

**On a New Histriobdellid.**

By

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With Plates 14 and 15.

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## INTRODUCTION.

DURING a recent visit to Tasmania I found the minute animals which form the subject of the present paper living in abundance in the branchial chambers of the fresh-water crayfish (*Astacopsis tasmanicus*) that occurs in streams in the neighbourhood of Hobart. I am greatly indebted to Mr. Alexander Morton, F.L.S., the Curator of the Tasmanian Museum, for his kindness in facilitating my work in Hobart by every means in his power, and also for afterwards procuring and sending to me in Sydney specimens of Tasmanian crayfishes.

*Histriobdella homari*,<sup>1</sup> the only known relative of the new animal, is found living among the eggs of the European lobster (*Homarus vulgaris*). The first recognisable account of it was given by P. J. van Beneden (2) in 1858. Our knowledge of this remarkable animal was greatly extended in 1884 by Alexander Fœttinger (6), who supple-

<sup>1</sup> Fœttinger's alteration of both the generic and specific names does not appear to be necessary, and van Beneden's name must apparently be restored. *Histriobdella* is certainly not a leech; but the name *Histriodrilus* proposed by Fœttinger does not indicate its true affinities with any greater exactness. Moreover the termination "-bdella" occurs in the accepted names of several genera that do not belong to the Hirudinea.

mented van Beneden's description of most of the internal organs, described the nervous system for the first time, and pointed out the erroneous nature of van Beneden's conclusions as to the animal's affinities.

Since the date of Fœttinger's paper *Histriobdella* has never been re-investigated, and a good many points in its structure still remain obscure.

The animal with which the present paper deals, though without doubt nearly related to *Histriobdella*, differs from it in a number of points of greater or less importance; and I have signalled these differences by giving it a new generic name—*Stratiodrilus*. The species I propose to name *S. tasmanicus*.

#### External Features: Movements.

Like *Histriobdella*, *Stratiodrilus* is a very small animal, the largest being only a little over a millimetre in length, and about one sixth of a millimetre in greatest breadth. In general shape (figs. 1 and 2) it approaches very near to *Histriobdella*. In front is a well-marked head, separated by a constriction from the body. The head is dorso-ventrally compressed, convex dorsally, nearly flat ventrally; in outline as seen from above it is approximately heart-shaped—the apex, which is rounded off, directed forwards. There is no distinction into prostomium and peristomium, and the mouth is situated on the ventral surface quite close to the anterior extremity. The head bears seven appendages, arranged exactly in the same way as the appendages of the head of *Histriobdella*, but differing in shape. Five of these appendages are tactile, and may be called tentacles. The other two aid in locomotion, and may be termed the anterior limbs. Of the tentacles, one (fig. 1, *t*<sup>1</sup>) is median, and projects forwards from a point immediately above and behind the middle of the anterior margin of the head; it is about one sixth of the length of the head, very slender, cylindrical, and unjointed. The most anterior pair of tentacles (*t*<sup>2</sup>) are a little longer than the

median, and each consists of two distinct segments, the basal much shorter than the distal. They are attached a little below and behind the antero-lateral border of the head at some little distance from the middle line. The second pair ( $t^2$ ) are nearly twice as long as the first, attached on the antero-lateral margin of the head a little behind the first pair; each consists of two segments, of which the basal is somewhat longer and thicker than the distal. All the tentacles are tipped with very fine non-motile sensory cilia, arranged in a circlet or spiral. The remaining pair of appendages of the head, the anterior legs (*l. a.*), are of a very different character. They are much thicker than the tentacles, unjointed, and retractile, being capable of becoming completely withdrawn into the interior of the head by the action of retractor muscles. They are situated on the ventral surface of the head, considerably behind the posterior tentacles. They are somewhat shorter than the latter, of subcylindrical form, broadest at the base, ordinarily directed outwards, forwards, and downwards. At the free end is a slight expansion, apparently of the nature of a sucker. Close to the base of each is a rounded mass of unicellular glands, about half a dozen in number, the ducts of which traverse the appendage to its extremity.

The body is regularly constricted at intervals, and may best be described as imperfectly divided into six segments. The nature of these can only be discussed after the internal organs have been dealt with. All the constrictions are much more strongly marked laterally than dorsally or ventrally. They are clearly marked in the living specimens. The first or neck segment is small, and is devoid of appendages. The second has on each side a mammiform elevation, on the summit of which is inserted one of the cirri of the first pair ( $c^1$ ). These are slender cylindrical appendages, similar in character to the tentacles, and each consisting of two segments, a thicker proximal and a thinner distal. Like the tentacles, the cirri are tipped with fine non-motile sensory cilia. Behind this are three rings, which are probably to be referred

to the next or third segment, the main part of which bulges out laterally like the second, and bears a similar pair of cirri ( $c^2$ ). On this follows a small annulus, probably belonging to the fourth segment. The main part of the latter is much broader than the segments in front, bulging out prominently at the sides. In the female this segment is devoid of appendages, but in the male it bears a pair of remarkable organs, the claspers (*cl.*). These are situated laterally in a position corresponding to that of the cirri on the other segments. They are not unlike the anterior legs in their general shape, but are considerably larger. They are of cylindrical shape, stouter at the base than towards the free end. The distal extremity is obscurely divided into two lobes, tipped with a few non-motile cilia; close to this, situated laterally, are two small rounded elevations. A large unicellular gland (fig. 14, *gl. cl.*) lies in the basal part of the interior of the clasper, its duct opening at the distal end.

The following segment, the fifth, is as wide as the third, but somewhat shorter. It bears laterally a pair of cirri ( $c^3$ ), similar to those on the more anterior segments. The part of the body which lies behind this is sharply marked off from the rest, as will subsequently be explained. It cannot be looked upon as a single segment, and it will be preferable to term it the posterior or caudal region. It nearly equals in length the two preceding segments put together, but is much narrower, being in fact the narrowest part of the body. It is divided by slight constrictions into six fairly regular annuli, which, however, may become obliterated when the body is greatly extended. At its posterior end, rather towards the dorsal side, is the anal aperture. At the sides of this lie the large posterior legs (*l. p.*). These are non-retractile, and in a state of rest usually extend first outwards and backwards, and then, towards their extremities, bend forwards. They are much larger than the anterior legs (as long as the entire caudal region); subcylindrical, stout at the base, constricted towards the free end, which is expanded into a flattened adhesive disc, the edge of which is divided by notches into

about ten minute lobes. A large mass of unicellular glands (*l. gland.*) lies just within the base of each leg, and the numerous ducts open on the terminal lobes. The expanded terminal part (foot) of these appendages is strongly adhesive—not owing to any sucker-like action, as there is no muscular arrangement for bringing this about, but on account of the sticky character of the secretion of the gland. On the posterior border of each leg is a short cylindrical tentacle or cirrus (*c*<sup>4</sup>), tipped with motionless cilia; and close to its base lies a shorter process of similar character.

*Stratiodrillus* differs from *Histriobdella homari*, as regards the external features, mainly in the presence of the cirri, of which there is no rudiment in the latter form. The anterior and posterior limbs and the claspers, though differing in minor points, are very similar in essentials. Foottinger has, however, failed to distinguish the adhesive glands of the posterior legs, with their ducts, from the muscular fibres that run close to them. He says, "Nous avons ici, comme dans les pattes antérieures, un amas de cellules musculaires composées de deux parties, une centrale, cellulaire avec noyau et une périphérique, sous forme de fibre. Tous les fibres se dirigent vers l'extrémité élargie du membre, et se terminent en divergeant à peu de distance de son bord aminci."<sup>1</sup> But the fibres referred to are the ducts of the glands, and the secretion may frequently be seen oozing through their fine terminal apertures. The greater development of the cephalic tentacles in *Stratiodrillus* is a minor point of difference.

