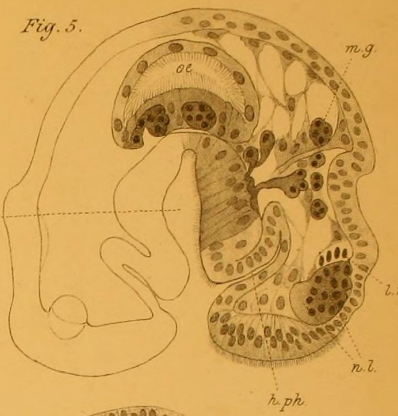
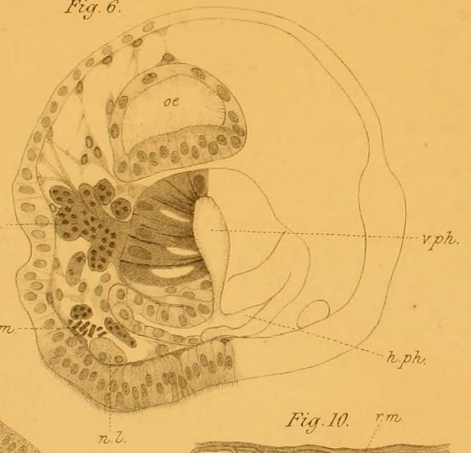


Fig. 6.



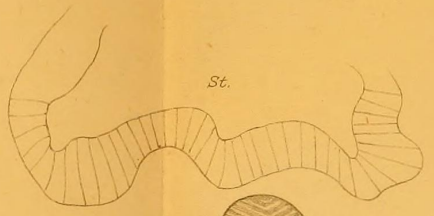


Fig. 7.

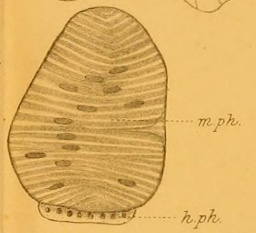


Fig. 8.

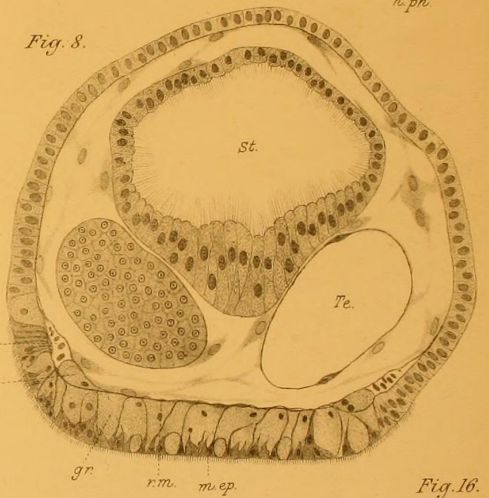


Fig. 9.

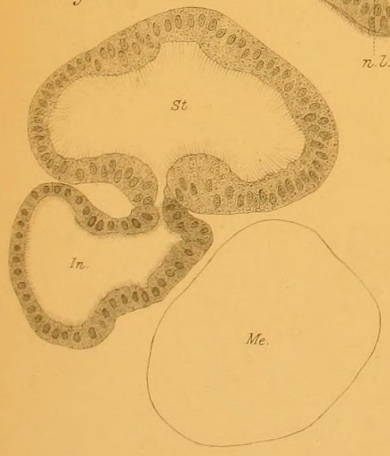


Fig. 10.

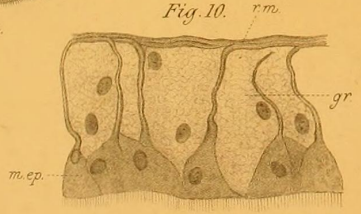


Fig. 11.

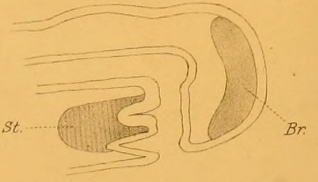


Fig. 12.

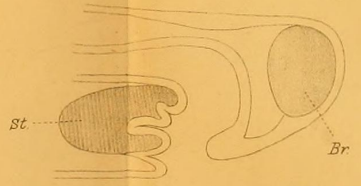


Fig. 13.

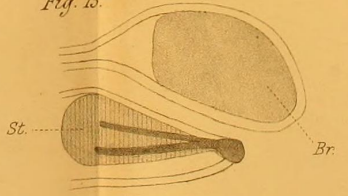


Fig. 14.

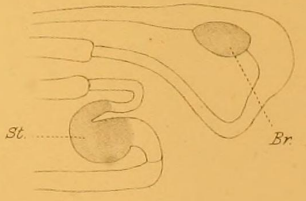


Fig. 15.

