

On the Anatomy of *Histriobdella Homari*.¹

By

Cresswell Shearer, M.A.,

Trinity College, Cambridge.

With Plates 17-20 and 5 Text-figures.

CONTENTS.

	PAGE
1. Introduction, Material, and Methods	288
2. Review of Literature and Remarks on Habits	291
3. Description of the Nephridia	300
A. First Nephridium	303
B. Second Nephridium	303
C. Third Nephridium	304
D. Fourth Nephridium	304
4. Body-cavity and Nephridia	305
5. Muscular System	308
A. Longitudinal Muscles	308
B. Special Muscles of the Generative Segment	309
C. Oblique Muscles	311
6. Digestive System	314
7. Nervous System	321
8. Sense-Organs	327
9. Reproductive System	328
A. In the Male	328
B. In the Female	334
10. Conclusion and Summary	346

¹ I have to thank the Director and members of the staff of the Marine Biological Association of Plymouth for their kind attention and interest in my work while at Plymouth.

1. INTRODUCTION, MATERIAL, AND METHODS.

OUR knowledge of the anatomy of *Histriobdella* is based on the papers of Van Beneden (1858), Foettinger (1884), and Haswell (1900). Of these, Foettinger's account is the most extensive, while Haswell's paper is perhaps the most valuable. Both accounts contain a more or less detailed description of the internal structure and organisation of the adult. Several years ago I described the presence of solenocytes in connection with the nephridia of *Dinophilus*. This discovery rendered it probable that these peculiar structures would also be found in *Histriobdella*, with which *Dinophilus* shows many relationships. Moreover, the different description of the nephridial system given by Haswell in *Stratiodrilus* from that of Foettinger for *Histriobdella* called for a re-investigation of these organs. For these reasons the present work was begun. I was soon led to undertake a detailed examination of the animal. It is some twenty-five years since the publication of Foettinger's paper, and during this interval the European species of *Histriobdella* has received no further attention. In the following account I have endeavoured to clear up Foettinger's description of several of the organs. I have had the advantage of having made use of the methyl-blue method of *intra vitam* impregnation, which has proved most valuable. With its use I have experienced no difficulty in determining the number of the nephridia and their relationship to the segments, and to make out new details in their structure quite impossible from ordinary sections of fixed material.

Good methyl-blue¹ preparations of the nephridia can be obtained by placing the lobsters bearing the parasites in small tanks of sea-water, to which sufficient blue has been added to colour the water a light shade. It is necessary for the animals to remain in the blue two or three days before it appears in the nephridia. As the blue is rapidly absorbed by the living tissues of the lobster, an additional quantity has

¹ This is "soluble blue," and not methylene blue.

to be added to the water from time to time. With good air-circulation and a little attention, a medium-sized lobster can be kept alive for several weeks in a tank of four or five litres capacity without change of water.

At the end of the second day the blue will have collected in dark granules on the walls of the nephridial canals, so as to outline these clearly. By this time it has been discharged from the nervous system and the sensory cells of the epidermis. About the bases of the legs of the head it shows a tendency to remain some time after it has disappeared from the brain. It is retained alone by the nephridia on the third day. Here it collects in dense masses on the courses and openings of the canals.

In the study of these methyl-blue preparations I have made use of long, thin cover-slips, such as are used in preparing large serial sections instead of ordinary slides, on which to mount my preparations. The use of a thin cover-slip used as a slide allows of the preparation being examined from each surface, as desired, under an oil-immersion lens. It is thus possible to trace a nephridium first on one side of the preparation, and then turn the slide over and trace it further on the other surface.

Histriobdella is a somewhat difficult animal to fix. The only reagent that has given uniform results is a saturated sublimate solution, with 5 per cent. acetic, used boiling hot. Hermann's solution and Flemming and the osmic acid mixtures give very irregular results, and are not to be depended on for their action. One lot of material will be excellent, while the next, fixed with the same solutions and under the same conditions, are useless. Picro-acetic and Bouin's solutions, used hot, give good results, but not as good as material fixed with sublimate-acetic. Picro-sulphuric was used for preparations to be studied whole, on account of the excellent preservation it gives of the external form. As stains, the following have given satisfaction: Hæmacalcium and Benda's iron-hæmatoxylin, paracarmine, lithium-carmine followed by Lyon's blue for eggs.

The nephridial canals are remarkably difficult to recognise in sections on account of the retraction they invariably undergo during fixing. It is impossible to trace them with any degree of certainty through consecutive sections. For this reason I have relied mainly in my investigation of the nephridia on methyl-blue impregnation preparations of living material. The figures accompanying the present paper therefore represent the appearance of the nephridia in living material. It is necessary to use the highest powers of the microscope to determine the structure of the nephridia, and even then the eye requires considerable practice and training to distinguish the motion of their cilia. It is difficult to convey any idea of the extreme delicacy and minuteness of these structures. The necessity of being compelled to use immersion-lenses for their study excludes the use of any of the ordinary dark ground systems of illumination. Doubtless these would offer an excellent means of investigating structures of this nature in an animal so transparent as *Histiobdella*, if they could be used successfully with the immersion-lens.

Of great service in the study of the methyl-blue preparations is, I have found, the use of a number of sodium glass screens of different shades, such as are used in orthochromatic photography to vary the exposure from five to fifteen times.

To obtain a uniformly constant light I have used an ordinary Welsbach gas lamp, with standard screens. This gives a light much superior to that of ordinary daylight in bringing out the finer structure of the nephridial canals.

For sections I have used the ordinary paraffin and the paraffin celloidin method. The sections were cut of the uniform thickness of 7μ . In the reconstructions of the nervous system shown in figures I have used a method which is in part a modification¹ of that described by Woodworth ('Zeit. f. wiss. Mik.,' xiv, 1897, p. 15). Each section, of which there

¹ This I owe to my friend, Mr. E. W. Nelson, of the Marine Biological Association, Plymouth.

were about eighty, was first outlined on paper with the aid of a camera lucida, and the nervous system carefully marked in. Each of these drawings was then measured transversely from side to side, and the measurements plotted out on millimetre paper, allowance being made for the magnification between sections. The nervous system was also measured, and likewise put in, all the distances being doubled to give an axial line. The ends of the plotted points were then joined up, and an outline of the external form and the nervous system obtained. The figures were then reduced to their present size, and at the same time transferred to ordinary drawing-paper by means of an eidograph. In the sagittal section shown in fig. 15 the dorso-ventral diameter was taken instead of the transverse. By this means the relationship of the ganglia to the segments can be accurately determined in a way that would be impossible with the ordinary reconstruction methods (figs. 15, 21, 28).

2. HISTORICAL REVIEW AND GENERAL REMARKS ON HABITS, ETC.

Histriobdella was discovered and briefly described by J. P. van Beneden (1) in 1853. He found it as a parasite on the eggs of some lobsters obtained from Ostend. He considered it a larval Serpulid, and placed it among the Polychætæ. Subsequently, in 1858, he (2) pointed out that it was an adult form. From its peculiar structure he remarked that it could not be easily classed with any known group of animals, although some of its features he thought were such as to place it among the leeches. He gave a more or less detailed description of both sexes, and figured the eggs and immature young.

To Foettinger (8) we owe the most extensive account of this animal. He describes the nervous system, nephridia, reproductive organs, and, in fact, was the first to give a detailed account of its anatomy based on sections. He supported the conclusions of Edouard van Beneden that it was an Archannelid, placing it near *Polygordius*, but separate from it,

in the family Histriodrilides. In his opinion many of its characters show its inferiority in organisation to *Protodrilus*. Among these the absence of any trace of the circulatory system, the feeble internal segmentation, marked by the complete absence of dissepiments and the small number of segments. On the other hand, the presence of well-developed ganglia points towards a higher organisation than that possessed by any known Archiannelid. Again, the complicated sexual apparatus of the male is different from anything at present found in this class. The presence also of chitinous jaws with striated muscles and the anterior and posterior feet he considered as distinguishing it as a type superior to *Polygordius*.