P. J. van Beneden's description of the extraordinary movements of *Histriobdella* applies so well to the form at present under consideration, that they may be quoted. "On peut dire sans exagération que c'est un ver bipède ou même quadrupède, quand il se déplace sur une plaque de verre, ou tout autre corps uni. Que l'on se figure un clown de cirque le plus complètement disloqué possible, nous allons même dire entièrement désossé, faisant des tours de force et

<sup>1</sup> L. c., p. 459.

d'équilibre sur une montagne de boulets monstres qu'il s'évertue à escalader, posant un pied (en forme de ventouse) sur un boulet, l'autre pied sur un autre boulet, balauçant le corps ou le roidissant, se tordant sur lui-même ou se courbant comme une chenille arpeuteuse, et on n'aura encore qu'une idée très-imparfaite de toutes les attitudes qu'il prend au bout de quelques secondes."

For the "immense balls" (eggs of the lobster) in the above description substitute "filaments of the branchiæ," and it would apply equally well to *Stratiodrilus*, except that the bending movements of the latter are not so free, being restricted by a certain stiffness of the body, due apparently to the firmer cuticle. When moving over the bottom of a glass vessel the mode of locomotion is very grotesque. The posterior legs are advanced alternately like the legs of a man in walking, the anterior portion of the body, and particularly the head, being strongly swayed from side to side. The anterior legs are also used, though not invariably, and support the weight of the head and front part of the body. It is from this entirely unique style of locomotion that I have derived the name I have given to the genus.

By means of the viscid secretion of the glands of the posterior legs the animal is able to adhere so firmly to the smoothest surface that it is difficult to detach it.

On one occasion I found four specimens, out of a number that had been placed in a glass dish, collected together, and executing the most remarkable movements. They were in ceaseless motion, creeping over and under one another, touching one another all over with their tentacles, and occasionally inflicting a bite sharp enough to cause the bitten individual to start back with a sudden movement. This went on for an hour or more without intermission.

#### Integument and Muscular System.

The integument consists, as in *Histriobdella*, of a cuticle and an epidermis. The former, though not very thick even

relatively, is remarkably firm, if one may judge from the fact that the form of the body is not readily altered under the action of various reagents. In *Histriobdella* this layer is described by Fettinger as structureless; in *Stratiodrillus*, on the other hand, it is marked by two systems of fine lines crossing one another nearly at right angles, as in the cuticle of many *Chaetopoda*. The epidermis is a thin layer of protoplasm in which cell outlines are not recognisable, but in which nuclei occur at wide and irregular intervals. No integumentary glands of any kind appear to occur with the exception of those situated at the bases of the legs and of the claspers, and a few small unicellular glands situated in the neighbourhood of the genital opening in the male.

The integument of *Histriobdella* would appear from Fettinger's description and figures to differ from that of *Stratiodrillus* not only in the structureless character of the cuticle, but in its relative thinness, and in the relative thickness of the epidermis.

The chief muscles of the body are the four longitudinal muscles (figs. 1 and 9—13, *m. d.* and *m. v.*). These have the form of thin flat bands, two dorsal and two ventral, extending from the neck constriction to the bases of the posterior legs. There is no layer of circularly arranged fibres. The fibres of these bands are flattened in a direction approximately at right angles to the surface of the body; each fibre, of which there are only about ten to twenty in each bundle, appears to extend through the whole length of the body.

In front of the neck constriction, in the posterior part of the head, the place of these longitudinal bundles is taken, to some extent, by oblique and transverse fibres, by means of which the movements of the head on the neck are effected, by two pairs of retractor muscles of the jaws, and by the retractors of the anterior legs. The transverse and oblique fibres form an imperfect partition between the *cœlom* of the head and that of the trunk.

In the third segment of the male are two pairs of retractor muscles of the claspers (fig. 1, *r. cl.*) running obliquely out-

wards from near the middle of the ventral body-wall; the fibres of the more posterior of these extend through the appendage to its extremity. In the following segment are two pairs of narrow bands of fibres which act as protractors and retractors of the penis, running inwards from the lateral body-wall, the latter in front of and the former behind the third cirrus, and becoming inserted into the processes at the base of the penis (figs. 1 and 14, *pro. m.*, *retr. m.*). In the same sex, in the interval between the second cirrus and the clasper, a pair of bundles of fibres run nearly vertically from the dorsal body-wall to the ventral, enclosing between them a mesial space in which lie the alimentary canal on the dorsal side and the nerve-cord on the ventral, with a portion of the testis between. Further back again a similar pair of dorso-ventral bands separate the alimentary canal, nerve-cord, and penis, situated mesially, from the testes and seminal vesicles at the sides. In the female a pair of bands of the same character (fig. 11, *m. ob.*) occur in the region of the anterior part of the ovary. In both sexes a strong band of transverse fibres extends across between the fifth and the following segments; it does not seem to form a complete partition. Throughout the body slender oblique bundles occur at fairly regular intervals, running from the cuticle of the lateral surface to that of the ventral near the nerve-cord.

The dorsal and ventral longitudinal bands both send contributions of fibres to a pair of large flexor muscles (fig. 1, *fl.*) which run through the posterior leg on its anterior side, and eventually terminate in the minute lobes at its distal end. From the ventral longitudinal band a bundle of fibres runs backwards and outwards to become inserted into the cuticle about the middle of the ventral surface of the leg. A few of the fibres of the extensor muscle run nearly transversely inwards as a narrow band which unites with the corresponding band of the opposite side. A narrow bundle runs obliquely inwards and backwards from the angle between the leg and the caudal region to the posterior median depression between



the legs; and from the latter point a pair of small bundles run forwards parallel with one another, one on each side of the anus. A small muscle runs along the posterior border of the leg, and another crosses its cavity nearly transversely from the base of the cirrus to the anterior border.

### Digestive System.

The mouth, a wide, somewhat quadrilateral aperture, is situated, as already stated, close to the anterior extremity of the head. From it a narrow œsophagus (figs. 6 to 8, *œs.*) leads backwards and slightly upwards through the head to open into the stomach. Below the œsophagus lie the jaws (figs. 1, 4, 5, 7, 8), the anterior extremities of which when they are retracted lie just within the mouth opening, while the posterior ends are at the posterior limits of the head.

The chitinous pieces of the jaw apparatus (figs. 4 and 5) are arranged in two sets, which, though linked together, are capable of being moved independently to some extent. One of these two sets—the upper jaws—consists of a median piece which I will call the fulcrum, and two sets of lateral pieces composing the rami. The latter set—the lower jaws—is paired throughout.

The fulcrum of the upper jaws (*f.*) is a slender, nearly straight rod lying between and somewhat above (dorsal to) the lower jaws. Articulating with its distal end is a small median piece, and with this articulate the right and left rami. The latter consist each of a number of freely articulated basal pieces supporting four teeth. The teeth are provided with hooked claw-like extremities, and their inner surfaces are beset closely with extremely fine transverse ridges, giving them on that aspect the appearance of minute curry-combs. When at rest the fulcrum is drawn back, so that its posterior end is nearly on a level with the posterior ends of the two lower jaws. When it is in this position the rami are folded up into a small compass with the teeth inwards, between and dorsal to the anterior portions of the lower

jaws. When this part of the apparatus is brought into use the fulcrum is pushed forwards by the action of its protractor muscles, and the two sets of rami, becoming thrust out through the aperture of the mouth, become widely divaricated with the teeth at their outer ends. When the upper jaw has been fully exerted in this way the right and left rami are brought together sharply, the fulcrum being jerked back slightly at the same time. This series of movements is effected with great rapidity, so that it is extremely difficult to follow and analyse them. The chief part of each of the two lower jaws is a stout, slightly curved rod (*j.*<sup>2</sup>), thickest behind and tapering slightly in front. These rods lie nearly parallel with one another, but diverging slightly anteriorly. The most anterior part of each (about one seventh of the length of the whole) articulates with the rest by a transverse joint. Behind this to about the middle of the posterior portion of the rod runs a thin, internally projecting flange with a smooth inner edge. Firmly fixed to the anterior portion of each rod along its inner edge is a broad plate, the inner edge of which is in contact with that of its fellow of the opposite side. The anterior edge of this plate is finely denticulated; its antero-lateral angle is produced into a pointed process directed outwards and backwards.

