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MEMOIRS:

On Temnocephala, an Aberrant Monogenetic Trematode.

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With Plates XX, XXI, and XII.

Historical.

About the year 1849 Gay discovered, in the environs of Santiago, on the surface of certain crayfishes, a leech-like animal, which, in a letter to Blainville, he described briefly under the name of Branchiobdella chilensis.[1] The genus Branchiobdella was first instituted by Odier, and, though apparently the name was applied by him to a species of the genus Branchellion of Savigny, it has been very generally adopted since for an external parasite of the fresh-water crayfish of Europe—the Branchiobdella astaci of Rudolphi.

Branchiobdella astaci, as is well known, is a well-marked Leech; it has an elongated body composed of about eighteen distinct rings, with an anterior and a posterior sucker, an anal aperture above the posterior sucker, and a median ventral nerve-cord. In Gay's 'Zoology of Chilé,'[2] Blanchard described Gay's species under the name of Temnocephala chilensis, recognising that the differences between it and Branchiobdella astaci are too great to admit of both species being placed in one genus. "Las Temnocefalas se distinguen aun

[1] I am not aware that the letter has been published, but it is quoted by Moquin-Tandon in the 'Monographie des Hirudinés,' p. 300.

[2] ii, p. 51.

del género Branchiobdella por la presencia de los ojos y de las divisiones cefalicas de que no existe traza alguna en él."

In 1870, Philippi[1] published some observations on Temnocephala, based on an examination of living specimens which he found on the surface of Chilian fresh-water crayfishes of the genus Æglea. He described the external form, the colouration, and the movements, and notices certain of the internal organs which he is able to see through the wall of the body, though without being able to give any precise account of their nature. He concludes that Temnocephala ought to be placed among the worms in the neighbourhood of Malacobdella.

During his scientific explorations in the Phillipine Islands, Carl Semper found, on the surface of fresh-water crabs, specimens of an external parasite, which proved to be the Temnocephala of Blanchard; but a more detailed examination showed him that the affinities of the animal were much more with the ectoparasitic Trematodes than with Malacobdella or the Hirudinea.[2]

Wood-Mason found, in 1875, a number of Temnocephalæ in a bottle containing some New Zealand crayfishes (Paranephropssetosus), to which they had evidently been attached, and some also in bottles containing specimens from the north-east frontier of India.[3]

At the beginning of last year, when on a visit to Tasmania, my attention was directed by Mr. Alexander Morton, the curator of the Tasmanian Museum at Hobart, to certain remarkable animals observable on the surface of a specimen of the large fresh-water crayfish of the northern waters of Tasmania, which he had alive in a tank. These proved to be

[1] 'Archiv für Naturgeschichte,' 1870.

[2] 'Zeitschrift f. wiss. Zoologie,' xxii Band (1872). I have not been able to see this paper, which is a very short one (three pages), and am indebted for my knowledge of it to Leuckart's "Bericht" in the 'Archiv f. Naturgeschichte,' xl Band (1874).

[3] "On the Geographical Distribution of the Temnocephala chilensis of Blanchard," 'Ann. Mag. Nat. Hist.' (4), vol. xv, p. 336 (1875).

Temnocephalæ; and I have since found that other species of this remarkable genus infest the fresh-water crayfishes of the rivers of New South Wales.

I must here acknowledge my indebtedness to various friends, through whose kindness I have been able to procure ample supplies of specimens, more especially to Mr. Alexander Morton, of Hobart; Mr. E. C. Merewether, and Mr. Harry Merewether, of Bondi and Mount Wilson; Mr. Alexander Hamilton, of Mudgee; Mr. J. D. Cox, of Mount Wilson; Mr. Charles Chilton, of Dunedin, and Mr. J. J. Fletcher.

General Description of Temnocephala.

Temnocephala (Pl. XX, figs. 1—5) is a leech-like animal, the largest about half an inch in length. In outline the body is ovate or pyriform, but much compressed from above downwards; the anterior end narrower than the posterior, and the lateral border fringed with a narrow, delicate fold. At the narrower anterior end there is, in the middle, in the case of the Tasmanian species, a rounded, dorso-ventrally compressed lobe, about a fifth of the length of the rest of the body, and on either side of this two very long and slender tentacles, which are filiform, and a half to two thirds of the total length of the body when fully extended, but are capable of being greatly retracted. In the case of the New South Wales species, and that from New Zealand, there are five equal slender tentacles. Close to the broader posterior end on the ventral aspect is a very large sucker of circular outline supported on a short stalk. Near the middle line of the dorsal surface, placed near together a little behind the bases of the tentacles, is a pair of small black eyes. On the ventral surface, not far from the anterior end, is the mouth—a well-marked aperture. Some distance behind it, a little way in front of the sucker, is the common genital aperture—a short transverse slit leading into the genital cloaca.

By incident light against a dark ground, the body of the larger New South Wales species (fig. 2) and of the Tasmanian

species (fig. 3) has a dark grey ground colour with rich brown mottling. In the New South Wales species there are several, usually three, broad transverse dark bands, separated from one another by lighter intervals. In the middle of the most anterior of these, towards its front edge, about a fifth of the total length behind the base of the tentacles, is the dark spot on which the eyes are situated, and in front of this is a lighter interval, succeeded in front again by a dark space about the bases of the tentacles; the latter are of a nearly uniform brown, rather lighter towards the tips. Slightly behind the eyes, and rather nearer the lateral margin than the middle line, there will be seen on either side a minute white spot, which marks the position of the opening of the excretory system.

Little is to be seen of the internal organisation on a surface view, the pigment of the integument being very dense. A few light reticulating lines may be observed, which indicate the position of the elements of the dorsal nerve-plexus, the alimentary canal may be discerned as a lighter patch of squarish outline towards the middle of the body, and a few, irregularly-placed, fine transverse lines may be observed, which marks the position of rudimentary intersegmental septa.

On the ventral side the colour is light grey; the sucker is colourless. The squarish intestine, of a darker colour, is seen through the body wall, and transverse divisions of its substance indicate the intestinal pouches or cæca.

Here and there among the full-grown Temnocephalæ, in the case of the larger New South Wales species, will be found smaller immature specimens, distinguished by their whiteness; and when these are examined under the compressorium a good deal is to be learnt regarding the internal organisation. They are almost entirely devoid of pigment, except a little in the neighbourhood of the eyes and along the back, and, strange to say, they have invariably six tentacles, whereas the adult has only five.

When undisturbed the Temnocephalæ adhere to the surface of the crayfish by means of the sucker, with the body extended and inclined at an angle of about 45° to the surface

of attachment, the long slender tentacles stretched to their utmost and waving about the water in search of food. Their food consists of small crustacea (small Amphipoda in the case of the New Zealand species, small Aselli and Entomostracans in the case of the New South Wales species) and insect larvæ. These they capture by means of the tentacles, and it is readily to be understood that living on the crayfish must be of advantage to the animal, the movements of the crayfish in searching for food amongst the stones and dead leaves and sticks on the bottom of the stream doubtless starting many of these Arthropods, and enabling the Trematodes to secure them.