More recently Haswell (13) has obtained, as already mentioned, a freshwater species from the branchial chamber of a Tasmanian crawfish. In the possession of cirri it differs externally slightly from *Histriobdella*. Haswell pointed out, among other new features, that the lateral organs which Foettinger considered penes are in reality organs that function as claspers, while the penis, as in *Dinophilus*, is a median unpaired structure. While Foettinger described the seminal vesicles he was unable to trace their ducts to a common receptaculum as Haswell has done in *Stratiodrilus*. The nervous system of *Stratiodrilus* seems to be different however from that of *Histriobdella*, in being more highly differentiated. In *Histriobdella* the ventral nerve-cord is still in complete continuity with the epidermal layer, while in *Stratiodrilus* it is situated much deeper. This difference may be in great part due to the close union of the epidermal and sub-epidermal tissues in contrast to those of *Stratiodrilus*. A more important difference is the separation shown by the two component halves of the ventral nerve-cord in *Histriobdella*, and the somewhat different position and number of the ganglia.

The greatest difference, however, is shown in the excretory system. It is impossible to reduce this to a common type. In *Stratiodrilus* the crossing and branching of the canals

in the anterior region, and their course in some instances through more than one segment, seems to preclude any comparison with *Histriobdella*.¹ Again, in *Stratiodrilus* the interior feet are retractile, and can be completely drawn into the head. This is not the case in *Histriobdella*, where the distal joint alone is retractile. The main mass of the foot is incapable of retraction, even under the action of strong reagents.

Histriobdella was found by van Beneden and Foettinger on the eggs of the European lobster, and was considered by them a parasite on these alone. It is, however, like *Stratiodrilus*, normally an inhabitant of the branchial chamber and gills. It passes to the eggs of the female from the gill-chamber when these happen to be present,² returning to the same situation when the eggs are hatched and the egg-membranes shed. In the branchial chamber it is quite difficult to detect at first, on account of its almost colourless condition and the fact that in this situation it does not show the excitable movements exhibited while on the eggs, but crawls slowly, keeping close to the mucous membrane. Examination of the branchial surface of the carapace, however, once the eye has become accustomed to distinguishing them, seldom fails to show their presence in this situation in either of the sexes. They prefer the carapace to the gill surface, as it affords a better footing, and the long hairs under which they move prevent their being readily brushed off. To the bases of these they attach their eggs in great numbers, especially towards the margin of the carapace, where the hairs are long and numerous. Comparison of the parasites from the "berry" with those from the chamber shows no difference between them, except that the jaws of the parasites from the chamber

¹ Professor Haswell informs me that since the publication of his account of *Stratiodrilus* he has re-examined the nephridia and has re-confirmed his statements regarding them.

² According to Herrick this takes place once in two years. "The Reproductive Period in the Lobster," 'Bull. of U.S. Fish Commission,' vol. xxi, 1901, p. 161.

seem a little better developed than those of the "berry." The parasites are evidently able to migrate rapidly from one situation to the other. On female lobsters whose eggs are about to hatch, many of them have already migrated to the gill-chamber. A certain number, however, are always to be found on the old egg-membranes, although the eggs have been hatched and the membranes are much discoloured with age, showing that the breeding period had passed some time. I have taken females in this condition, and placed them in tanks with air circulation and kept them under observation. In the course of several weeks the membranes drop off, but no parasites are found about the tank, showing that they have all taken refuge in the gill-chamber. In the gill-chamber and on the eggs both sexes are present in equal numbers. When the lobster ova are well advanced and about to hatch, the male *Histriobdellid* would seem to preponderate over the female. On the ova the immature young are found in greater numbers than in the gill-chamber.

Frequently a large female can be seen carrying a male attached to its back by means of its claspers. These would seem to throw out some sticky secretion, for once the male has taken hold of the female it is unable readily to let go, and gets carried about by the female although it makes violent efforts to free itself.

In the gill-chamber, as on the eggs, the parasites show the same tendency to collect in small groups, huddling close together and crawling over and over one another. When disturbed they separate, to re-collect shortly in another group. Why they do this is not obvious, as the individuals are sometimes all males or immature young, in which the sexual organs have not yet developed. This habit of collecting in groups therefore can hardly be for the purpose of the impregnation of the females.

I have examined a considerable number of "berried" crabs and rock lobsters, both at Plymouth and Naples, without finding *Histriobdella*. They would seem to be exclusively confined to the lobster.

Nothing is known regarding geographical distribution beyond the fact that *Histriobdella* is common on the lobster of the Channel region. J. P. van Beneden (2), as already mentioned, obtained it at Ostend. He also states in his second paper that he had observed it on the lobster of the Norwegian coast. I have been unable to find it on the lobster at Naples. My observations were, however, limited by the rarity of this animal in the Bay of Naples. I only had the opportunity of examining a few adults. So far it has not been reported as occurring on the American lobster.¹ It is remarkable that an animal of such peculiar structure should be represented in Europe by a single species, while its nearest ally should be found in fresh-water streams of Tasmania.

Little is also known of its life-history and habits. If a small mass of lobster ova with the parasites is placed in a watch-glass of sea-water, it will be noticed that they never crawl on any foreign body brought in contact with them. When left to themselves they collect in groups, twisting their bodies together, and remaining quiet for long periods. On being disturbed they show singular excitement, twisting themselves violently and throwing their heads rapidly from side to side, all the time remaining firmly attached by their powerful hind legs. From time to time they can be seen to bite one another with their strong jaws.

While the parasite can be obtained from the branchial chamber or "berry" of almost any lobster on the coast of England, the manner in which it gains access and passes from one host to another has not been determined. Like most parasites, it has limited powers of locomotion, being unable to swim, and crawling very slowly. It has no larval stage that might assist in its distribution. The eggs are attached in capsules to the lobster ova, and the young undergo their entire development within this capsule, emerging in almost the adult condition. There can be no larval

¹ Professor Herrick informs me that he has never found it on the American lobster.

stage during which it can live, either internally or externally, on some other host.

The parasites are able, however, to pass from one host to another without apparent difficulty. This can be readily demonstrated by placing a lobster in a solution of neutral rose in sea-water until the parasites it bears are stained, and then placing it in company with a number of normal unstained lobsters. In the course of a day many of the stained parasites will be found to have gained access to the normal lobsters, while many unstained parasites will be found on the stained lobster. This takes place readily in large tanks where the animals have room to keep well apart. How this passage is accomplished under these conditions I have been unable to observe, as the female lobster is very shy when "in berry," and unsociable, strictly avoiding its mates and companions.

Both Foettinger and Haswell have drawn attention to the remarkable chitinous jaws with which *Histriobdella* is furnished. Haswell has made a careful study of these in *Stratiodrillus*, and has shown how the movements of the component parts of the mechanism are brought about. In *Histriobdella* the jaws are almost identical, as far as I can determine, with those of *Stratiodrillus*. Foettinger represents them as furnished with many more teeth than I can find to be the case. Their use is not known, as neither Foettinger nor Haswell have made any observations on this head. Unfortunately the intestinal contents are reduced to such a fine amorphous condition as to afford no evidence as to the animal's food. It is probable that the parasites feed on small algæ to a certain extent, as the intestinal contents are usually of a greenish tint. Diatoms occasionally are present, and in some instances would seem to compose the greater portion of the food. This is so in the case of the parasites living on the "berry." In the parasites of the gill-chamber they seem absent, and the intestinal contents consist of a fine brownish mass, among which reddish granules are seen. It is certain that the jaws are not used for tearing the membranes of the lobster's ova as has been supposed.