Connecting together the rami of the upper jaw with the lower jaws on each side is a sort of bridle (*br.*) composed of two pieces, the posterior of which curves over the rod of the lower jaw, and slides along it when the upper jaw is protruded or retracted. The effect of this arrangement is to restrict the forward movement of the upper jaw, the curved piece being checked when it reaches the anterior broad plate of the lower jaw above described, and further movement of the upper jaw forwards being thus prevented. At the same time, as will be explained presently, it is through the inter-mediation of the bridle that the biting movements are carried on. Whether the lower jaws have any function beyond merely supporting the upper jaw and controlling its movements is not clear. I have not observed them performing any inde-

pendent movements; but the strength of their muscles and the toothed character of their anterior edges would seem to indicate that they play something more than a merely passive rôle.

In addition to the bundles of fibres which play the part of protractors and retractors, the jaws have three other sets of muscles concerned with their movements. One of these is a pair of large bundles of non-striated fibres, each of which is wrapped round the ventral side of the corresponding lower jaw, the fibres running forwards parallel with the latter throughout their length. These two muscles are in close apposition with one another along the mid-ventral line, separated, however, by a thin septum of nucleated material continuous with the lining of the head cœlom, of which it appears to be a thickening. They are continuous with the retractor fibres behind. The ventral edge of each is infolded, and becomes continuous with the ventral edge of the corresponding muscle of the second pair. The latter (figs. 4 and 7, *str. m.*) are a pair of bundles of transversely striated muscular fibres, which are in immediate contact with the lower jaws and enclosed ventrally by the muscles just mentioned; behind they arise from the main shaft of the lower jaw, towards its posterior end; in front they are inserted into the chain of pieces which I have called the bridle. The third set consists of a number of non-striated fibres which run forwards parallel with and close to the slender central shaft of the upper jaw (fig. 7, *j.*<sup>1</sup>).

The precise mode of action of these various muscles is very difficult to determine with certainty. But there cannot be much doubt that the striated bundles bring about some movement which has to be performed with special rapidity and strength. From their connections, and what I have been able to observe with regard to their mode of action, I am led to conclude that, acting through the bridles on the lateral parts of the upper jaw, their function is to bring about the sharp movements by which these are brought to bear on an external object in the act of biting.

Føetinger's figure of the jaws of *Histriobdella homari* resembles in essentials that given by P. J. van Beneden, and represents a structure widely different from that of the jaws of *Stratiodrillus*, though probably reducible to the same general type. Both figures are very general; but it would appear that one of the most striking differences lies in the shape of the lower jaws, which are comparatively wide, and in the larger number of teeth in the upper jaw. The bridles are figured by both authors, but their significance was apparently not detected by either. Van Beneden's description is as follows:<sup>1</sup>

“ Il y a d'abord deux mâchoires placées symétriquement et qui se correspondent complètement sous tous les rapports. Elles ont une couleur bistre, s'allongent en arrière sous forme de lames jusque près de l'extrême limite de la région céphalique, et laissent un certain espace entre elles. On pourrait les comparer à des élytres très-allongées de Coléoptère légèrement écartées l'une de l'autre, surtout vers leur extrémité postérieure. . . . Ces mâchoires sont également larges sur toute leur longueur; leur extrémité libre en arrière est tronquée obliquement.

“ En avant, ces organes chitineux se touchent au point de se confondre, en s'unissant à la troisième pièce dont nous allons parler.

“ Ces mâchoires, vers leur extrémité libre antérieure, qui est logée au fond de l'entonnoir, deviennent rugueuses à la surface et se hérissent même de courtes aspérités qui leur donnent une apparence de brosses. Au lieu d'être terminées en pointe en avant comme on le voit communément pour ces pièces de la bouche des parasites, ces organes sont tronqués en travers.

“ À la base de cette portion rugueuse, on aperçoit encore une éminence crochue, dont la pointe est dirigée en dehors et en arrière, et qui semble empêcher le retrait de ce singulier appareil de succion, quand il a perforé les parois des œufs dont il suce la masse vitelline.

<sup>1</sup> L. c., p. 14.

“À ces pièces paires se joint une troisième pièce impaire plus courte et beaucoup plus grêle que les précédentes, de la même couleur et de la même consistance, et qui fait, par son extrémité postérieure, l’effet d’un stylet, dont les autres formeraient la gaine. Cette dernière, en effet, est étroite dans toute sa longueur, et son extrémité postérieure est entièrement libre.”

Føttinger does not add much to this. He merely states, “Les mâchoires sont au nombre de trois, une médiane et deux latérales; celles-ci, réunies en avant par une partie impaire et situées du côté ventral, ont assez bien la forme d’élytres très allongées de Coléoptère ainsi que le décrit P. J. van Beneden. À côté de leur terminaisons antérieures se trouvent deux petites languettes chitineuses, et plus en avant deux masses de même nature, à surface hérissée de pointes, articulées par leurs extrémités postérieures avec la partie impaire, et pouvant se mouvoir latéralement de façon à rapprocher ou à écarter leurs bords antérieures. La mâchoire médiane, placée au dessus des deux autres leur est réunie en avant. Je ne m’étendrai pas plus longuement sur l’aspect de cet appareil, P. J. van Beneden en ayant donné une description complète.”<sup>1</sup>

It will be observed that both van Beneden and Føttinger agree in connecting the part bearing the teeth with the paired lower jaws rather than with the median upper jaw.

From the mouth a narrow œsophagus runs backwards through the head to open into the stomach. The latter is a tolerably wide sac extending through the first, second, and third segments. In the fifth segment there succeeds a very narrow canal, much more contracted in the female than in the male, leading to the intestine, a comparatively wide tube running through the caudal region to the anal aperture.

The wall of the alimentary canal is composed throughout of a single layer of cells, beset on their inner surfaces with numerous long cilia. Here and there in the wall of the stomach is to be distinguished a non-ciliated cell, which

<sup>1</sup> L. c., p. 462.

becomes affected by staining agents much more strongly than the rest; these are probably of the nature of unicellular digestive glands. External to this there is merely a thin peritoneal layer without any muscular fibres.

The stomach and intestine invariably contain a quantity of miscellaneous granular particles which are so finely comminuted as to afford no clue to their nature.

#### Body-cavity.

There is an extensive body-cavity sending a prolongation into the head. In *Histriobdella*, Fœttinger describes this cavity as lined by a cœlomic epithelium having the usual relations of such a membrane, a splanchnic layer covering the surface of the digestive canal, and a somatic layer lining the inner surface of the body-wall. But such a description does not give a correct idea of the cœlomic wall, at all events in *Stratiodrilus*. Covering the stomach and intestine throughout is the splanchnic layer of cœlomic epithelium, a thin layer of flattened cells with small nuclei. But the somatopleure remains in a very primitive condition. Closely applied to the inner surfaces of the dorsal and ventral longitudinal bands of muscle is a single layer of cells, the protoplasm of which is seen in the best series of sections (fig. 3) to be completely continuous with the muscle substance of the fibres. These cells, which are obviously the cells by means of which the muscular fibres have become formed, are also the only representatives of the somatic layer of the mesoderm. This condition of things corresponds exactly to what has been described by Fraipont as occurring at a certain stage in the development of *Polygordius*. In the latter the somatic layer of the cœlomic epithelium subsequently becomes formed by the division of this single layer into two; in *Stratiodrilus* the embryonic condition remains permanent.

There are no mesenteries of any kind, the wall of the stomach and intestine being simply fused on the dorsal side with the ectoderm as described by Fœttinger. In this

position the ectoderm is thicker than in most other situations, and in transverse sections a pair of nuclei are most regularly to be observed in this thickened area; the double row of cells which those represent would thus seem to form a cord having the function of supporting the digestive canal. The special developments of the cœlomic epithelium in the genital region will be described in the section on the reproductive organs.