The Temnocephalæ move from place to place with a sort of "looping" action very like the movements of a leech. The body is applied to the surface of the crayfish and then stretched out; the tentacles become shortened and flattened out on the surface of the crayfish and play the part of anterior suckers; the large sucker is relaxed and the body drawn forwards by means of the tentacles, until the sucker is fixed again close up to the latter, the body being now bent double; the tentacles then let go their hold, the body is stretched out again and so on. The body can be rotated from side to side through a very large arc by the action of the sucker, which is capable of a considerable amount of rotation around its short stalk. The rapidity of all these movements and the extreme sensitiveness of the animals are surprising. A slight touch from an instrument will cause an instantaneous turning aside of the body, drawing in of the tentacles, and frequently rapid flight in a different direction from that in which the attack was made. In turning aside from a touch the little animals show a very definite sense of direction, and if a succession of taps be made on the bottom of a vessel in which they are living, alternately on opposite sides of them, they will turn from one side to the other according to the direction of the tap. If they are detached from the surface of the crayfish—which it is very difficult to do owing to the slippery character of their integument and the firmness with which the sucker adheres—they contract themselves for a moment into a ball, then stretch-

ing themselves out to their full length and extending their tentacles, they are often able by strong flexions of the body while falling through the water to seize on some other part of the surface and regain their position on the crayfish. The movements thus made in the attempt to regain a hold are not unlike the movements made by the leech when swimming, but the Temnocephalæ are incapable of directed movement or even of sustaining themselves in the water by this means. When the body is pinched or cut, the tentacles are very often turned backwards and clasp the instrument used as if to ascertain its nature or to repel the attack, and the tentacles are to be regarded as special organs of touch as well as instruments of prehension and aids to locomotion.

Four very distinct species of Temnocephala frequent the Australian and New Zealand crayfishes, and all of them, so far as I am able to judge from Philippi's figures, differ from T. chilensis. That found on the surface of the larger Tasmanian crayfish is distinguished by the possession of a short compressed lobe instead of the median tentacle. All the others have, like T. chilensis, five equal or nearly equal tentacles; but are to be distinguished from one another by certain differences in the structure of the reproductive organs to be noticed later on. I propose the following names for the four species:

1. Temnocephala fasciata, on Astacopsis serratus, streams of New South Wales.

2. T. quadricornis, on Astacopsis Franklinii, northern rivers of Tasmania.

3. T. minor, on Astacopsis bicarinatus, streams of New South Wales.

4. T. novæ-zelandiæ, on Paranephrops setosus, rivers of New Zealand.

Integument, Muscles, and Parenchyma.

The body wall is composed of the following layers—cuticle, epidermis, basement membrane, circularly arranged layers

of muscular fibres, longitudinal layer of muscle, nervous layer.

The cuticle (Plate XXI, fig. 1, *c.*) attains a thickness of ·006 mm. in T. fasciata. It is beset with numerous vertical pore-canals, the presence of which gives it the appearance in sections of being made up of close-set papillæ. On a surface view it appears slightly corrugated, the rugæ being exceedingly minute, irregular, and mostly transverse.

The epidermis (*e*) is of nearly equal thickness with the cuticle. It is composed of a thin layer of protoplasm, with regularly distributed nuclei, but without a trace of cell-boundaries. The nuclei are spherical, of a diameter nearly equal to the whole thickness of the epidermal layer, and with a finely granular interior. In vertical section the substance of the epidermal layer appears to be divided into a series of vertical columns by a number of parallel lines. This appearance is produced by the presence of very numerous pore-canals, which run perpendicularly through both epidermis and cuticle to open on the surface of the latter; and a surface view of the epidermis shows the numerous and closely-placed rounded openings. In T. minor the cuticle is smooth, and the nuclei in the epidermis much less numerous than in T. fasciata.

The basement membrane (*b.*) on which the epidermis rests is a perfectly homogeneous membrane of, comparatively, considerable thickness, being as thick as the epidermis itself. It stains deeply with carmine dyes—much more deeply than the epidermis, but is not readily stained with hæmatoxylin. It is devoid of nuclei or other evidence of structure; like the superficial layers it is perforated by the pore-canals, but it is difficult to see them unless in parts where the secretion of the subcutaneous glands, which is readily acted on by staining agents, is passing out. Like the cuticle and epidermis the basement membrane varies little in thickness in different parts of the body. In T. minor cuticle, epidermis, and basement membrane are very delicate, and together are only ·008 mm. in thickness.

The external muscular layer (*c. m.*) is a thin stratum of circularly arranged fibres, not more than one or two fibres in thickness. It is situated in a stratum of finely fibrous matter containing a layer of pigment cells, which in T. fasciatus on the dorsal side form with their anastomosing processes a dense and regular network; this pigment-bearing stratum is much more strongly developed on the doral side than on the ventral.

The internal layer of muscle (*l. m.*), the fibres of which run longitudinally, is much more strongly developed than the external layer, and is composed of thicker fibres; it is most powerfully developed on the ventral side, but extends over the whole surface and is specially well developed in the tentacles on the ventral side. The fibres on the dorsal side are arranged in bundles, separated from one another by very narrow interspaces occupied by interstitial fibrous matter containing pigment; on the ventral side they are arranged in thin fasciculi.

The muscular fibres of these two layers are usually angular, sometimes oval in cross section, ·004 mm. in diameter in the internal layer, rather less in the external. They are finely striated longitudinally, non-nucleated, and are separated from one another by finely fibrillar interstitial matter. In cross section they are seen to consist of two substances, one forming a narrow darker central core, the other clearer and constituting the principal bulk of the fibre.

The nervous layer is a thin layer of the parenchyma, distinguished by the presence in it of a considerable amount of pigment, and by being the seat of the superficial nerve-plexuses. It passes insensibly into the general parenchyma of the centre of the body.

In the structure of the body wall Temnocephala resembles the marine ectoparasitic Trematodes such as Tristomum and Onchocotyle, and differs essentially from the Distomidæ in the presence of the pore-canals and the absence of distinct cell-boundaries in the epidermis; the inner cell-layer described by Sommer[1] in the liver-fluke is not represented,

[1] "Die Anatomie des Leberegels," 'Zeitschr. f. wiss. Zool.,' xxxiv Band.

but its existence in the latter species has been denied by Mace.[1] The layer of oblique muscular fibres found in the body wall of some Polystomidæ, though absent in others, is not here represented.