When the animals are excited they have a rapid way of opening and closing the jaw teeth, but they are never seen to use them to tear open the lobster ova. When suddenly disturbed they sometimes secure themselves by means of their jaws to the egg membranes. They possess the power of protruding the jaw apparatus considerably beyond the mouth orifice, and in crawling they are sometimes seen to seize some object in front of them by protruding their jaws in this manner, after the fashion of many Polychæts.

Histriobdella is remarkably sensitive to any changes in the sea-water. The circulation of water through the branchial chamber of the lobster insures their receiving a continual change of water under normal conditions. Likewise, on the "berry" the water is kept in constant circulation round them by the ceaseless motion of the lobster's swimmerets. With any slight impurity of the water they fall off their hosts, and are found on the bottom of the tank in a half paralysed condition. They are quickly killed by the addition of small quantities of fresh water, and die very readily when exposed to bright light. This is of interest when it is recalled that *Stratiodrilus* is found in fresh water.

Fertilisation takes place internally. The male drives its penis through any portion of the body-wall of the female. In one instance I saw a male drive its penis into the head and discharge a considerable quantity of spermatozoa. These could be seen under the microscope working their way down into the generative segment. In many cases the males fertilise young females without eggs, and the spermatozoa apparently remain in the body till the ova develop. Many females can be observed carrying spermatozoa but no eggs.

The female exercises apparently little choice in the selection of a site in which to deposit her eggs. On the "berry" these are usually attached to the membranes of the lobster ova, while in the branchial chamber the carapace side is the one selected. They are usually deposited in groups of four or five, and this would indicate that these are all deposited at one time by the female. The eggs are all of one size, and it is

impossible to distinguish the sex of the immature young. They develop at once on being laid, showing that they have already been fertilised within the body. Even when the female is isolated in pasteurised sea-water the eggs develop immediately on being deposited; no sperm can therefore fertilise them in the sea-water.

The egg-laying is done at night, as every morning fresh capsules are to be seen adherent to the coatings of the lobster "berry." The eggs within these are always in segmentation or gastrulation stages. They are laid in great numbers, so that it is easily possible to obtain all the stages of development up to the time the young worm leaves the capsule. Development is direct and would seem to be rapid, for by the end of the fortieth hour the young are fully formed and appear ready to quit the capsule. On leaving this they move about the gill-chamber or pass immediately to the lobster ova, where they soon attain maturity. They are readily distinguishable at this time by their small size and the undeveloped condition of the generative segment. The young of both sexes resemble the female in shape. Van Beneden (2) has figured a number of the young stages, and Haswell (13) mentions that he has obtained a number of the stages in the development of *Stratiodrilus*.

Regarding the nephridia, Foettinger (8) stated that in the male there were five pairs of these organs, while in the female there were four. Each nephridium consisted of an intracellular tube running backwards on the border of the longitudinal muscle-strands. They turn in sharply towards the median line, to terminate ventrally, on the surface of the succeeding segment to that in which they arise, in a small pore. He could observe no internal openings or funnels. Their heads at their point of origin are on the dorsal surface; since they terminate on the ventral surface they run backwards in an oblique plane between the dorsal and ventral muscle-bands. The first pair arise in the neck segment close to the head, and run backwards to terminate on the ventral surface of the second segment. The second pair arise in the

posterior portion of this segment, and terminate in a similar manner in the third segment. The third pair arise in the third segment to terminate in the fourth. In the female the third and fourth pairs overlap, while in the male the fourth pair arises much farther back between the posterior portion of the fourth and the anterior border of the fifth segment.

In *Stratiodrillus*, on the contrary, according to Haswell, the nephridial system would seem to extend into the head region. Each nephridium at its anterior end divides into an external and an internal branch. The external branch runs forward into the head, while the internal crosses over to join the internal branch of the opposite side. From the fact that the motion of the cilia of this pair of organs is always from behind forward, their openings are probably in the head. The other nephridia are not 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 the 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 in and terminate in the cœlom in the middle line." In the fourth segment, according to Haswell, it is probable that the oviducts represent the nephridia, while in the male they are represented by the vasa deferentia. In both sexes, in the fifth segment there is a pair of organs (beginning in a loop in the male) which run back in the caudal region to terminate near the anus. The direction of the movement of the cilia in these organs is from behind forwards. Thus, in the male there are three pairs of organs, while in the female there are four ; so that the nephridia do not partake of the metamerism

of the body, *Stratiodrillus* having the same number of segments as *Histriobdella*. In no part of the canals were ciliary flames observed.

3. GENERAL DESCRIPTION OF THE NEPHRIDIA.

From the inspection of figs. 1, 7, and 9, it will be seen that the nephridia have much the same positions as those assigned them by Foettinger (8). Apparently in the male the fourth pair, figured by him in the genital region, have no existence. Like the female, the male has only four pairs of organs. It will be seen that they are the narrow, delicate, S-shaped structures he has described (figs. 4, 5, 6, 10, 14), running in the mesodermic tissue of the body-wall. Their position in sections can be seen in figs. 37 and 43. Each organ takes its origin in a small space—a prolongation or part of the general blastocœlic cavity that surrounds the gut—in the anterior portion of the segment to which it properly belongs, and runs back to terminate on the ventral surface of the following segment near the median line. It arises in a knob-like process that projects slightly into the space. This process is thick-walled, and sometimes contains refractive granules. It is shown in fig. 14. Its structure is difficult to determine, and especially the relationship it bears to the space. What I take to be the real head of the organ is shown in section in fig. 42. Here the space into which it projects is surrounded by darkly staining nuclei. These are not seen in the living condition. It bears no cells that have any resemblance to solenocytes, and these structures would seem to be entirely absent in *Histriobdella*. In a number of preparations it was obvious that the internal ends of the canals were closed, and that they did not open into the space into which they project.

The main portion of the nephridial canal is a thin-walled intra-cellular tube, the anterior end of which contains a few refractive granules and nuclei. It runs directly backwards in an oblique plane, and is much longer than the terminal

portion. It reaches its greatest length in the case of the second nephridium (fig. 14). Frequently the lumen can be seen to be enlarged into small spaces or lacunæ. These would seem similar to the spaces I have described on the nephridial canals of *Dinophilus*. A number of these are usually seen on the course of the second organ (fig. 6). One large one is often found on the posterior part of the third. From the terminal portion of the canal they seem to be absent. The nephridial flagella pass through their centre while their walls themselves are unciliated. It is possible they are due to the somewhat abnormal conditions under which the parasites are kept in the process of their impregnation with methyl-blue, as I have never been able to observe their presence in the unstained living *Histriobdella*, although something like their appearance can be detected in sections.

The terminal portion of the nephridial canal turns towards the median line, close to which it ends in a darkly staining pore (fig. 14). About this the blue usually collects in thick granules, which can sometimes be seen vibrating to and fro in the fluid escaping from the canal. The lumen of this terminal portion is greatly restricted in size.

Throughout the length of the nephridial canal the ciliary action of the flagella in their interior can be plainly observed during life. The movement of this is always in the one direction—from before backwards—and I have never observed any reversal of this motion as Haswell has described in *Stratiodrillus*. Despite numerous observations, I have been unable to determine whether the flagella are derived from the walls of the canal or from the knob-like head of the organ. In some preparations they seemed derived from the wall, in others they seemed derived from the nephridial heads. In sections they would seem to be derived from the walls.

In no case can the canals be seen dividing, as Haswell has described in the case of the first pair in the male of *Stratiodrillus*. I am quite positive in saying no such division takes place in *Histriobdella*. They run through

only one segment, in every case terminating in the next segment to that in which they arise in the manner similar to the nephridia in Annelids.

In both sexes the first three pairs of nephridia hold the same position, but the fourth varies according to sex. In the male it is situated much farther back—at the junction of the generative with that of the following segment, while in the female it is much more forward—in the anterior portion of this segment. In the female the third and fourth pairs overlap and cross one another in different planes.