The cœlom of the head is almost completely cut off from that of the trunk by the muscular fibres of the neck constriction and the gland cells that lie in that region. But this separation is not complete, as evidenced by the fact that in several female specimens sperms were found to have penetrated into this region.

#### Nervous System.

The nervous system (figs. 1 and 2) consists, like that of *Histriobdella* as described by Fœttinger, of a brain, a pair of œsophageal connectives, and a ventral nerve-cord with ganglia at intervals. The brain (figs. 1, 2, 6, 8), situated in immediate relation to the integument of the dorsal surface of the head, consists dorsally of a mass of nerve-cells (*br. c.*), and ventrally of a mass of fibrillated material (*br. f.*). Of the nerve-cells, special groups (tentacular ganglia) (fig. 6) situated opposite the bases of the tentacles give off peripherally nerve-fibres which run to the extremities of the latter. The fibrous material is in the form of a curved transverse band obscurely divided into two portions, anterior and posterior. Running back from the main mass of the brain at the sides of the œsophagus is a pair of processes which are perhaps to be looked upon as representing the visceral nervous system ("nerfs sympathiques" of Fœttinger).

The ventral nerve-cord consists of a strand of finely fibrillated material and groups of small nerve-cells similar to those of the brain. In transverse section the fibrillated cord

has the shape in different regions sometimes of an entire oval, or is bilobed, or more or less deeply cleft, or even completely divided. The ganglia consist of very slight enlargements of the fibrillated cord, covered on its ventral and lateral aspects with the nerve-cells; where a nerve is given off, the group of nerve-cells is produced for a short distance around its base.

There are five ganglia, one for each segment, in the internal region of the body. The first ganglion is short, but (as regards its group of nerve-cells) expanded transversely. The fibrillated cord is here deeply divided into right and left portions, each continuous with the œsophageal connective of its side. The second ganglion, which is very close to the first, is of much larger size; it is situated opposite the cirri of the first pair, and gives off a pair of nerves ending in a pair of ganglia at the bases of the cirri. From the nerve-cells of these lateral ganglia nerve-fibres pass along the axis of the cirri to the extremities, where they terminate in connection with the sensory cilia. In transverse section the second ganglion appears very distinctly double, especially in its posterior portion; in the female it is completely divided into two parts, separated by a definite gap. The connection between the second and third ganglia is of considerable length, and is very distinctly double. The third ganglion gives off a pair of nerves to a second pair of lateral ganglia. In the male the fibrous cord is not distinctly divided, but further back it is divided into two completely separated though closely apposed portions; in the female it is deeply divided throughout. The connection between this and the fourth ganglion is not cleft, but only obscurely divided in the male; in the female it is deeply cleft. The fourth ganglion is situated opposite the claspers in the male, and in a corresponding position in the female. It gives off a pair of nerves which in the male supply the claspers, while in the female they end in a pair of small lateral ganglia. In the anterior part of this ganglion the cord is not divided; further back it is bilobed; yet further back it is undivided and



dorso-ventrally compressed. In the male the cord just behind this ganglion and immediately in front of the penis gives off a pair of strong branches, and then becomes greatly reduced, passing towards the dorsal side as a double cord, to run between the intestine and the penis, in which position it enlarges into a small ganglion, the fifth, completely divided into two lateral bodies; this gives off a pair of nerves to the ganglia at the bases of the third pair of cirri. In the female the nerve-cord becomes extremely attenuated behind the fourth ganglion (in the neighbourhood of the dilated median part of the ovary), but retains its ventral position; the fifth ganglion is dorso-ventrally compressed in its anterior portion, but loses this character further back where it gives origin to a pair of nerves passing to the ganglia at the bases of the cirri of the third pair.

In the caudal region the ventral chain may be described either as represented by a single elongated ganglion imperfectly divided into five or six portions, or as consisting of five or six imperfectly separated ganglia. Nerve-cells clothe the nerve-cord ventrally and laterally through all this portion of its extent, except that there are about five narrow intervals in which they are almost absent, the breadth of the intervals differing in different specimens according to the degree in which the body is contracted. Throughout this posterior region the cord is deeply cleft. From the posterior end of the cord nerves pass to the posterior legs, and to a pair of ganglia situated at the bases of the cirri which they bear.

The account of the nervous system of *Histriobdella homari* given by Føttinger corresponds fairly closely with what I have found in *Stratiodrillus* as described above, except that in the former in the caudal region there are only three ganglia, somewhat better defined than those in the corresponding region of *Stratiodrillus*, and that the lateral ganglia are absent, or at least have not been recognised. A more important point of difference is that the nerve-cord of *Histriodrillus* would appear to be in complete continuity with the epidermal layer, while in *Stratiodrillus* it is much more dis-

tinctly differentiated; a comparison of my figures of transverse sections with those of Føttinger will show how marked this difference is.

There are no organs of special sense, unless we reckon as such the tentacles and cirri; there are no vestiges of eyes, and the ciliated pits described by Føttinger as occurring in *Histriobdella* are not present.

### Excretory System.

The excretory organs (fig. 1) take the form of a series of pairs of ciliated canals. These are for the most part very thin-walled, so that they are only to be traced in the living animal by the movement of the cilia, and are not to be followed with any certainty in any of my series of sections, except in one or two localities where their walls are thicker. A good many details thus remain to be elucidated, but the following general features have been satisfactorily made out.

The arrangement of these canals differs considerably in the two sexes. In both the system extends forwards into the head, and backwards as far as the posterior end of the body. Each nephridium of the most anterior pair divides in the first segment into an external and an internal branch. The former runs right forwards into the head. The latter crosses obliquely over to the opposite side, and joins the external branch of the opposite nephridium. Judging from the direction of movement of the cilia, which is always from behind forwards, the external apertures of this pair of nephridia must be in the head. None of the other nephridia are branched. In the female an apparently continuous line of cilia is traceable backwards on each side from the head canals to a point some little distance behind the second cirrus, where a canal is clearly traceable, which, after bending round in a loop, opens on the exterior on the ventral side. But as the direction of movement of the cilia is from before backwards in the posterior part of this line, it would

appear probable that there are two pairs of canals in this anterior region in the female. In the male, on the other hand, there is no such evidence of division, the pair of nephridia which branch in the head being traceable backwards, without change in the direction of the cilia, nearly as far as the bases of the second cirri, at which point they bend inwards and terminate in the cœlom near the middle line. In some specimens each tube seemed to end in a loop, in others this was clearly not the case; a difference in the degree of contraction may have been the cause of this discrepancy. In all cases the posterior part of the canal, from the point where it begins to bend inwards, has comparatively thick granular walls. The extremity of each is not funnel-like, but is enlarged into a rounded knob which has the appearance of having a narrow cleft on it; but I am not certain of the existence of a cœlomic aperture. The two knob-like ends lie in a compartment of the cœlom, bounded by the stomach above and the ventral nerve-cord below, and at the sides by a pair of fibrous partitions passing vertically from the stomach to the ventral wall of the body.

In the fourth segment the nephridia are probably represented in the female by the oviducts, in the male by the vasa deferentia.

In both sexes a pair of nephridia, which begin in the fifth segment (in a loop in the male), run backwards through the caudal region at the sides of the intestine, and terminate close to the anus. The direction of movement of the cilia in these is from behind forwards.

The arrangement of these canals, though to some extent partaking in the metamerism of the body, is not strictly a metameric one, there being apparently only three pairs in the male and four in the female.

Ciliary flames have not been observed, and, I think I may say positively, do not occur in any part.