The interstices between the various organs and the wall of the body are occupied by the parenchyma, which consists of a variety of areolar fibrous tissue with very delicate anastomosing fibres with plates and nuclei. In the interspaces of this network are occasionally cells which having no distinctive character may be called parenchyma cells; but these only occur irregularly and are entirely absent in many places. To be regarded perhaps as modified cells of the parenchyma is a layer of very large cells (Pl. XXI, figs. 3 and 4) lying between the longitudinal layer of muscle of the body wall and the testes, and extending from the region of the pharynx in front to that of the genital aperture behind. These are the subcutaneous gland-cells whose function is the secretion of slimy and viscid matter to be discharged on certain areas of the outer surface. The fibrous tissue of the parenchyma forms wide meshes in which these cells are contained. The cells themselves are of colossal size, averaging ·066 mm. in diameter, with a large vesicular nucleus like that of an ovum, and a spherical solid-looking nucleolus. The substances of the protoplasm of these cells presents three principal modifications. In the first of these forms there is only a very delicate protoplasmic network in which the threads have a tendency to radiate outwards from the nucleus to the periphery. In a second form there occur in the interstices of the network a greater or smaller number of rounded granules, ·004 mm. in diameter. In the third variety the place of the network is more or less completely taken up by numbers of bacilliform bodies, about ·02 mm. in length, slender, and with a slight enlargement at one end. Intermediate stages between the two last forms are also to be observed, the contents of the cell consisting of oval bodies, each of which is enclosed in a clear

[1] "Recherches anatomiques sur la grande douve du foie (Distoma hepaticum)." [Abstract in 'Zool. Jahresb.,' 1882, i, pp. 230, 231.]

spherical space. The secretions of these cells have two distinct destinations. In the case of the more posterior cells of the gland (Pl. XXI, fig. 2, *d.*) the secretion passes out of the cell by a narrow elongated neck or duck without well-defined walls, and reaches the exterior by perforating the muscular layers and passing through basement membrane, epidermis, and cuticle by means of the delicate pore-canals. The numerous "ducts" of these cells, which branch and anastomose in their course, pour their secretion over a considerable area of the ventral surface in front of and behind the genital aperture, and all over the ventral surface of the sucker. The function of these cells which discharge around the genital opening is, doubtless, the secretion of the viscid matter by means of which the eggs adhere together, while that of the cells discharging on the sucker is the formation of a similar sticky secretion adding to the adhesive power of the organ. The most anteriorly placed of the cells discharge their contents into a system of narrow anastomosing channels which run between them. These channels unite on each side anteriorly to form a larger duct which runs forwards into the region of the head, past the excretory sac, and breaks up in front into branches which open on the exterior (through the pore-canals) on the ventral aspect of the tentacles. The secretion here voided is a viscid matter similar to the secretion of the posterior part of the gland, and its function is obviously to add to the prehensile power of the tentacles.

Scarcely to be distinguished from those subcutaneous unicellular glands are certain gland-cells at the base of the penis, secreting a substance containing spherical granules which reaches the interior of the ejaculatory duct to become mingled with the testicular secretion; but, though apparently merely a part of the subcutaneous system of unicellular glands, this group of cells on account of the special destination of its secretion is best considered along with the reproductive organs.

The system of muscular fibres of the parenchyma is highly developed. In general they occur either singly or in narrow bands, running (Pl. XXII, fig. 17, *d. v. m.*) either trans-

versely or obliquely through the parenchyma from the dorsal to the ventral aspect, and inserted at their extremities into the basement membrane. In the region of the intestine, however, the muscular fibres of the parenchyma form a series of about twelve incomplete transverse dissepiments (Pl. XXI, fig. 8, *sept.*), constricting the intestine at regular intervals, and dividing the peri-intestinal region into a series of incompletely separated segments. Continuous with these are the layers of muscular fibres investing the alimentary canal and the reproductive organs.

The muscular fibres of the sucker are derived both from the muscle of the body wall and from that of the parenchyma. There are six sets of fibres to be distinguished, viz. (1) fibres which pass from the dorsal wall of the body to near the centre of the concavity of the sucker; (2) oblique fibres which run through the substance of the outer part of the sucker from the dorsal to the ventral surface; (3) fibres which run longitudinally from the ventral body wall obliquely through the lateral parts of the stalk; (4) radial fibres; (5) circular fibres running round the margin; (6) accessory fibres.

Alimentary Canal.

The mouth is situated on the ventral surface, near the anterior end of the body, rather behind the plane of the eyes and the excretory openings. It is a transverse opening of considerable width, leading directly into the cavity of the muscular pharynx. The latter is a subspherical organ with thick walls and a relatively small cavity. The wall of the organ (Plate XXI, fig. 6) is constituted as follows. Most internally is a thick membrane (*ep.*), almost homogeneous in character, but very finely granular, and very finely striated in a vertical direction. The substance of which this membrane is composed is not cuticular, but, though entirely devoid of nuclei, is to be taken as the equivalent of an internal epithelium. Running right through the substance of the wall of the pharynx is a series of radially arranged muscular fibres (*rad.*);

each of those divides both externally and internally into two or three parts; internally, these pass into the internal layer, in which they are traceable for a little distance as vertical lines; externally, they are affixed to the most external layer. Between the radiating fibres, which are not closely placed, is a finely fibrous material, which is little acted on by staining agents, and embedded in this, here and there, is a large ganglion-cell. Besides these radiating fibres the wall of the organ comprises four layers of circularly arranged fibres; the most internal layer (*i. c. l.*) is longitudinal in direction, the second and third (*e. c. t.* and *i. c. t.*) transverse, and the fourth (most external *e. c. l.*) longitudinal.

The intestine (Plate XXI, fig. 5) is a wide, dorso-ventrally compressed sac of rectangular outline, nearly as broad as long, which occupies about the middle third of the length of the body and more than half its breath. It is surrounded on all sides, and to some extent also in front and behind, by the rounded lobes of the vitelline glands; in the middle in front it comes into relation with the pharynx, while behind the receptaculum seminis and ovary lie in the concavity of a sort of recess between two very slight postero-lateral prolongations.

The walls of the intestine are deeply sacculated, a number of incomplete partitions running inwards from the body wall, as already described, and producing a series of circular constrictions, so that the internal cavity consists of a central space and a series of annular cæca lying between successive constrictions.

The intestinal wall (Plate XXI, fig. 7) is of considerable thickness. It is composed of greatly elongated epithelial cells (*e.*) with rounded inner ends which are devoid of cilia. In the granular substance of the cells themselves, as well as in little special reservoirs (*c.*), which appear to be intracellular, are very numerous large granules which show a distinct concentric structure; these, which colour darkly with hæmatoxylin, but are little affected by carmine, are most numerous towards the bases of the cells. This epithelium is supported externally by a thin musclar coat (*m.*).

Excretory System.