The most posterior nephridium in *Stratiodrillus* is in that segment that would correspond to the fifth in *Histriobdella*. In neither of the sexes are organs found in this region in *Histriobdella*.

Foettinger, in figuring a pair of nephridia in the region of the penis, evidently mistook the motion of the cilia in the vas deferens, or the slit in the vesiculæ, for the ciliary motion of excretory organs. The slit in the vesiculæ was first described by Haswell in *Stratiodrillus*, and as such was evidently overlooked by Foettinger. They are even better developed in *Histriobdella* than in *Stratiodrillus*. They are edged with very stout cilia, that could readily be mistaken for nephridial flagella. With methyl-blue it is easy to determine, however, that no excretory organs exist at this point in *Histriobdella*.

In *Histriobdella*, unlike *Stratiodrillus*, the nephridia partake to some extent of the metamerism of the body. In the third and fourth segments this is masked in the male by the great development of the reproductive organs. In the case of the nephridia there has resulted a pushing forward in the female of the fourth organ, while in the male this has been reduced in size and moved backwards.

Unlike *Dinophilus*, we do not find the sharp specialisation of the different parts of the nephridial canal into a thick-walled anterior excretory portion and a thin-walled posterior part. It is more uniform throughout in structure.

A. The First Nephridium (figs. 1, 7, 9, 37, and 42).

The first nephridium arises in the segment immediately behind the head, and opens on the exterior in the second segment. The head of the organ I have never been able to see plainly in the living condition, as it is hidden by the muscle-bands. These are always undergoing contraction during life; the lumen of the canal in its anterior portion is continually compressed, and thus the action of its cilia rendered very intermittent. The head of the organ at its point of origin is very close under the epidermis; in one case seeming to be almost under the limiting membrane of the epidermis. In section the head of the organ appears as shown in fig. 42, which is taken in a horizontal plane in the dorsal region of the first segment. The space into which the nephridial head projects is shown surrounded by a number of darkly staining nuclei. The canal with its flagella is shown cut in section in the body-cavity. The actual projection of the head into the space is not seen in this section.

The neck segment is very clear, and were the canal prolonged into the head, as in *Stratiodrilus*, it could easily be seen at this point passing into the head. As this can never be done, it is apparent that the organ takes its origin in the neck segment and is not prolonged into the head. It is also certain that it does not divide and send a branch to join one from the opposite side, as in *Stratiodrilus*. Throughout its course it is a simple, unbranched, intra-cellular tube, being in the same position in both sexes.

B. The Second Nephridium (figs. 1, 6, 7, 9, 14, and 37).

The second nephridium arises in the anterior portion of the second segment, and runs back to terminate in the anterior part of the third. It is much the longest, being twice the length of the first. Its course is straight backwards along the border of the muscle-bands. The action of its cilia is much more constant than that of the others, and for this reason it

is the one most readily observed. The main portion of its canal is slender and thin-walled. The general course of the organ is shown in figs. 1, 6, 7, 9, 14, and 37. It will be seen from these figures that Foettinger observed the organ only at the point where it passes from the second to the third segment, and that he was unaware of its considerable extension into the anterior region of the second segment. In the female the segments through which it stretches are somewhat more compressed, and for this reason it appears in the female shorter than in the male.

c. The Third Nephridium (figs. 1, 3, 4, 10, and 13).

The third nephridium has much the same position in both sexes. It arises in the anterior part of the third segment and runs back to bend outwards in the male and slightly inwards in the female, and terminates in the anterior part of the generative region. When the body is retracted it overlaps the posterior third of the second. The head of the organ, as already mentioned, at its point of origin is in the normal condition on a level with the opening of the second. It is situated close under the epidermis, as in the case of the first nephridium, and on the dorsal surface. It runs backwards, and about the middle of its course makes a sharp turn ventralwards (fig. 5). In the female it overlaps considerably the fourth, its opening on the exterior being internal to the course of this organ. While in the male it makes only one turn outwards, in the female it is **S**-shaped, the terminal portion running inwards (fig. 3).

d. The Fourth Nephridium (figs. 1, 3, 10, and 13).

In the male the fourth nephridium arises in the posterior part of the generative segment in the region immediately behind the clasper. It runs backwards and terminates in the anterior part of the caudal segment. Its course is short and somewhat difficult to observe. It is much the smallest of all

the nephridia, and its action more feeble than that of the others, as the motion of its flagella is the first to stop when the animal is compressed under a cover-slip. It, however, assumes a much darker colour on impregnation with methyl-blue than do the other nephridia, and for this reason seems to play a considerable part in the excretion of waste products. Its position in the male has been correctly indicated by Foettinger, who remarks that no organ is to be found in this position in the female.

Unlike *Stratiodrillus*, the organ does not begin in a loop or run back so far in the tail region, but opens on the exterior just over the line of separation between the generative and the caudal segments (fig. 12).

4. BODY-CAVITY AND NEPHRIDIA.

As in *Dinophilus*, there is an extensive blastocœlic cavity surrounding the gut, which sends prolongations into the head region, and also into the anterior and posterior feet. It has been described by Foettinger as lined by a more or less definite cœlomic epithelium. I cannot find that this is strictly the case. The gut surface of the cavity is covered by a delicate cuticle, in which at rare intervals are seen small flat nuclei. It is difficult to say if this membrane is a definite structure or a mere secretion from the blastocœlic ends of the cells of the gut-wall. The somatopleuric side of the cavity is not lined by any such membrane. The longitudinal muscles, as in *Stratiodrillus*, are surrounded by a similar delicate cuticle, but no nuclei are to be seen in it as in the gut membrane. I believe in neither of these cases can this membrane be considered a true peritoneal or cœlomic epithelium. No mesenteries are present, nor can I observe the fusion of the gut to the dorsal ectoderm as mentioned by Foettinger. The gut is more or less closely applied to the dorsal wall, but I cannot find that any true fusion takes place.

In the head the blastocœlic space sends prolongations into

the feet, and forward on the under side of the brain. It is more or less separated from the cavity of the trunk by the neck muscles and the narrow constricted condition of this region. Its extension into the posterior feet is in free communication with the trunk, so that in living preparations the eggs in the female can sometimes be forced into the leg portion of the cavity by slight compression of the cover-glass. They slip back, however, to the main blastocœlic space surrounding the gut when this pressure is removed. The whole of the blastocœlic cavity is very irregular in outline, and is divided, as has been described, in the trunk region by the oblique muscle strands into two lateral chambers.

In every respect it corresponds with the same cavity surrounding the gut in *Dinophilus*. There is this difference, however, that the numerous brown granules seen in it in *Dinophilus* are wanting in *Histriobdella*, although *Histriobdella*, like *Dinophilus*, has no specialised vascular system. It is sharply divided from the sac of the ovary, there being no communication between the two. When the ova are forced into the blastocœlic space of the hind limbs the sac of the ovary is either pushed with them, or is definitely ruptured, and the ova pass directly into the blastocœle. Both at the anterior and posterior regions the wall of the ovary is considerably thickened where it crosses the blastocœlic space between the body-wall and the gut. In the male the sac of the testis is likewise sharply cut off from the blastocœlic space in the anterior and posterior part of the generative region. *Histriobdella*, like *Dinophilus*, shows the primary and secondary body-cavity existing together, but sharply divided from one another. The nephridia, as in *Dinophilus*, are in relation with the blastocœlic cavity alone.

From the fact that we get two nephridia in the generative region in the female, there is considerable reason for concluding that the oviduct and its funnel can hardly represent a transformed nephridium as Haswell has suggested. The arrangement of the ganglia and the external appearance of the

segmentation bear out the conclusion that in the male and female this region is composed of two segments. Haswell, in *Stratiodrillus*, states that "in the fourth segment the nephridia are probably represented in the female by the oviducts, in the male by the vasa deferentia." I have shown in the male and female that two nephridia are present in the generative region, although holding slightly different positions in the two sexes. It is therefore impossible that the oviduct and vasa deferentia represent transformed nephridia, unless we consider the generative region to be composed of three segments, for which there is no evidence.