To judge from Föttinger's description and figures, there is an important difference between *Histriobdella* and *Stratio-drilus* as regards the excretory system. "Ces canaux ne se

rencontrent pas dans toute l'étendue du corps de *Histriodrillus*. Je n'en ai pas vu la moindre trace dans la tête; aussi, sans en vouloir nier d'une façon absolue la présence, je suis porté à croire qu'ils n'y existent pas."<sup>1</sup> "Dans la partie tout à fait postérieure du corps je n'ai jamais pu découvrir d'organes excréteurs."<sup>2</sup>

### Reproductive System.

The male reproductive organs (figs. 1 and 14—16) consist, in addition to the claspers, of two testes fused together in part of their extent, two seminal vesicles (*ves.*), two lateral vasa deferentia (*v. def.*), a median ejaculatory duct, a median chitinous penis (*p.*), two sets of granule glands (*gr. gland.*), and a pair of accessory glands (*ac.*). The claspers have been already referred to. In the interior of the base of each is a large unicellular gland (fig. 14, *gl. cl.*), the duct of which opens at the extremity. The testes when fully developed fill the greater part of the cavity of the third, fourth, and fifth segments. Anteriorly (in the third and partly in the fourth segment) the right and left testes are separated from one another by a distinct space; posteriorly they are completely fused. They consist of oval masses of spermatidia and sperm, the fully developed sperms being in later stages of formation, most abundant towards the posterior end. A thin envelope invests the whole.

The seminal vesicles (*ves.*) are a pair of oval sacs situated laterally in the interior of the testes, just in front of the third cirri. Each has on its dorsal aspect a wide, nearly longitudinal slit, the edges of which are beset with vibratile cilia. In the interior, in mature specimens, is always a large mass of sperms. On the ventral surface are usually to be observed several curved ridges, which are found when carefully traced to be continuous with the ducts about to be described as

<sup>1</sup> L. c., p. 469.

<sup>2</sup> *Ibid.*, p. 471.

those of the granule glands. These ridges are formed by accumulated masses of the secretion of these glands.

The glands which I have termed granule glands, on account of their resemblance to the glands so named in the Turbellaria and some Trematodes, are situated on each side immediately behind the base of the clasper. In each of the two groups there are about half a dozen of these glands, which are pear-shaped and unicellular. The narrow end of each, which is directed inwards, is prolonged into a delicate duct which runs to the seminal vesicle, into which it opens on the ventral side. The rod-shaped granules which the glands secrete are thus mixed with the sperms in the cavity of the seminal vesicles. Sometimes the ducts are found to be distended with accumulated masses of the secretion.

The vas deferens is a thin-walled, widish tube, which runs inwards to a point in the middle line close to the base of the penis, where it unites with its fellow to form the median ejaculatory duct.

The penis (figs. 14—16) is a hollow chitinous spine, perforated throughout by the ejaculatory duct. At its base it is produced into three processes, one median and two lateral, for the insertion of the protractor and retractor muscles. It is broadest at the base and tapers gradually distally, ending in a sharp point. At the free end it is cut off obliquely like the needle of a hypodermic syringe. Near the extremity it bears two very minute spinules, one dorsal and one ventral.<sup>1</sup> When at rest the penis lies enclosed in a folded integumentary sheath, which projects more or less prominently on the ventral surface, its pointed extremity directed backwards and downwards, and just protruding through the median ventral reproductive aperture. In a good many preserved specimens it was found fully protruded when it extends forwards and slightly downwards from the reproductive aperture at the end of the everted sheath.

The glands which—their function being unknown—I have

<sup>1</sup> The shape of the penis and its processes differs somewhat in different specimens.

termed accessory glands are small, sharply contoured, oval bodies .02 mm. in length, lying one (*ac.*) on either side of the penis behind the vas deferens. The long axis is directed forwards and inwards, and from the narrower inner end there arises a thin-walled duct, which opens into the sheath of the penis. In the interior of the gland is a well-defined lumen; the wall is composed of a small number of cells arranged in a single layer, each bulging somewhat in the middle into the cavity.

Foettinger has failed to recognise the significance of various parts of the male reproductive apparatus in *Histriobdella*, owing mainly to his having followed P. J. van Beneden, and taken the claspers for a pair of penes. He describes the seminal vesicles, though without fully recognising their nature or their relations and tracing their ducts (in which he observed sperms) to their union to form a median duct. Of the median structure on which this opens he says, "Celle-ci est cylindrique et pourvue d'un canal assez étroit qui, d'après ce que j'ai vu sur le vivant, doit être le tube impair; elle a une structure peu déchiffrable; on dirait avoir affaire à un pénis."

The chitinous hollow spine of *Stratioidrilus* is not represented, but a number of very minute spinules, not represented in his woodcut on p. 488, though not referred to in the text, have probably a similar function.

The granule glands are the cells which Foettinger describes and figures as "cellules pariétales." With regard to these he states,<sup>1</sup> "Au niveau de la partie antérieure de ces vésicules, on voit les cellules pariétales qui avoisinent le tube digestif et les muscles dorsaux faire fortement saillie dans le segment et se recourber vers le bas en longeant les extrémités internes de leur congénères. Les parties recourbées sont très étroites et arrivent à la face dorsale des vésicules; où elles se divisent en deux feuilletés nucléés formant une sorte de revêtement cellulaire." From the figure (pl. 29, fig. 2) to which reference is made it is evident that what are here referred to as the "parties recourbées" are the ducts of the granule

<sup>1</sup> L. c., p. 487.

glands. The irregular masses which he figures as projecting into the cavities of the vesicles, and which he describes as "des corps allongés, plus ou moins cylindriques, droits ou non, homogènes, très réfringents sur le vivant et qui semblent unis aux parois par une base assez larges,"<sup>1</sup> are probably the masses of the accumulated secretion of these glands to which reference is made above.

In the female the ovaries (figs. 11 and 12; *ov.*, fig. 17) occupy a corresponding position in the body to that occupied by the testes in the male. Anteriorly they diverge; posteriorly they are coalescent. The formation of the ova begins in the anterior portion of each ovary (fig. 11), and as we pass backwards they advance in development. In nearly all the specimens examined the whole of the posterior part of the united ovaries is composed of a single immense ovum, very much larger than any of the rest, and occupying nearly the entire interior of the body in this situation, the alimentary canal and also the nerve-cord being in this position greatly attenuated. The diameter of this relatively enormous ovum is as much as .2 mm.; its nucleus about .02 mm. Its cytoplasm is coarsely granular, in which it contrasts strongly with that of the smaller ova. In a few cases, however, there is a second ovum, somewhat approaching the largest in size, and resembling it in the coarsely granular character of the cytoplasm.

The entire ovary is invested in a layer of nucleated material, which is probably to be regarded as specially developed peritoneal epithelium. Probably it is from the cells of this layer that new ova are formed. It forms a complete investment for all the larger ova, and this investing follicle, which is of considerable thickness in an ovum approaching maturity, has doubtless the function of ministering to its nourishment.

A pair of specially modified nephridia appear to act as oviducts (fig. 11, *od.*). These open on the exterior in a lateral position behind the second pair of cirri, and opposite the anterior paired portions of the ovary. Each runs first

<sup>1</sup> L. c., p. 487.

forwards and inwards, and then bends round, following the line of the anterior border of the ovary, and runs backwards to open near its fellow of the opposite side into the anterior part of the space (uterus) containing the large mature ovum. It is a comparatively wide tube, ciliated internally, with thick walls, having a granular appearance, due evidently to the presence of numerous minute bright granules or vesicles. In close relation to it is a glandular body (*vit.*), of varying size, consisting of finely granular material, with a large nucleus here and there, but without cell limits and without lumen. When well developed this body fills up a good deal of the space between the wall of the body, the alimentary canal, and the lateral paired portion of the ovary. It appears to terminate behind in close relation to the corresponding oviduct. I am in doubt whether these bodies are to be looked upon as shell glands or as vitellaria. I think the latter view is the more probable, and accordingly I have provisionally given them that name. If they have this function the shell must be secreted either by the cells of the follicle or by the wall of the oviduct.

When a ripe ovum has become discharged its place is taken by the next in size. This must receive accessions of vitelline matter with great rapidity, as the median ovum in mature animals is nearly always greatly larger than the next in point of size. From their arrangement it is evident that the ripe ova are derived from the right and left sides alternately. The shrivelled follicle of the ovum which has been last discharged is sometimes to be found pushed on one side by the ovum which has succeeded.