The excretory system of Temnocephala differs from that of most Trematodes[1] in opening on the exterior by two apertures. These are situated on the dorsal surface slightly behind the eyes, as already described. The surface in this position is usually found to be elevated on each side into a rounded eminence, and in the centre of this is easily to be distinguished the minute circular opening. This leads into the cavity of a non-ciliated sac (Plate XXI, figs. 9 and 10) with thick walls, of a pyriform shape, but slightly bent on itself. From the narrower posterior end proceed two large vessels which pass backwards along the lateral edge of the alimentary canal, and two (or a single one which speedily bifurcates) passing forwards towards the bases of the tentacles. As ordinarily seen these canals are twisted into spirals owing to the contraction of the whole body, but when the body is fully extended they are straightened out. The arrangement and final destination of these vessels and their branches I did not succeed in tracing. It would seem probable that the branches open directly into the spaces and channels in the parenchyma, and the "Schwingende Läppchen" found in other forms do not seem to be present.[2]

The above-described arrangement of the excretory system would seem to be very characteristic. Paired external openings, where they occur in other Trematodes, are to be found on the ventral and not on the dorsal surface, with the single doubtful exception of Polystomum.

The wall of the terminal sac (fig. 10) is composed of a thick layer of very finely fibrous substance (*e.*) without a trace of nuclei, but with occasional rounded vacuoles, and a thin layer of a similar substance lines the longitudinal vessels (fig. 11). External to this protoplasmic layer is a thin sheet of the parenchyma muscle (fig. 10, *m.*) which completely invests the

[1] Vide Fraipont's "Recherches sur l'appareil excréteur des Trematodes et des Cestodes," 'Archives de Biologie," ii (1881).

[2] Taschenberg states that they are absent also in Tristomum (see 'Zoologischer Jahresbericht,' 1879, i, p. 319).

organ. The external aperture is capable of being dilated or contracted by specially arranged fibres of the muscular layers of the body wall. At the narrow end of the sac, where the branches are given off, are two large ganglion-cells (figs. 9 and 10, *g*.).

Nervous System.

The cerebral ganglion (Pl. XXI, fig. 12, and Pl. XXII, fig. 1) is a six-sided body situated immediately beneath the longitudinal layer of muscle on the dorsal aspect, just in front of the pharynx. It consists of a clump of non-nucleated granular material, having ganglion-cells symmetrically arranged around it, with lateral, anterior, and posterior commissures of nerve-fibres. Laterally, it gives off in front a pair of nerve-trunks, each of which divides into three branches entering the tentacles —the middle tentacle being supplied by a branch from each side. Lateral branches pass outwards to supply the sides of the anterior region of the body. Posteriorly, the ganglion gives origin to three pairs of nerve-cords, which pass backwards towards the posterior end of the body. The ganglion bends downwards laterally towards the ventral aspect of the body, but the origin of the branches are still all distinctly dorsal in position. The first of these—the dorsal (Pl. XXI, fig. 12)—are the smallest, and are rather more superficial in position than the others. They leave the cerebral ganglion at its posterior and lateral angles, and run along on the dorsal aspect of the body immediately beneath the longitudinal layer of muscle in the pigmented "nervous" layer, the distance between the two cords being less than their distance from the lateral border. Branches are given off from these cords as they pass backwards, both internally and externally at frequent and fairly regular intervals. The internal branches of each cord pass inwards at right angles to the long axis of the body, and unite with the corresponding branch of the opposite side, sometimes after dividing into two. The external branches bifurcate again and again, the system of fine twigs thus produced anastomosing freely, and giving rise to a fine meshwork

of fibres. Finally, the longitudinal cords, much diminished in size, unite together near the posterior border.

The whole course of these dorsal cords and their branches can be made out much more readily than in the case of the others. If an alcoholic specimen of T. fasciata be macerated for a day or two in weak bichromate of potash and weak alcohol, and the cuticle, epidermis, and muscular layers, with the outer layer of pigment carefully stripped off, the nerves are readily traced by the light lines which they form among the pigment of the nervous layer. In young specimens of the same species in which the outer layer of pigment is imperfectly developed, more or less of the course of this series of nerves can usually be seen, and in the New Zealand T. novæ-zelandiæ in which the outer layer of pigment is little developed or absent, the nerves are readily traceable even in the adult. In the case of the other sets of nerves resort must be had in tracing them to the study of series of sections, and I am not able to give more than a general account of their distribution.

The second pair or dorso-lateral cords (Pl. XXI, fig. 4, and Pl. XXI, fig. 12, *d. l. n.*) run backwards on the dorsal aspect of the body immediately outside the testes, not far from the lateral border. It is of larger size than the dorsal, and sends off branches between the organs. The ventral cords (*v. n.*) are the largest. From the ganglion they curve round the pharynx and run along the ventral aspect in the angle between the testes externally, and rather farther from the median line than from the lateral border. The ventral and lateral longitudinal cords are connected by transverse branches, and the ventral cords of opposite sides are united similarly by numerous transverse commissures.

The nerve-fibres (Pl. XXII, figs. 2 and 3) of which these longitudinal cords and their branches consist, are large fibres averaging ·01 mm. in diameter, of very delicate material, which is not readily acted on by staining agents, enclosed in a more resistent sheath. The central material shrinks greatly in preserved specimens, and this with its being little affected by dyes

very often gives the fibres the appearance of hollow tubes; when perfectly preserved it presents a reticulate appearance such as is represented in fig. 3; but this is very rarely to be observed. Within the sheath, besides the delicate substance constituting the nerve-fibre, there are also in the commissural nerves that form an important part of the cerebral ganglion, though not, so far as I have observed, in the course of the peripheral nerves, numbers of bipolar ganglion-cells.

This arrangement of the nervous system is, as regards the posterior part of it—the six longitudinal cords—very similar to that described by Lang as observed by him in the Tristomidæ.[1] The development of the tentacles in Temnocephala, and the consequent greater relative importance of the anterior region of the animal, are accompanied by a greater development of the nerves running forwards from the cerebral ganglion.

The single pair of eyes (Pl. XXI, fig. 13) are of extremely simple structure. They lie almost over the brain, so that the nerves which pass up to them are very short. The eye consists of a cup-shaped mass of dense pigment (*p.*), at the mouth of which are one or two nerve-cells (*g.*) not differing from those of the cerebral ganglion. Enclosed in the cup, the mouth of which is directed upwards and outwards, is a highly refracting body (*r.*) of a spherical form. This stains with difficulty and not very darkly, and is obscurely fibrillar in minute structure; it contains a nucleus near the mouth of the cup, and towards the base shows a trace of division into separate segments. Completely enclosed in the substance of the pigment of the cup on its inner side is a spherical cell (*t.*), of nearly the same dimensions as the body contained in the cavity of the cup; this exhibits a fine protoplasmic network and contains a solid-looking nucleus.

[1] "Untersuchungen zur vergleichenden Anatomie u. Histologie des Nervensystems der Platyelminthen," 'Mittheilungen aus der Zool. Station zu Neapel,' ii Band. A very similar arrangement is described in Distomum isostomum by E. Gaffron ("Zum Nervensystem der Trematoden," 'Zool. Beiträge,' herausg. v. A. Schneider, 1884, known to me through an abstract in the Biologisches Centralblatt,' iv).

The tentacles are also to be regarded as sense organs as well as aiding in locomotion and prehension. There is nothing, however, in the structure of these organs, except the presence of large nerves, specially connected with their sensory functions; the epidermis and the muscular layers resemble those of other parts of the body.