In my paper on the nephridia of *Dinophilus tæniatus* I have given some reasons for opposing the view brought forward by Schimkewitsch (28) and Harmer (12), that the oviducts and vasa deferentia in the male of this animal represent modified nephridia. Here there are four pairs of close solenocyte-bearing nephridia in the male and five in the female. They show the same primitive relationship with the blastocœlic cavity as do those of *Histriobdella*. Harmer's suggestion is that in the male the fifth nephridium has been modified into the vesiculæ seminales and vasa deferentia, while it remains unmodified in the female as the fifth nephridium. In the male he holds that one of the pairs of nephridia has lost its primitive relationship with the blastocœlic cavity, and here becomes highly modified into the large ciliated apparatus of the vesicula seminalis and the vasa deferentia. The principal evidence relied on by Harmer in making this comparison is the resemblance of the funnel-like opening of the vasa deferentia into the cavity of the testis, to the funnels with which he thought the nephridia were furnished. I have shown that these do not exist, and that the nephridia of *D. tæniatus* are definitely closed. Therefore the funnels of the vasa deferentia cannot be derived through modification from those of the nephridia.

In *Histriobdella* and *Dinophilus*, I believe the oviducts, funnels, and vasa deferentia represent structures

belonging to an entirely different set of organs from those of the nephridia, viz. the coelomoducts of Lankester's nomenclature.

5. MUSCULAR SYSTEM.

The muscular system has been described by Foettinger, whose account is correct in its main particulars. The muscles of the trunk region, as described by him, consist of two groups, the dorsal and ventral longitudinal, and the irregular oblique or transverse muscles. It is to these last that I wish to call particular attention in the present account, as they are only mentioned briefly by Foettinger.

In addition to this I have been able to add new details in the division and arrangement of the fibres of the longitudinal muscles that escaped Foettinger's observation.

A. Longitudinal Muscles.

The chief muscles of the body are these powerful longitudinal bands. They have already been described by Foettinger in considerable detail. They consist of two dorsal and two ventral sets. Each band is composed of from twenty to thirty fibres, flattened dorso-ventrally. They are attached by their outer margins to the cuticle, while their free edges project into the body-cavity. In the generative segment their number seems reduced, but this is due to their confinement within a limited space—against the gut dorsally and the nerve-cord ventrally. In the caudal region they spread out, forming a more or less complete wall round the segment, only interrupted dorsally by the gut and ventrally by the nerve-cord. They split up in the head and tail regions, sending fibres to the jaws and the anterior and posterior feet. In the head dorsally they converge on one another, uniting in the median plane, and are inserted in the anterior surface of the jaw apparatus. The ventral bands, on the other hand, divide into two sets of fibres, the outer of which split again to supply fibres to the anterior and posterior surfaces of the

anterior feet, while the other set run forward and are inserted ventrally into the anterior part of the jaw mechanism. In the posterior region each band splits likewise, the ventral sending fibres to the foot of the same side, other fibres crossing to be inserted in the small appendage of the posterior limb. The dorsal send part of their fibres into the leg on the same side, while the internal ones cross over to be inserted in the leg of the opposite side, these fibres thus forming a cross dorsal to the anal part of the gut. The dorsal longitudinal bands give off a few fibres to the two segments of the caudal region, which run towards the median line and are inserted into the cuticle. It is due to the action of these fibres that the contraction of the caudal segment is brought about.

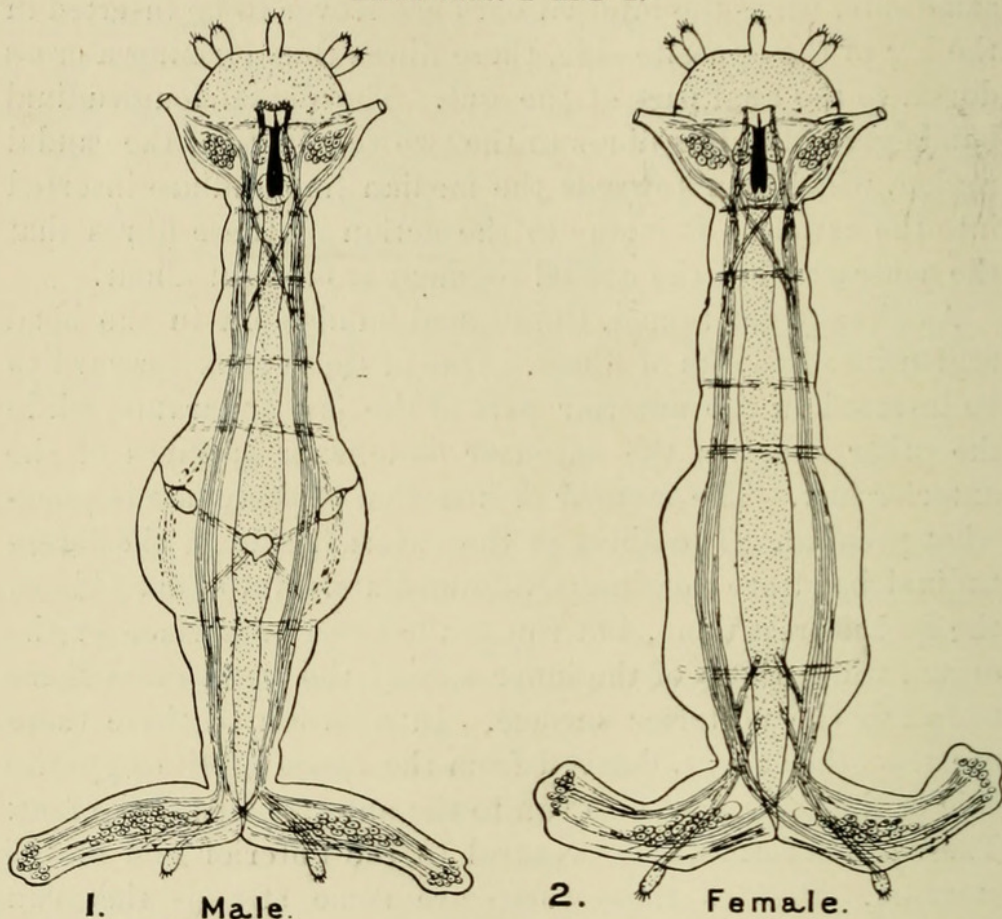
As already mentioned, the ventral bands split in the head region into two sets of fibres. One of these runs forward to be inserted in the anterior part of the jaw apparatus, while the other supplies the extensor and flexor surfaces of the anterior feet. The manner of insertion of these last is somewhat peculiar. The fibres of the external side of the longitudinal band are not inserted immediately into that side of the foot nearest them, but run to the anterior surface of the organ, while those of the inner side of the band cross these to run to the posterior surface. In addition to these there are also other fibres, derived from the bands of the opposite side of the body, that also run to the anterior face of the foot. These fibres form a cross ventral to the anterior end of the stomach. Besides these there are some strands that run from the same side of the foot directly towards the median line, and appear to be inserted into the anterior end of the jaws. All these are inserted into the distal joint of the foot. The course of these different fibres can be readily understood on reference to text-figs. 1 and 2.

B. Special Muscles of the Generative Segment.

In the anterior and posterior part of the generative segment, in the intersegmental region, a few transverse fibres are present, running beneath the epidermis.

In the male special muscles are developed in relation with the claspers and the penis. These are similar in their arrangement to the same muscles of *Stratiodrillus*. The penis possesses a pair of protractors and retractors. The retractor muscles also function as the retractors of the claspers. They

TEXT-FIGS. 1 AND 2.