Föttinger's account<sup>1</sup> of the female reproductive organs in *Histriobdella* differs from the above in several important points. The structure of the ovaries is evidently similar in all essential respects, except that in *Histriobdella* there is not, as in *Stratiodrillus*, a single ovum greatly predominating in size over the rest—several ova of approximately equal size occurring together; and that in the former the

<sup>1</sup> L. c., p. 473.



posterior portion of the organ extends nearly to the posterior end of the body. The ducts would appear, however, to be widely different. From each female aperture there runs a very short canal opening into an ampulla, the cavity of which is drawn out into digitations. This often contains a granular material, which passes out and spreads over the surface for some distance around the reproductive aperture. Usually one only of the digitations communicates with another ventrally placed vesicle of spherical form, containing bodies supposed to be sperms. This vesicle communicates by a constricted portion with a flattened canal, having cellular walls ciliated on the dorsal side only; this opens into the body-cavity.

Living sperms were found in abundance in the body-cavities of several females. In one instance they had penetrated in large numbers into the head, the cœlom of which is not completely cut off from that of the trunk. In one instance they were found in the tail region—the partition between this and the segment in front apparently not being sufficiently complete to prevent their passage.

In several specimens dense masses of sperms were found, always in the neighbourhood of the ripe ovum. But it was only in one specimen that I happened to meet with the appearances represented in fig. 12, which appear to explain the mode of impregnation. Here a darkish body (*spr.*), having the size and shape of a cast of the internal cavity of the penis, with short prolongations representing the three basal processes, was found with its point directed inwards, close to the single large ovum and close to the internal opening of the oviduct. Close to it in front, in the next section, is a mass of sperms which had begun to become scattered. Obviously the foreign body is the case of a spermatophore, thrown off from the inner lining of the penis. After having been discharged—the penis having previously been thrust through the body-wall—the spermatophore had become ruptured and its contents liberated. In the other specimens in which sperms were found in masses, the case of the spermatophore had apparently become absorbed.

This observation renders evident the purpose of the pair of claspers with their adhesive glands and the peculiarly shaped penis. In the act of copulation the male, holding the female fast by means of the claspers, drives the sharp-pointed penis through the body-wall in the neighbourhood of the mature ovum, and discharges a spermatophore into the body-cavity.

Fertilisation is thus internal, but the fertilised ovum would appear to be deposited at once, as no segmenting ova were ever found. The section represented in fig. 12 shows definite processes given off by the ovum towards the mass of sperms; these may be of the nature of receptive prominences, or perhaps are processes formed during maturation. The body lettered *pl.* in fig. 12 is most probably a polar body.

As it passes out the oosperm becomes enclosed in a firm shell, and is attached to the axis of a gill-plume or an epipodite, usually near its base.

Only a few stages in the development of the embryo have been examined; a full account of this part of the subject I hope to be able to communicate at some future time when sufficient material is available. So far as they go, my results are in full conformity with the hypothesis dealt with in the following section, that the *Histriobdellidæ* are derived from the *Rotifera*. When it escapes from the egg, the young *Histriodrilus* is fully formed in all respects, except as regards the reproductive organs.

#### Affinities of the *Histriobdellidæ*.

P. J. van Beneden (1) in his earliest communication on the subject referred *Histriobdella* with doubt to the *Polychaeta*, as perhaps the larva of a *Serpulid*. In his later paper (2) he assigned it to the *Hirudinea*.

Foettinger (6) enters into a full discussion of this question, and comes to the conclusion that *Histriobdella* is nearly related to *Polygordius* and *Protodrilus*, and ought to be looked upon as a member of the class *Archiannelida*, and

this view has been generally accepted by later writers, though frequently with some reservation.

Harmer (12, p. 22) assents to Fœttinger's views as to affinities, and adds, "In the number of segments, in the segmentation of the ventral nervous system, and in the arrangement of the muscular system *Dinophilus* more nearly approaches *Histriodrilus* than any of the other Archiannelida." Hatschek (15) suggests that *Histriobdella* may be a degenerate Eunicid. Eisig (5) expresses the opinion that in *Histriobdella* we have to do with a strongly modified and degenerate animal, and not with an Archiannelid.

Though I have not been able to trace a closer affinity between the *Histriobdellidæ* and any other group of the Annulata, I have come to the conclusion that to class them as nearly related to *Protodrilus* and *Polygordius* is altogether unjustifiable. Of the common features which Fœttinger adduces as affording evidence in support of his view, nearly all are general annulate characteristics. To the alleged primitive condition of the nervous system no weight can be attached, since, as I have shown above, this condition scarcely obtains in *Stratiodrilus*; and since, as has been pointed out by various observers, it is a condition which is by no means confined to the Archiannelida, but which occurs also in various Chætopoda that do not, in other respects, present any primitive features.<sup>1</sup> To the purely negative feature of the absence of setæ, also, it is impossible to attribute much importance.

In both the *Polygordiidæ* and *Histriobdellidæ* the body is segmented; but the nature of the metamerism differs greatly in the two cases. In the former group the segments are numerous; they are not very sharply defined externally, but internally their cavities are separated by transverse partitions or mesenteries. In the *Histriobdellidæ* the segments are few in number: they are defined externally by constrictions, and, in the case of *Stratiodrilus*, by the occurrence of the paired appendages; but only one intersegmental partition,

<sup>1</sup> See Mensch, 21.

and that an imperfect one, is developed, namely, that at the commencement of the tail region.

In both families a head is present, and is clearly marked off from the rest. Its composition, however, does not in any way correspond in the two cases. In the Polygordiidae it consists, as in most Chætopods, of a prostomium lodging the brain, and of a peristomium, on the ventral surface of which the mouth opens. In the Histriobdellidae it is undivided, and the mouth opens far forwards, near its anterior extremity in front of the brain. The presence on the head of the remarkable retractile anterior limbs is highly characteristic of the Histriobdellidae, as is also the presence further back of the retractile claspers in the male. The highly developed posterior limbs with their glands are also special structures.

One of the most characteristic features of the structure of the Histriobdellidae is the presence of the elaborate jaw apparatus, which is not represented in the Polygordiidae, though the muscular sac appended to the œsophagus in the members of the latter family may correspond to the sac in which the jaws are lodged in the Histriobdellidae.

A blood-vascular system is fairly well developed in the Polygordiidae, but is not present in the Histriobdellidae. The nervous system is much more highly developed in the latter than in the former, and the ventral nerve-cord takes the form of a chain of ganglia metamericly arranged, whereas in the Polygordiidae there is no trace of ganglia.

The reproductive organs of the Polygordiidae are of a generalised character, and are constructed on the same general plan as those of the Polychæta. In the Histriobdellidae they are highly specialised. On the whole it appears to me that the relationship between the Histriobdellidae and the Polygordiidae is extremely remote, and not such as to justify their inclusion in the same class.

A comparison with *Dinophilus* reveals certain common features not shared with the Polygordiidae. In both *Dinophilus* and the Histriobdellidae the animal consists of a distinct head, and a trunk consisting of a small number of

segments. In *Dinophilus* there is sometimes (*D. metameroides*) an undivided post-anal or tail region, beset with small adhesive papillæ, with glands serving as organs of attachment. In both groups the ventral nervous system consists of metamericly arranged ganglia, though in *Dinophilus* there are two separate chains connected by transverse commissures (at least in Schimkewitsch's species) into a ladder-like structure (25). *Dinophilus* wants the tentacles and cirri; possesses bands or a cavity of cilia, and a pair of eyes. In some species the metameric condition of the nephridial system is more pronounced than in the *Histriobdellidæ*, in others less so; there is an extension forwards into the head. In Schimkewitsch's species there are metamericly arranged bundles of annular muscular fibres, and a pair of ventral longitudinal muscles. In the alimentary canal there is a close resemblance between the two groups, though the horny jaws are absent in *Dinophilus*. Though *Dinophilus* possesses a mesoderm, segmented in the larval condition, developed from primitive mesoderm cells, its general body-cavity has no epithelial lining, and the equivalent of the cœlom is reduced to the cavity of the reproductive organs. In the reproductive organs there is a considerable similarity between the two groups, especially in respect of the male apparatus with its median penis and associated hypodermic mode of impregnation, and the paired vesiculæ seminales.