Reproductive Organs.

The common genital aperture (Pl. XX, fig. 5, *g*.) is a tolerably large slit-like opening situated a little distance in front of the sucker. It is surrounded by a special set of muscular fibres which serve the purpose of a sort of sphincter. It leads into a common genital cloaca, into which on one side projects the penis, while on the other is situated the female opening. This cavity is lined by a continuation of the cuticle and epidermis of the outer surface, the cells of the latter being, however, considerably elongated, forming an almost columnar epithelium, external to which is a thick layer of muscle.

The testes (*te*. in Pl. XX, fig. 6; Pl. XXI, fig. 4; and Pl. XXII, fig. 17) are two pairs of large glands of cylindrical form, with the long axis longitudinal, lying at the sides of the alimentary canal, and extending throughout the length of the body from the pharyngeal region to some distance behind the sexual aperture. The two testes of the same side are connected by a slender duct. They are invested with an extremely delicate layer of muscle, which is continued into the wall of the duct and of the vas deferens. Though there are only two pairs of testes, these partake to some extent of the segmented character of the animal—being partially subdivided at the sides by a deep transverse incision opposite each of the muscular partitions through which, however, the main substance of the gland is continued uninterrupted. The spermatozoa have pear-shaped heads, about ·0046 mm. in diameter, and slender flagella, ·083 mm. in length.

The two vasa deferentia are slender tubes, which, passing inwards from the posterior testes towards the middle line of the body, meet to form a large seminal vesicle or spermatic

reservoir (Pl. XXII, fig. 17, *e.j.*), which is always found to be distended with spermatozoa. This is an elongated sac, much dilated proximally, which runs almost transversely from near the middle line of the body where the vasa deferentia open into it towards the right, and opening into the base of the canal of the penis. The latter organ (Pl. XX, fig. 6, *p.*) is contained, when retracted, in an elongated muscular sac lying transversely with the mouth directed towards the left and towards the dorsal side. It is a cylindrical, slightly curved, chitinous body, having a wider proximal and narrower distal end. In T. fasciata (Pl. XX, figs. 5—7) and T. quadricornis (Pl. XX, fig. 8) the distal end is provided with a knob or glans (*gl.*); in T. minor and T. novæ-zelandiæ, this is merely represented by a slight rim (Pl. XXII, figs. 9 and 10). The whole is enclosed in a sheath composed of circular and longitudinal muscular fibres—the latter the stronger, and enclosed by the former. At the opening of the penis the sheath is continuous with the proper chitinous wall of the organ, it is continuous also proximally with the sheath of the spermatic reservoir and distally with the muscular investment of the genital cloaca. In T. fasciata, where it turns back to become continuous with the proper wall of the penal cylinder, it is provided with a number of chitinous spines, which, when the penis is retracted, lie in the interior of the terminal knob or glans in a radiating manner, their outer ends, which are the broader, embedded in the sheath and the acute inner ends pointing into the narrow lumen. When the penis is protracted this inverted part of the sheath will become everted, and the spine project on the exterior of the end of the penis, thus enabling the organ to retain a firm hold during the act of copulation. In T. minor and T. novæ-zelandiæ there is only a slight rim to effect this purpose; but in the latter species (Pl. XXII, fig. 19) the female opening is provided with inwardly directed spines, which doubtless effect the same object. The interior of the penis and spermatic reservoir is lined with a protoplasmic layer containing nuclei, but without cell boundaries. Into the lumen of the ejaculatory duct there

is discharged the secretion of the unicellular glands already mentioned as apparently forming a part of the system of subcutaneous glands. The secretion consists of or contains little spherical, highly refracting bodies, which stain darkly with hæmatoxylin; probably the foreign particles found in the receptaculum seminis with the spermatozoa are the products of this secretion.

The female organs consist of receptaculum seminis, or single ovary, oviduct, uterus, vitelline, and uterine glands, together with certain of the subcutaneous glands opening around the sexual orifice, which probably secrete the viscid matter by means of which the eggs adhere together.

The receptaculum seminis (Pl. XX, fig. 6, *re.*, and Pl. XXI, fig. 8, *rec. sem.*) is a large rounded sac which lies in the middle line in a deep bay of the posterior wall of the intestine. Its walls are formed of a granular protoplasmic matter, without differentiation, into cells, but with large nuclei here and there. External to this is a thin layer of muscular fibres. In all the specimens examined the cavity of the sac was found to be full of spermatozoa, with frequently small particles of amorphous matter, probably derived from the accessory glands of the male organs.

Opening out of the left-hand corner of the receptaculum seminis is the oviduct (*o. d.* in Pl. XX, fig. 6; Pl. XXI, fig. 8; and Pl. XXII, fig. 12), a rather narrow, curved tube which opens below into the uterus. The wall of the oviduct (Pl. XXII, fig. 12) consists of an external circular and an internal longitudinal layer of muscular fibres, and is devoid of epithelium, but is lined internally with a homogeneous layer of some delicate non-nucleated material, which is not readily acted on by staining agents. Into its lumen open the ducts of a few of the shell-glands.

The wall of the uterus (Pl. XXI, fig. 8) resembles that of the oviduct in structure; but the muscular layer is thicker, and the fibres cross one another in all directions. Most of the shell-glands open into the uterus. Each shell-gland (*s. gl.*) is a single, irregularly.shaped cell of very large size, with a large

nucleus; passing from it to the oviduct or uterus is the narrow duct (*d.*), which is essentially a process of the cell substance. As the duct passes through the wall of the uterus it acquires definite boundaries, and presents a little vesicular enlargement (*d.*) just before it opens into the uterus. Leading from the uterus to the genital cloaca is the vagina, a short, narrow passage, which in T. novæ-zelandiæ is provided at its mouth with a series of chitinous teeth.

The vitelline glands (Pl. XXII, figs. 15 and 16) consist of a number of rounded lobules arranged in narrow branching lobes, which, for the most part, take a transverse direction. These lobes are very closely applied to the wall of the intestine, which they almost entirely cover, both on the dorsal and on the ventral aspect. The muscular septa pass outwards from the wall of the alimentary canal, and through between the lobules of the vitelline gland in such a way as to bring about an imperfectly metameric arrangement in irregular transverse lobes, which, however, branch and anastomose with one another. The arrangement of the lobes and the degree to which the glands are developed vary somewhat in different individuals. The lobules are invested in a thin layer of the parenchyma muscle, which is continuous with that constituting the septa, and similar to the layer investing the intestine. The central substance of the lobules is composed of large irregular cells with ill-defined boundaries, whose protoplasm is clear and colourless in the fresh state, but with a number of large granules which become more evident in hardened specimens; the nuclei resemble those of the alimentary epithelium; throughout the protoplasm there are frequently large rounded vacuoles.