The muscles seen from the dorsal side in the male and female.
The division of the longitudinal bands in the head and caudal regions is also represented.

run from the base of the penis to the base of the claspers, and by their contraction at the same time retract the penis and claspers. The claspers have also, as in *Stratiodrillus*, a set of protractor muscles, which run obliquely forwards and inwards in the generative segment, and also a few fibres that run from the bottom of the clasper sheath to the anterior lip of the same.

It will be seen that there is some difference between the arrangement of the main muscles in *Histriobdella* as compared with *Stratiodrillus*. In the neck region I cannot find the complicated crossing of fibres shown by Haswell in his fig. 1. Nor in the posterior legs can I distinguish some of the fibres he represents. The muscular system of *Stratiodrillus* is much better developed, and the presence of cirri and the retractile condition of the anterior feet give it a more elaborate muscular system than that of *Histriobdella*.

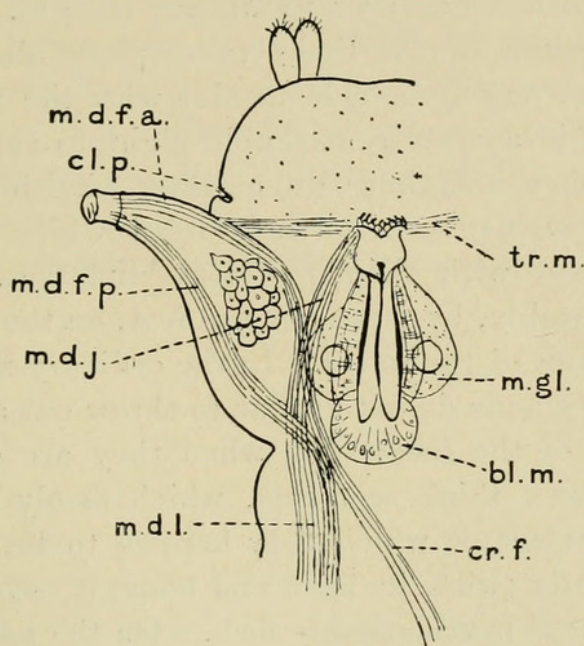
c. Oblique Muscles.

If we examine a number of transverse sections we will see the body-cavity traversed occasionally by oblique strands (figs. 39, 40, 41, 43, and 44). Foettinger mentions their resemblance to the oblique muscles of *Protodrillus*, but he was somewhat uncertain as to their nature. He says, "*Je n'ai pu m'assurer si elles étaient de nature musculaire*" (p. 457). They divide the body-cavity, as in the Archiannelids, into a circular portion surrounding the gut and a right and left lateral chamber. In some of my sections they form almost a continual sheet of fibres, and they are much better developed than one might suppose from Foettinger's remark. They are found as irregular bundles crossing the body-cavity from the head to the tail region. They are well marked in the posterior part of the head; commencing at a point on a line with the chitinous jaws, they are continued back into the neck region in an unbroken succession. In the middle of the segment they almost disappear, while they are more prominent in the intersegmental regions. In the anterior and posterior parts of the generative segment they are also present, but are entirely missing from the middle in the male, being interrupted by the muscles and accessory glands of the penis. Anteriorly they divide the testis in two portions, forming a right and left chamber (fig. 39). In the anterior part of the first segment they are shown in fig. 43. Here, during part of their course, they touch the wall of the gut.

In *Stratiodrillus* their presence has been observed by Haswell (13), who states: "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" (p. 306). Here, however, they would seem to be much less developed. I think there is no doubt that they correspond to the oblique muscles of *Polygordius*. It is interesting to note that the nephridial canals, as in *Polygordius*, are always within the limits of the lateral cavities formed by them. Another point of similarity consists in the manner of their insertion into the dorsal body-wall. They spread out in a fan-like manner, as Hempelmann (15) has shown takes place in *Polygordius* (see his text-fig. 14). This same arrangement of the fibres, it will be seen, is found in *Histriobdella* (fig. 41). The anterior and posterior feet, in addition to the fibres they receive from the longitudinal bands, also possess a special musculature of their own. In the anterior foot this consists of a series of parallel fibres that run from its base to the distal, flat, saucer-like pad of the foot. The foot itself is composed of two parts, a distal retractile portion and a larger non-retractile, cone-shaped basal portion. Some of the fibres are applied closely to the cuticle of the outer part of the basal portion, while those of the bands, as already mentioned, are inserted into the retractile distal portion. They surround and run into the basal gland of the foot. There is a collection of granular mucus cells at the base of the foot, abutting internally on the jaw musculature. They stain deeply with carmine, each cell having a darkly granular periphery, with a clear centre hollowed out in a small cavity. The gland gives off a number of straight tubes, that open on the pad surface of the foot. They run up amongst the muscle-fibres, and can be readily distinguished from these by the manner in which they take the stain. The gland pours out on the surface of the pad some sticky secretion, by means of which the animal is enabled to obtain a firm hold. In the case of the posterior limbs a similar, but larger, gland is present. It extends from the wall of the gut out of

the centre of each leg to the commencement of the outer third, where it gives off a mass of fine, darkly staining tubules, which open on the pyramidal pad of the foot. This gland is able to pour out a copious viscid secretion. Frequently, when the animals are irritated, this secretion can be

TEXT-FIG. 3.



3.

Head showing the muscles in connection with the feet and the jaws. *bl.m.*, Bulb-like muscular organ of the jaws; *cl.p.*, ciliated pit of the head; *cr.f.*, crossed strands of the dorsal longitudinal muscles; *m.d.f.a.*, dorsal longitudinal muscles running into anterior surface of the foot; *m.d.f.p.*, dorsal longitudinal muscles running into posterior surface of the foot; *m.gl.*, salivary gland of the mouth; *m.d.j.*, dorsal longitudinal muscle running to jaw apparatus; *tr.m.*, transverse muscle-strands running into the feet.

seen pouring out from the ends of the tubules, forming minute round drops on the end of the foot. Like the anterior limb, the posterior has some muscular fibres apart from those it receives from the longitudinal muscle-bands. These are a delicate set of fibres just under the cuticle on the posterior surface, that run from the extremity to be inserted on either side of the anus. In addition to these there are some oblique

fibres, as in *Stratiodrillus*, but they are but feebly developed. A considerable prolongation of the blastocoelic cavity takes place into the posterior limbs, running out along each leg between the muscle-fibres and the glands. Into this space the ova in the female are sometimes forced when the animal is compressed under a cover-slip, showing that it is in free communication with the cavity surrounding the gut.

The movement of the limbs takes place alternately, the head being swung from side to side with the movement of the feet. It is a most remarkable sight to see the animals rear up, as they sometimes do, on their hind feet, and stand executing movements with their head while they remain firmly attached with their powerful hind feet. They also crawl quite readily, by means of the feet, on the underside of the surface-film of the water. In the ordinary movements of crawling the glands do not appear to throw out any secretion on the pads of the feet; only when they are disturbed do they pour out a thick secretion, which firmly attaches the feet to the surface on which they happen to be. While the animal violently twists its head and body, it never moves its feet. This hold is remarkably firm. On the lobster ova the parasites can be seized by the middle of the body by means of a pair of fine forceps, under a dissecting microscope, and the body pulled off, leaving the feet still attached, the limbs having been torn from the body without loosening their hold.

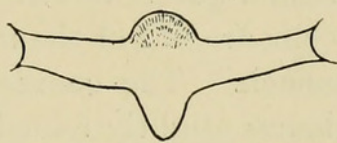
As already mentioned, the front limbs in *Histriobdella* differ from those of *Stratiodrillus* in that they are non-retractile. I have never been able to observe any retraction of the feet in the living condition, or in preserved specimens treated with different reagents.