On the whole I consider that there is more reason for including *Dinophilus* and the *Histriobdellidæ* in one class than for grouping either of them with the *Polygordiidæ*.

It is obviously of radical importance in connection with this question to determine if those features of the *Histriobdellidæ* which seem to be of a primitive nature can be explained as a result of degeneration. If the *Histriobdellidæ* are degenerate they must be degenerate *Chætopods*, or, at all events, degenerate achætous *Annelids*. If we are to take this view, we must at the same time acknowledge that, side by side with the supposed degeneration, there must

have gone on a special development in certain directions; that, while the definite character of the segmentation became lost, a special set of locomotor organs with an elaborate musculature became evolved, the mouth became shifted forwards, and complex reproductive organs of a specialised type were developed. This view appears to me to involve difficulties so great that they render the degeneration theory extremely improbable, and it seems more in accordance with the facts of the case to conclude that the *Histriobdellidæ* are really primitive Annulates, and that the rudiments of their specialised features have been inherited from forms lower in the scale.

A connection between *Dinophilus* and the Rotifera has been insisted on by various writers, notably by Schimkewitsch (25), who says, "Ohne Zweifel sind auch einige Züge vorhanden die *Dinophilus* mit den Rotatorien verbinden: die Furchung des Eies, die Anwesenheit des Schwanzanlages, der mit dem Fusse der Rotatorien übereinstimmt, der geschlechtliche Dimorphismus: man muss auch gestehen, dass im Baue des Nervensystems und der Hautmuskulatur der Rotatorien die Tendenz zur Erwerbung der Metamerie bemerkt werden kann; bei *Dinophilus* aber erstreckt sich diese Tendenz auch auf das Mesoderm und die Excretionsorgane. Auch bei den Rotatorien erscheinen, wie bei *Dinophilus* die Genitalhöhlen als einzige Homologa des Cöloms. . .

"Es giebt aber auch ausser der Metamerie des Mesoderms einen fundamentalen Unterschied in der Entwicklung; die Rotatorien besitzen nach den Beobachtungen Zelinka's gar kein Mesoderm, wogegen bei *Dinophilus* die mesoepitheliale Anlage vollkommen entwickelt ist. . .

"Es können also die *Dinophiliden* entweder als oligomeren Archianneliden deren Cölom sehr spät im Laufe der Entwicklung erscheint und gänzlich auf die Bildung der Genitalhöhlen mit ihren seitlichen Anhängen geht angesehen werden, oder man kann sie auch als Rotatorien auffassen, die eine echte metamere mesoepitheliale Anlage, vielleicht durch das Anwachsen der Genitalanlage, und die metamere angeordneten Segmentalorgane bekommen haben" (p. 74).

It will be observed that in order to connect *Dinophilus* genetically with the Rotifera we have not only to assume the development of metamerism, but also the loss of the mastax and the appearance of the external ciliation.

Let us now consider what assumptions must be made if we are to regard the *Histriobdellidæ* as direct descendants of the Rotifera. The evolution of an incomplete metamerism must of course be assumed. But there are indications of such a tendency not only externally, but in both the muscular and nervous systems of the Rotifera.

In the general shape the *Histriobdellidæ* more nearly resemble the *Gastrotricha* than the Rotifera proper—in the narrow body, in the presence of a distinct head region having the mouth at its anterior end, and in the foot being represented by a pair of processes each with its pedal gland, with the anus situated nearly between them on the dorsal side. But in *Paraseison* (23) we have a true Rotifer in which the trochal disc is not developed, and in which there is a definitely separated head region, containing the brain and the mastax, and having the mouth at its anterior end.

The tail region of the *Histriobdellidæ* corresponds to the tail of the Rotifer; the posterior legs of the former to the "toes" of the latter. The tail of the Rotifer is always entirely post-anal; but, as shown by Tessin and by Zelinka (27), its interior is filled at an early stage with endoderm cells, from which circumstance the latter author comes to the conclusion that the anus originally opened at the end of the tail. In the *Histriobdellidæ* the terminal position of the anus was retained.

The resemblance between the glands in the bases of the posterior legs of the *Histriobdellidæ* and the foot glands of the Rotifers will be obvious. In some cases the latter would appear to consist of homogeneous masses of protoplasm, not divided into cells, with scattered nuclei (Plate, 24); but in others (*Callidina*), as in *Stratiodrillus*, each is a group of distinct, apparently dust bearing, cells (Zelinka, 27).

In *Paraseison*, as already noted, there is a head region

closely comparable with that of the *Histriobdellidæ*. From the mouth, situated anteriorly, a long narrow œsophagus runs back; and contained in a diverticulum of this, given off close to the mouth, is lodged the mastax.

The various tentacles or papillæ tipped with sensory cilia on the anterior region in the *Rotifera* are closely comparable to the tentacles of the *Histriobdellidæ*. Homologues of the anterior or head legs of the *Histriobdellidæ* are not of general occurrence in the *Rotifera*. But the groups of unicellular glands forming a viscid secretion, the ducts of which, in *Paraseison*, open at certain definite spots on the surface of the head, appear to perform a similar function in connection with locomotion to the glands of the anterior legs in the *Histriobdellidæ*, and may be homologous to them. And still closer come the pair of mobile retractile tentacles of *Floscularia Hoodii*, which would appear to be provided with glands at their bases.<sup>1</sup> Homologues of the cirri of *Stratiodrillus* are readily to be found in the processes or papillæ tipped with sensory cilia on the body of various *Rotifera*.

The nervous system of the *Histriobdellidæ* differs from that of the *Rotifera* in the presence of the ventral chain of ganglia, but the discovery by Zelinka (27) of a subœsophageal ganglion in *Callidina* and *Discopus* serves to greatly reduce this difference.

The nephridial system, like the nervous, differs from that of the *Rotifera* in partaking (though in this case only to a slight extent) in the metamerism of the body, and also in the absence of ciliary flames.

The reproductive system is readily capable of being construed as a direct development from that of the *Rotifera*. One of the most striking points of resemblance is the median penis with the associated mode of impregnation. The rela-

<sup>1</sup> I obtain my information on this point from Hudson and Gosse's '*Rotifera*,' in which it is stated (p. 55), "Mr. Hood tells me that both in young and adult specimens he has seen brown granular matter discharged from their free ends."



tions of a pair of nephridia in the genital segment to the reproductive apparatus is a special development following upon the establishment of metamerism, such as we could not expect to see foreshadowed among the Rotifera. The secondary male character of the presence of the claspers seems to be paralleled in some species of *Asplanchna*, in which there is present only in the males a pair of lateral processes which seem to have glands at their bases.

If, as the evidence adduced above seems to indicate, the *Histriobdellidæ* are primitive Annulates which retain certain Rotiferan features that have become lost or disguised among higher forms, it becomes necessary to account for *Dinophilus* in a similar manner, unless we are to suppose that the annulate features of the latter have had an independent origin. Now *Dinophilus*, while in most respects distinctly less advanced than the *Histriobdellidæ* towards the normal annulate type, has at the same time fewer Rotiferan features, and is looked upon by most of the zoologists who have paid special attention to it as directly related to the *Turbellaria*. If, however, the evidence in favour of the derivation of the *Histriobdellidæ* from primitive Rotifers is sufficiently strong, we must look on *Dinophilus* as having diverged from the direct line of descent between the two groups, and as having lost some of the Rotiferan features that in the *Histriobdellidæ* have undergone a further evolution.