The ovary (Pl. XXII, fig. 11) is an oval solid body ·16 mm. in length, attached to the right wall of the receptaculum seminis, close to the beginning of the oviduct. The ova are narrow pyramids about ·083 mm. in length, each of which passes transversely through the entire thickness of the ovary. The impregnated ova are received singly into the uterus, where they become surrounded by a considerable quantity of vitelline

matter, and become enclosed in a chitinous shell secreted by the shell-glands. The egg is now compared with the animal, a very large structure (as much as a sixth of the length of the animal), and greatly distends the walls of the uterus. When extended (Pl. XXII, fig. 18) it has a short stalk, by means of which it becomes attached to the shell of the crayfish, and is enclosed in viscid matter, which when it hardens serves to cement the eggs together. The eggs are found in considerable numbers from October to February, attached chiefly to the under surface of the abdomen, some also at the sides of the mouth and the lower edges of the branchiostegites. The development of the embryo has not yet been studied; there is, as in other ecto-parasitic Trematodes, no metamorphosis. Temnocephalæ, perfect in every respect, being found still enclosed in the egg.

Affinities of Temnocephala.

Though most nearly related to the Tristomidæ, Temnocephala presents so many special peculiarities that it becomes necessary to regard it as the type of a distinct family. The principal characteristic features in its structure may be summarsied as follows :

The cephalic end of the body is produced into four, five, or six slender, filiform tentacles, which are capable of being used for prehension and touch, and in locomotion take the place of anterior suckers, their adhesive powers being increased by the secretion of certain special unicellular glands. There is a single, large, radiated posterior sucker without hooks. The body presents traces of a rudimentary form of segmentation in the shape of incomplete transverse dissepiments formed by specialised portions of the parenchyma muscle. The intestine is constricted at regular intervals by these septa ; its epithelium is not ciliated. There are three pairs of longitudinal nerve-trunks, a dorsal, a dorso-lateral, and a ventral, connected by numerous commissures. The excretory system opens by two apertures, placed far forwards on the dorsal surface. There is a single genital aperture leading into a genital cloaca, into

which the ejaculatory duct and the vagina open; there are two pairs of lobed testes, vitelline glands, which partake of the imperfect segmentation of the body, a single ovary, receptaculum seminis, oviduct and uterus.

The broader questions suggested by the imperfect segmentation of Temnocephala, and by other features in its organization which seem to point to a possible genetic relationship with the segmented worms, cannot well be dealt with until the development has been investigated.

EXPLANATION OF PLATES XX, XXI, & XXII,

Illustrating Mr. William A. Haswell's paper "On Temnocephala, an Aberrant Monogenetic Trematode."

PLATE XX.

Fig. 1.—Temnocephala fasciata in various positions. Natural size.

Fig. 2.—Temnocephala fasciata, from living specimens. Magnified.

Fig. 3.—Temnocephala quadricornis. Magnified.

Fig. 4.—Temnocephala minor, dorsal view, from preserved specimen. Magnified.

Fig. 5.—Temnocephala minor, ventral view. *g.* Genital aperture. *m.* Mouth. *s.* Sucker. *te.* Tentacles.

Fig. 6.—Diagram of the general organization of Temnocephala. *ph.* Pharynx. *i.* Intestine. *ex.* Excretory sac. *ex'.* Anterior canal of excretory system. *ex''.* Posterior canal of excretory system. *br.* Brain. *cl.* Genital cloaca. *te.* Testes. *v. d.* Vas deferens. *p.* Penis. *re.* Receptaculum seminis. *ov.* Ovary. *od.* Oviduct and uterus. *vit.* Vitelline glands. *s.* Sucker.

PLATE XXI.

Fig. 1.—Transverse section through the body wall of Temnocephala fasciata. *c.* Cuticle. *e.* Epidermis. *b.* Basement membrane. *c. m.* Circularly arranged layer of muscular fibres. *p.* Pigment layer. *l. m.* Longitudinal layer of fibres. *par.* Parenchyma.

Fig. 2.—Longitudinal section of the ventral body wall, in the neighbourhood of the genital opening, to show the ducts of the subcutaneous glands, *d*. Other letters as above.

Fig. 3. Cells of subcutaneous glands.

Fig. 4.—Transverse section of a young specimen of Temnocephala fasciata, in the region of the genital cloaca and penis. *c*. Cuticle. *e*. Epidermis. *b*. Basement membrane. *p*. Pigment layer. *l. m*. Longitudinal layer of muscle. *par*. Parenchyma, with subcutaneous gland-cells and dorso-ventral muscular fibres. *d. l. n*. Dorso-lateral nerve. *v. n*. Ventral nerve. *cl*. Genital cloaca. *pe*. Penis. *vit*. Lobule of vitelline gland. *te*. Extremity of testis (here imperfectly developed).

Fig. 5.—Outline of the alimentary canal of a young specimen of Temnocephala fasciata. *ph*. Pharynx. *i*. Intestine.

Fig. 6.—Vertical section of the wall of the pharynx, from a longitudinal section of the body. *ep*. Internal layer of granular matter. *i. c. l*. Internal circular longitudinal layer of muscle. *i. c. t*. Internal circular transverse layer. *e. c. t*. External transverse. *e. c. l*. External longitudinal. *rad*. Radiating fibres. *g*. Ganglion-cells.

Fig. 7. Section of the wall of the intestine. *m*. Layer of muscle. *e*. Epithelium. *c*. Reservoirs of granules.

Fig. 8.—Longitudinal and vertical section of Temnocephala minor. *s*. Sucker. *v*. Ventral body wall. *d*. Dorsal body wall. *int*. Cavity of the intestine. *sept*. Septa. *vit*. Lobules of vitelline gland. *gl*. Subcutaneous gland-cells. *od*. Oviduct. *ut*. Uterus. *rec*. Receptaculum seminis.

Fig. 9.—Excretory sac of Temnocephala fasciata in the fresh condition, viewed from the dorsal aspect. *o*. External opening. *l. c*. Longitudinal canals. *g*. Nuclei of ganglion-cells.

Fig. 10.—Section of excretory sac, on a level with the external opening. *e*. Proper wall of sac, with vacuoles. *m*. Investing layer of muscle. *g*. Ganglion-cell.

Fig. 11.—Longitudinal section of posterior excretory canal.

Fig. 12.—Diagram of dorsal portion of nervous system, showing the arrangement of the tentacular nerves, and the dorsal longitudinal trunks with their branches and commissures.

Fig. 13.—Transverse section through the eyes of Temnocephala fasciata. *p*. Pigment cup. *r*. Contained substance. *g*. Ganglion-cells opposite the mouth of the cup. *t*. Peculiar cell enclosed in the pigment of the optic cup. *u*. Large cells lying between the eyes.

PLATE XXII.

Fig. 1.—Transverse section through the brain ganglion of Temnocephala fasciata.

Fig. 2.—Transverse section of a portion of the ventral nerve.

Fig. 3.—Longitudinal section of nerve-fibre from dorsal nerve-plexus.

Fig. 4.—Elements of testis.