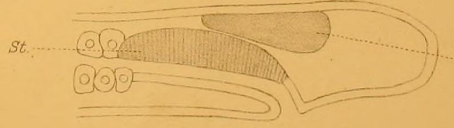
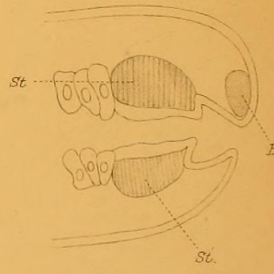
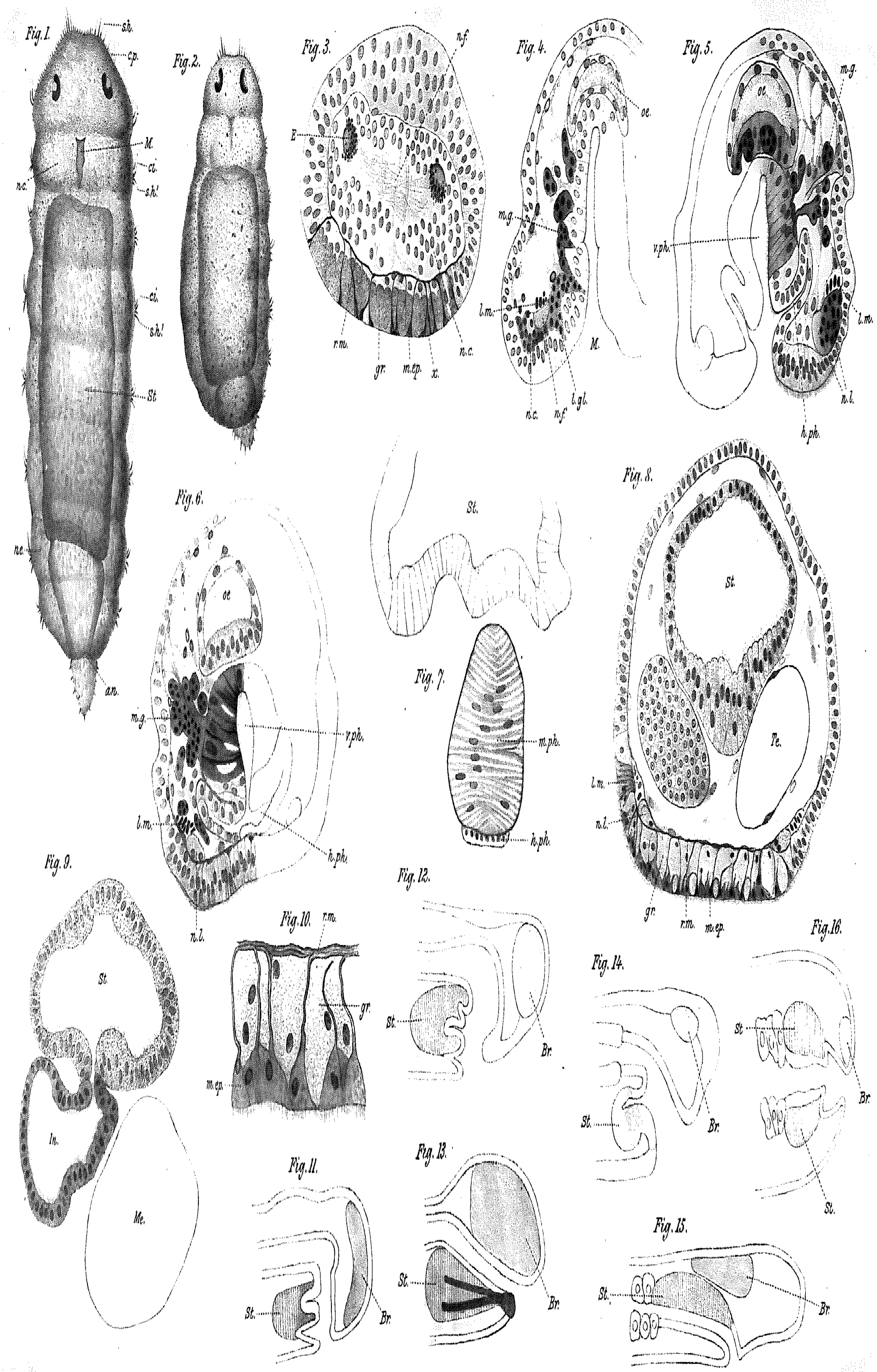


Fig. 16.





Weldon del.

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