The phase of metamerism which the *Histriobdellidæ* exhibit is of great interest. The metamerism of *Stratiodrillus* and that of a *Chætopod* must be acknowledged to be of the same nature, though the former is less complete in certain respects. In an animal which, whatever may be the nature of its food, is of extremely alert and active habits, great degeneration does not seem to me probable; and yet, unless we are to look upon the *Histriobdellidæ* as degenerate, it is impossible to avoid the conclusion that in them we have a metamerism tending in the direction of that of the *Annulata*, but in an incipient condition. If this be granted, it carries with it the conclusion that the metamerism of the

Annulata did not result from the modification of a chain of zooids developed by serial budding as supposed by Haeckel, Hatschek, and others ; but by the dividing up of the body of an elongate animal into a series of similar parts (Lang, Meyer, Eisig). In whatever manner the mesoderm bands, the mesoderm somites, and the resulting secondary mesodermal structures may have first originated, whether by modification of reproductive cells as supposed by E. Meyer, or by the proliferation of primitive mesodermal elements, it appears probable that the various organs passed through a condition of pseudo-metamerism, which became converted into nascent true metamerism as the ciliary mode of locomotion became completely given up, and a creeping mode fully adopted.

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## EXPLANATION OF PLATES 14 and 15,

Illustrating Prof. William A. Haswell's paper "Ou a New  
Histriobdellid."

*List of Reference Letters.*

*ac.* Accessory glands of male reproductive apparatus. *br.* Bridle pieces of jaws. *br. c.* Nerve-cells of brain. *br. f.* Fibrous matter of brain. *c.* Cirrus. *cl.* Clasper. *cn.* Œsophageal connective. *ca.* Cælom. *cæ. ep.* Cælomic epithelium. *f.* Fulcrum of upper jaw. *fol.* Follicle of large ovum. *gl. cl.* Gland of clasper. *gn. cd.* Ganglion of nerve-cord. *gn. t.* Tentacular ganglion. *gr. gland.* Granule glands. *int.* Intestine. *j.<sup>1</sup>* Upper jaw. *j.<sup>2</sup>* Lower jaw. *l. a.* Anterior legs. *l. ol.* Leg gland. *l. p.* Posterior leg. *m.* Mouth. *m. d.* Dorsal longitudinal muscles. *m. ob.* Oblique muscles. *m. v.* Ventral longitudinal muscles. *neph.* Nephridium. *n. l.* Lateral nerve. *od.* Oviduct. *œs.* Œsophagus. *ov.* Ovary. *p.* Penis. *p. j.* Muscular fibres supposed to act as protractors of jaws. *pro. m.* Protractor muscles of penis. *r.* Ramus of upper jaw. *r. cl.* Retractors of clasper. *retr. m.* Retractor muscles of penis. *r. j.* Retractor muscles of jaws. *r. l. a.* Retractors of anterior legs. *st.* Stomach. *str. m.* Striated muscle of jaws. *t.<sup>1</sup>* Median tentacle. *t.<sup>2</sup> t.<sup>3</sup>* Lateral tentacles. *te.* Testis. *v. def.* Vas deferens. *ves.* Vesicula seminalis. *vit.* Vitellarium.

FIG. 1.—Entire male of *Stratiodrillus tasmanicus*. × 200. The outline drawn from a living specimen with the aid of camera lucida: nervous system coloured blue, muscles red, nephridia (including vasa deferentia) green. To avoid too great complication the ganglion situated on the dorsal side of the penis and the œsophageal connectives have been omitted.

FIG. 2.—Outline of female specimen with the nervous system (coloured blue).

FIG. 3.—Transverse section of a portion of one of the longitudinal bands of muscular fibres, the cælomic surface below. × 1500.

FIG. 4.—Jaws with the rami retracted, ventral view. × 800.

FIG. 5.—Jaws with the rami everted, ventral view.

FIG. 6.—Approximately transverse section of head in the brain region.

FIG. 7.—Transverse section of head behind the brain region in the region of the anterior legs.

FIG. 8.—Longitudinal vertical section of head, approximately median.

FIG. 9.—Transverse section of the second segment, immediately behind the first pair of cirri.

FIG. 10.—Transverse section of female in the region of the second pair of cirri.

FIG. 11.—Transverse section of the same series as that represented in Fig. 10, in the region of the anterior paired portions of the ovaries.

FIG. 12.—Section (somewhat oblique) of female specimen in the region of the posterior unpaired part of the ovary, showing spermatophore; *pr.* processes of ovum.

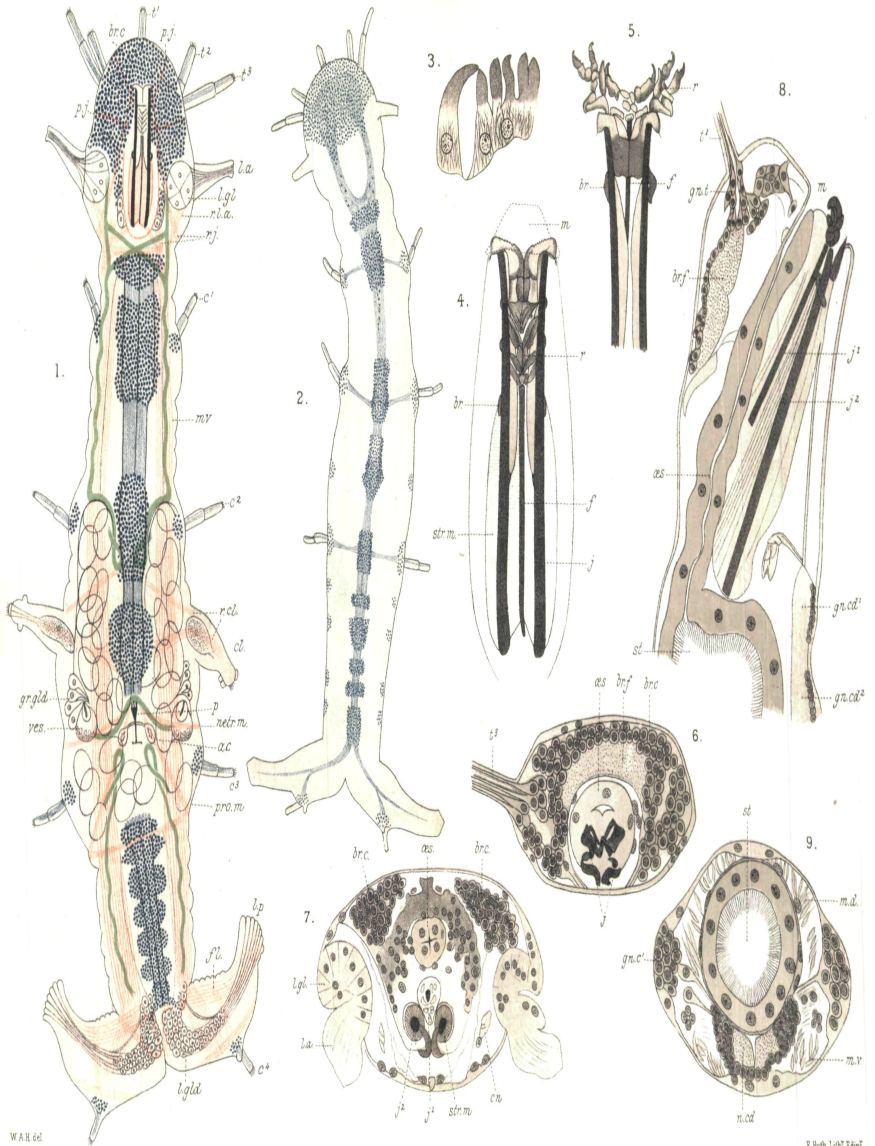
FIG. 13.—Transverse section of caudal region.

FIG. 14.—General view of the male reproductive organs.

FIG. 15.—Ventral view of penis.

FIG. 16.—Lateral view of penis, partly protruded.

FIG. 17.—Ovary. The follicle cells are not represented.



STRATIODRILUS.

W.A.H. 66

F. Hahn, Lith. 1867