Fig. 5.—Penis and penis-sheath of Temnocephala fasciata. *cl.* Genital cloaca. *sh.* Penis-sheath. *gl.* Terminal enlargement of "glans."

Fig. 6.—Transverse section of the distal end of the penis of Temnocephala fasciata, through the "glans." *sh.* Sheath. *sp.* Inverted chitinous spines.

Fig. 7.—Oblique section through spermatic reservoir, penis, and penis-sheath of Temnocephala fasciata, from a horizontal section of the body. *cl.* Genital cloaca. *sh.* Sheath. *ej.* Spermatic reservoir (ejaculatory duct).

Fig. 8.—End of penis of Temnocephala quadricornis.

Fig. 9.—End of penis of Temnocephala minor.

Fig. 10.—End of penis of Temnocephala novæ-zelandiæ.

Fig. 11.—Ovary of Temnocephala fasciata.

Fig. 12.—Transverse section of the oviduct of Temnocephala fasciata. *c. m.* Circular layer of muscle. *l. m.* Longitudinal layer of muscle. *p.* Internal homogeneous substance. *f.* Investing reticulum of fibrous tissue.

Fig. 13.—Vertical section of the wall of the uterus in the same species, with the shell-glands and their ducts. *s. gl.* Shell-glands. *d.* Ducts. *d'.* Terminal enlargements of the ducts. *m.* Muscle. *p.* Thin internal homogeneous layer.

Fig. 14.—Oblique section of uterine wall nearly parallel with the surface, showing the terminal dilatations of the ducts of the shell-glands with the investing plexus of muscular fibres.

Fig. 15.—Outline of the ventral part of the vitelline glands of Temnocephala fasciata. *i.* Outline of the wall of the intestine.

Fig. 16.- Section through a lobule of the vitelline glands. *m.* Investing layer of muscular fibres. *v.* Vacuoles in the protoplasm of the gland-cells.

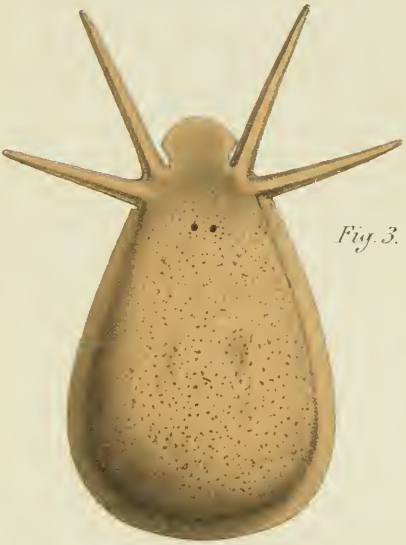
Fig. 17.—Portion of a transverse section of a young specimen of Temnocephala fasciata, just behind the pharynx. *c.* Cuticle. *e.* Epidermis. *b.* Basement membrane. *l. m.* Longitudinal layer of muscle. *v. l. m.* Ventral longitudinal layer of muscle. *par* Parenchyma, with subcutaneous glands. *d. v. m.* Dorso-ventral bundles of muscular fibres. *d. l. n.* Dorso-lateral nerve. *v. n.* Ventral nerve. *int.* Intestine. *te.* Anterior end of testis.

Fig. 18.—Eggs of Temnocephala fasciata. Magnified.

Fig. 19.—Opening of the vagina of Temnocephala novæ-zelandiæ.

Fig. 1.

Fig. 2.



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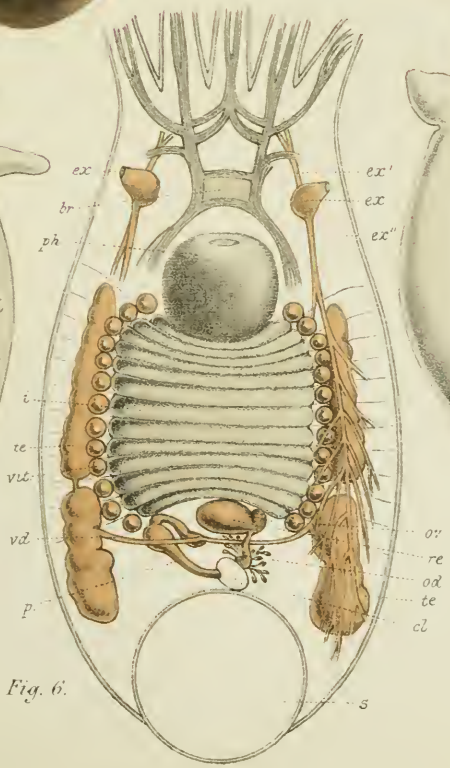

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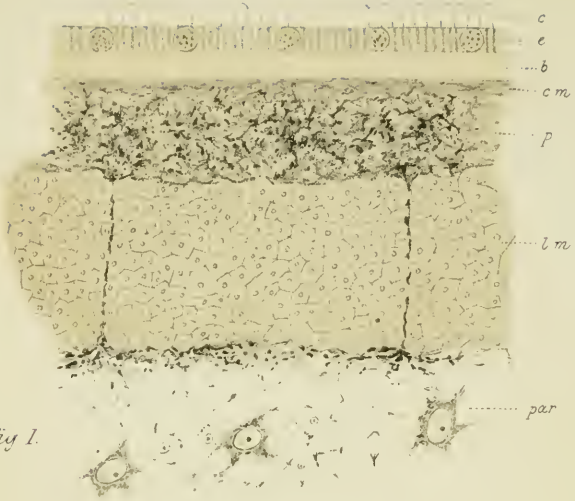

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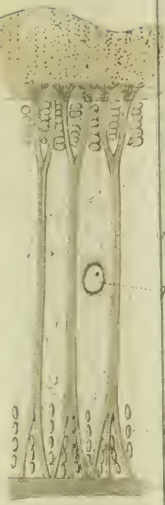

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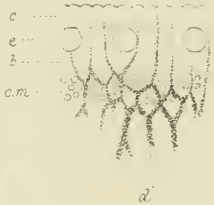

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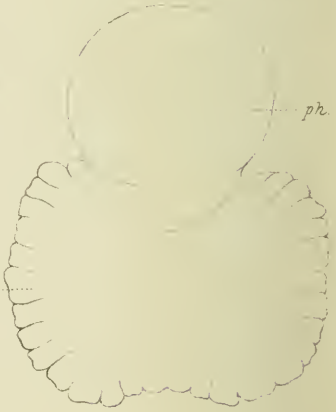

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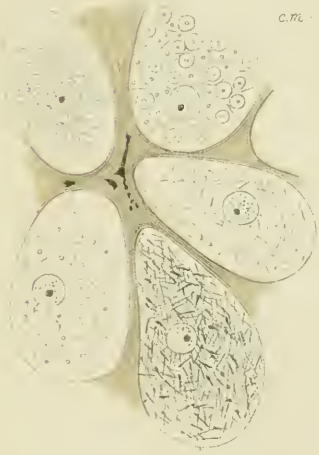

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Fig. 4.