6. DIGESTIVE SYSTEM.

The digestive system is sharply specialised into a number of divisions. These are readily seen in the figure of an immature parasite (fig. 30). Here they are more marked

than in the adult. A more or less slender œsophagus leads dorsalwards and backwards from a quadrilateral-shaped mouth (text-fig. 4). This, although small, is capable of considerable expansion. It is completely everted in allowing the jaws and teeth to be protruded in the act of biting. It commences in a slight ciliated depression, which rapidly deepens into a groove in the anterior part of the head. The œsophagus terminates, on a line with the posterior boundary of the jaw musculature, in a narrow constriction leading into the stomach. It is difficult to say where the mouth ends and the œsophagus commences. The mouth and œsophagus are lined throughout with fine cilia, those of the œsophagus being much stouter than those of the mouth.

TEXT-FIG. 4.



4.

Showing the outline of the mouth when partially closed.

The stomach may be defined as that portion of the intestinal tract lying between the first and the third segment. Its wall is composed of a single layer of cubical cells. It is for the most part uniform in thickness. The rounded internal ends of cells project irregularly into the lumen and are ciliated. At the anterior end, near the œsophagus, the cells are very columnar and contain many granules. They have probably to do with the elaboration of the digestive secretions, as they are seen to be very opaque after the animals have taken food. Those of the ventral wall in this part are somewhat larger than the dorsal. The nuclei are always placed at the bottom of the cell, that is, farthest from the internal ciliated surface. In the anterior region they are long and oval in shape, while in the middle and posterior regions they are spherical, and the cells themselves cubical in outline. In the posterior

region of the stomach the wall is relatively thin in comparison with that of the anterior part, and its cells on the ventral side are furnished with very long, dense cilia.

About the middle of the end of the third segment the stomach contracts into a narrow mid-gut, which runs through the generative region to widen somewhat in the caudal region into a more or less straight hind-gut. The lumen of the intestinal tract, from the stomach backwards, is greatly reduced in size, and, in the contracted condition of the animal, somewhat folded on itself. The character of its ciliation is also different from that of the stomach. At the point where the stomach passes into the mid-gut there is a sort of valve formed by the thickening of the stomach-wall. A similar valve is found at the point of union with the hind-gut. The wall of the mid-gut is relatively the thinnest part of the tract, and its cells are not of the marked yellow colour of those of the stomach. The course of the mid-gut is irregular, from its being slightly folded on itself. That of the hind-gut is comparatively straight, but its lumen is irregular and wavy in outline, due to the irregular thickening of the wall at different points on its course. Throughout the generative segment the gut is very closely confined against the dorsal body-wall. The anus is dorsal. The cells of the hind-gut are of a character quite different from those of the other parts of the tract. They are quite irregular in size, and extend into the lumen so as to make its outline very broken, as if thrown into a number of convolutions. In no part of the wall of the stomach or gut are any contractile muscular fibres to be seen. In the body-cavity, ventral to the anus, and close to the point where the gut joins the body-wall to form the anus, there is usually present a conspicuous cell on either side. The anus itself is an oblong, vertically placed, T-shaped slit placed more towards the dorsal than the ventral side of the animal. It is apparently kept closed by some contractile fibres of the cuticle which function as a sort of sphincter muscle.

The digestive tract of *Stratiodrillus* agrees in all essen-

tial details with that of *Histriobdella* as far as can be judged from Haswell's somewhat brief description. There is the same reduction of the tract in the generative region, this being much greater in the female than in the male, and its expansion into a more or less large hind-gut in the caudal region.

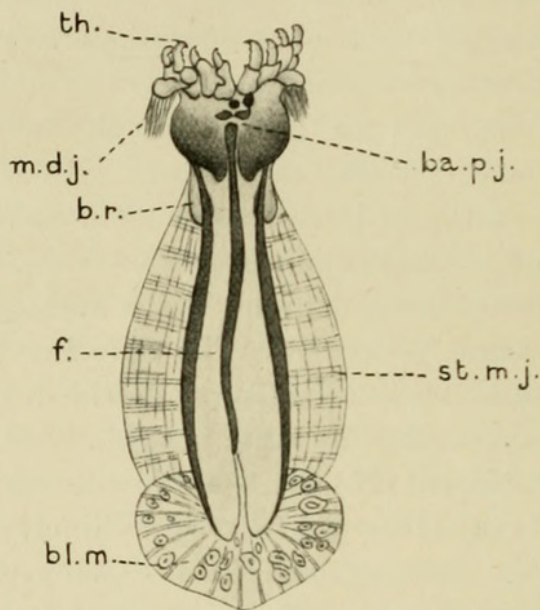
As compared with *Dinophilus* there is a greater difference. Yet with the exception of the peculiar mid-gut portion of the tract, which is a development due to the peculiar condition produced by the presence of a special generative segment, there is considerable resemblance between *Histriobdella* and *Dinophilus*, and in many of the finer histological details there is a very close resemblance. In the first place, the appearance of the cells of the stomach, each composed of a single layer of ciliated cells, the yellow vacuolated appearance of their protoplasm, and the basal arrangement of the nuclei, are the same in the two. The terminal dorsal position of the anus and the configuration of the œsophagus and pharynx are remarkably the same in both.

According to Nelson (25) there is a feeble strand of muscle-fibres that act in *Dinophilus* as sphincter ani, as in *Histriobdella*. Throughout the stomach region there is a lack of muscular strands, and the stomach is not supported by mesenteries, but is closely applied to the dorsal wall, as in *Histriobdella*. The blastocœlic surface of the stomach, as in *Histriobdella*, is covered with a fine cuticle.

The jaw apparatus of *Histriobdella* is very similar to that of *Stratiodrillus*. Haswell has given an extensive description of this, so that I need only briefly consider it. As in *Stratiodrillus*, it consists of two portions—the upper and the lower. The upper consists of a median rod (fig. 36), which Haswell has called the fulcrum. This is slender, round, and slightly curved; it articulates by means of a number of basal pieces with a series of jointed arms, each terminating in a curved tooth (text-fig. 5). It lies in the median plane dorsal to the two blades of the lower jaws, being set at a different angle to these. Its length is somewhat less

than these last. The cubical basal pieces with which it articulates support four arms on each side, each being composed of three or four pieces, the last of which is fashioned into a sharply-curved claw-like tooth. This is strongly serrated on its inner edge. One difference between the jaw parts of *Histriobdella* and *Stratiodrilus* consists in the length of the middle joint of these arms. They are much

TEXT-FIG. 5.



5.

Jaw apparatus. Enlarged figure showing the structure of the teeth and the arrangement of the jaw-muscles. *ba.p.j.*, basal piece of jaws; *bl.m.*, bulb-like muscular organ of the jaws; *f.*, fulcrum; *m.d.j.*, strands of the dorsal longitudinal muscle-bands running to the jaws; *st.m.j.*, striated muscles of the jaws; *th.*, teeth.