Fig. 10.

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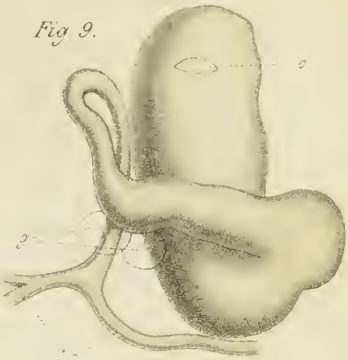

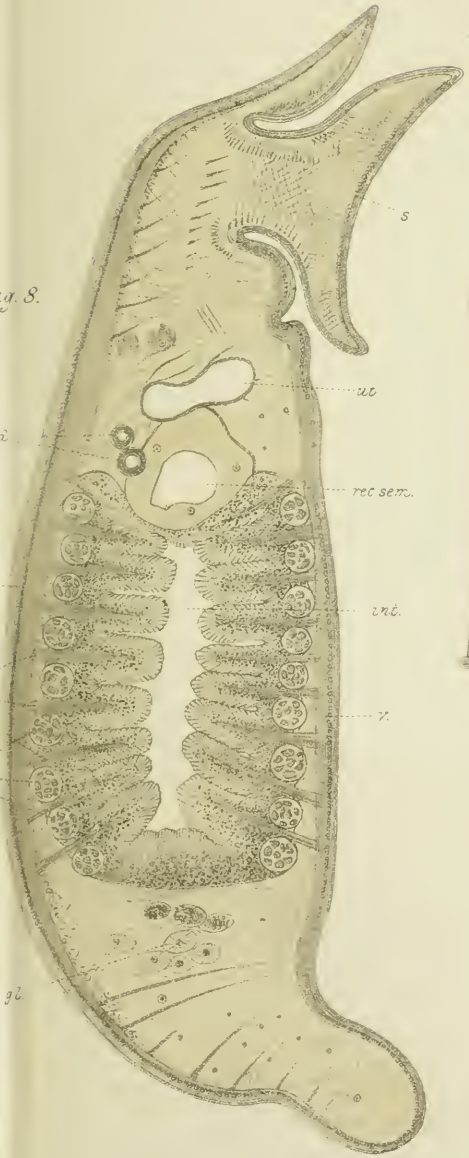

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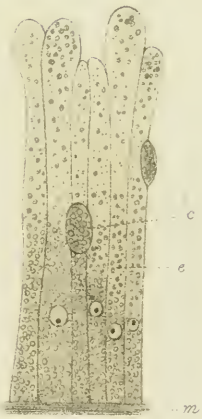

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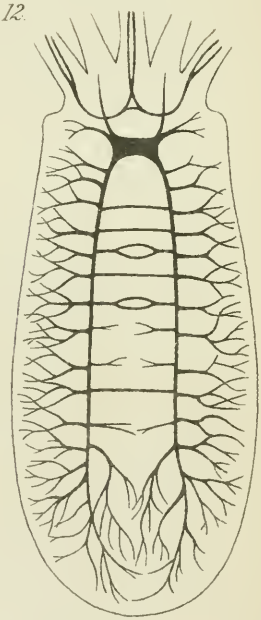

Fig. 13.

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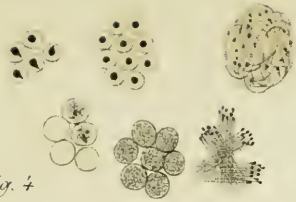

Fig. 4

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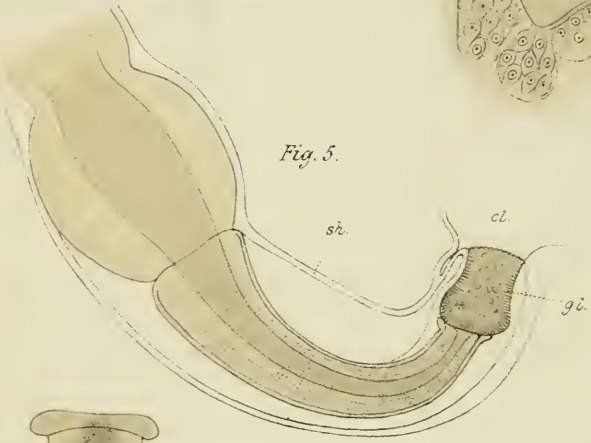

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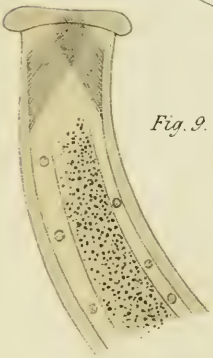

Fig. 10.

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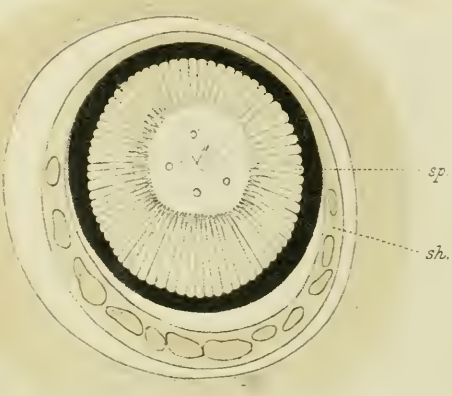

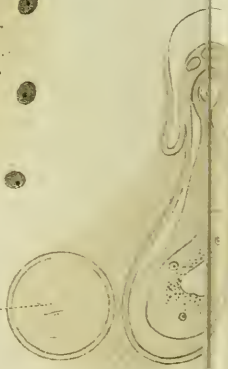

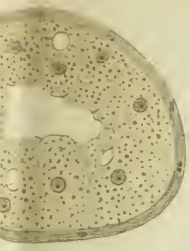

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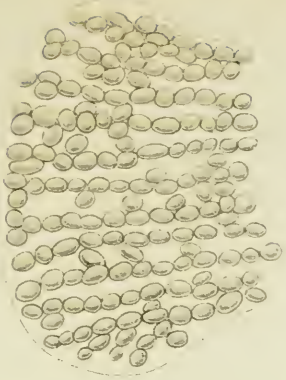

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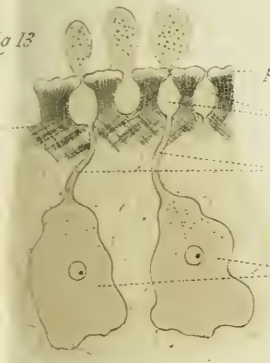

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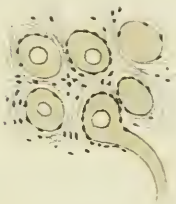

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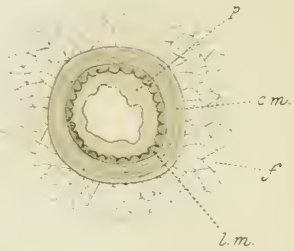

Fig. 19.

Fig. 18.

Fig. 17.

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