longer in *Histriobdella*, and allow of the teeth being folded back in the mouth or œsophagus to a greater extent than in *Stratiodrilus*. When at rest in the ordinary position the teeth are not folded back to their full extent. The middle piece of the arm projects at right angles to the jaws, and in this position the most anterior part of the arm is the distal joint, the tooth being strongly flexed. When the

arms are folded to their full extent the fulcrum is drawn back on a level with the extremity of the blades of the lower jaws. These are paired throughout. They consist of two long wide blades, thickened at their outer margins, and articulating at their basal ends with two curved wedge-like pieces, the pointed end of the wedge being directed forward in the ventral lip of the mouth. Ventrally they articulate with one another in the median line, and turn up dorsally to form a support for the upper jaws. The upper anterior angle of each plate is turned outwards and backwards, some of the fibres of the dorsal longitudinal muscle-bands being inserted into it. The internal interior edges of these plates are finely serrated, and evidently assist the teeth in their action. As far as can be judged from Haswell's figures, the shape of these plates differs slightly in *Histriobdella* from that of *Stratiodrillus*. They fold up dorsally to a greater degree. The main portion of the lower jaws are the wide blade-like portions which project backwards parallel with one another. They are widest behind, and taper slightly in front, where they articulate with the wedge-like portions. Connecting the upper with the lower jaws are the pieces that Haswell distinguishes as "bridles." Into the posterior extremities of these are inserted the powerful striated muscles. Apart from their action in binding together the jaw-sets I have not satisfactorily determined their function. They would seem to be composed of a single curved piece in *Histriobdella*, and its chitinous substance is broken up into a number of dark hairs where the muscle is inserted, giving it a furred appearance. The powerful nature of these fibres shows that their action in pulling on the bridles has to do with some essential movement of the jaws. It is likely that the actual process of biting is brought about by their contraction, as Haswell has suggested, while the fulcrum has merely to do with their protrusion and opening. In addition to these there is the peculiar bulbular muscular organ, not unlike the sub-oesophageal muscle pad of *Dinophilus*. This is attached to the posterior ends of the ventral surfaces of the lower

jaws. Its fibres form an oval mass attached directly to the jaw blades. Into this mass some of the striated muscle-fibres are inserted. Its action is hard to understand. It is well shown in Foettinger's figures. In the movements of the jaws the lower blades are sometimes seen to separate considerably from one another posteriorly, and it is possible this motion is brought about by them. What this movement has to do with the teeth I have been unable to observe. This muscular organ appears to be wanting in *Stratiodrillus*, as it is not shown in Haswell's figures.

On either side of the jaws about their middle there protrudes laterally a small pear-shaped gland composed of from three to four large granular cells with conspicuous nuclei (text-figs. 1 and 2). This gland opens into the mouth or the anterior part of the œsophagus, and is evidently of a mucous nature, as it absorbs the methyl-blue colour very strongly when the parasites are placed in it for a short time. The protoplasm of the gland-cells is finely granular, each having a very large, darkly staining nucleus with a prominent nucleolus. The duct of the gland converges and opens on the ventral side of the mouth. The posterior portion of the organ lies against the muscular pad of the ends of the lower jaws, while its dorsal surface touches the cuticle of the dorsal surface of the head.

In position and structure it is in all respects similar to the glands occupying the same position in *Dinophilus*, and undoubtedly answers the same purpose. In *Protodrillus*, also, similar glands are present. It appears to have been overlooked by Foettinger. In fig. 1 of his paper he shows a mass of tissue on either side of the jaws, which in great part belongs to these salivary glands, and not to the jaw muscles, as he evidently thought. Haswell makes no mention of its presence in *Stratiodrillus*, although it is probably present here also, for he shows a number of round cells in the position that it occupies in *Histriobdella*.

7. THE NERVOUS SYSTEM (figs. 15, 21, and 28).

The nervous system extends throughout the body, and is composed of a brain, œsophageal commissures, and ventral nerve-cord, with ganglia at intervals corresponding to the external segmentation. The brain is situated well forward in the head, its main mass being anterior to the oral opening, and close to the dorsal surface. It is composed externally of a mass of nerve-cells surrounding a clear fibrous core. The nerve-cells are distributed over its dorsal surface. Behind, the brain is deeply cleft ventrally, descending in lateral lobes on either side of the anterior part of the mouth. This cleft runs forward, forming a small closed sinus in the anterior end of the organ.

The brain terminates rather abruptly at a point about on a line with the anterior third of the jaws; here it gives off two fine commissures that run directly ventralwards and backwards, connecting it with the first ganglion of the ventral nerve-cord. At the point where these come off some fibres go to the anterior legs, and others run directly backwards in the dorsal region. They probably correspond with the "nerfs sympathiques" of Foettinger. In addition to these, the brain supplies nerves to the anterior tentacles.

The commissures are closely applied to the œsophagus, and are difficult to follow in sections on account of their small size.

At about on a line with the posterior boundary of the brain, and slightly in front of the anterior feet, there is a small ciliated pit on either side of the head. The anterior lip of this protrudes slightly, forming a sort of papilla. This pit is undoubtedly sensory in nature, and appears to have some fine nerve-fibres running to it from the brain. The nerve-cells of the dorsal surface of the brain are distinctly differentiated from the cells of the ectoderm. They are recognisable by the elliptical outline of their nuclei, and the marked way in which they take the stain when treated with the hæmatoxylin mixtures. As compared with the ectoderm

cells, their nuclei are rich in chromatin. This peculiarity renders them distinguishable from the supporting cells of the surrounding tissues. Some of the ganglion cells are clearly multipolar, but axons and dendrites are not recognisable. At the base of the tentacles the cells are bipolar, one process going into the tentacle while the other enters the neuropile. They form a dense mass of cells on the anterior dorsal surface of the brain-core. They are, however, quite distinct from it, only sending a few fine threads into its substance. In the median plane a small space, a prolongation of the general blastocœlic space, extends up under the brain, and separates them from the core, dividing them into two lateral masses. The central core of the brain is composed of a dense mass of interwoven nerve-fibres. It is distinguishable by its yellow colour and its non-nucleated character. It is remarkable that both in relation with the brain and the ventral cord the nerve-cells seem quite apart, and outside the fibrillar part of the nervous system. Their relationship seems closer with the ectodermic tissues of the head and the mesodermic and ectodermic tissues in the trunk than with the fibrillar material of the nervous system in these regions.

The fibres of the ventral portion of the neuropile seem to run from side to side, while those of the superficial layers run more longitudinally. In sagittal sections it is lenticular in outline, and in the median plane is divided by a transverse fissure into an anterior and posterior part. Haswell also shows these divisions in the brain of *Stratiodrillus* (fig. 8). This division is only limited to the median plane; laterally the neuropile swells out into two large lobes on either side. Thus it consists, as in *Dinophilus*, in a median and two lateral lobes, the median being in turn divided into an anterior and posterior portion. In the figures of the brain accompanying this paper these divisions do not show, as the brain surface is taken from the ganglion cells and not from the central core. Behind the brain, and dorsal to the muscular apparatus of the jaws, there is a second accumulation of nerve-cells. These may possibly have to do with the

innervation of the jaw muscles; they are dorsal and median to the oesophageal commissures. I have been unable to make out their connection with the muscles. They take up methyl-blue much more readily than do the other cells of the brain, and retain it considerably longer.

The ventral nerve-cord, like the brain, consists of a similar central fibrous core, surrounded with nerve-cells. The two halves of the cord are separated in the intersegmental regions, joining up in the middle of the segments to form a ganglion. From what can be judged from Haswell's drawings, in *Stratiodrillus* this separation is much less than in *Histriobdella*. Unfortunately, most of the sections drawn by Foettinger are taken through the middle of the segments, and do not properly illustrate the extent to which the two portions of the cord separate in the intersegmental regions. The two halves of the cord are crescentic in transverse section, the nerve-cells being imbedded on the ventral surface. Where the cords unite these cells are drawn out laterally to form considerable masses on either side.

The main ganglia, as already mentioned, correspond closely with the five main segments into which the trunk is divided. The first is situated in the anterior region of the first segment, and is of considerable size. The second is somewhat smaller, and is situated about the middle of the second segment. It has fewer nerve-cells, and, like *Stratiodrillus*, it is placed nearer the first than the third ganglion. The third is the largest, taking up the greater part of the length of the cord in the third segment, and having a great number of nerve-cells. Between all the ganglia in the intersegmental regions of the anterior segments the component parts of the cord separate as already mentioned; between the third and fourth ganglia this is hardly perceptible, and from this point backwards to the tail region the two portions of the cord are in close union, with the exception of a small area near the end.

The fourth ganglion is the largest of all, and occupies the middle of the generative segment. The fifth is in the middle of the caudal segment. The position of these ganglia can be

seen from the reconstructions shown in figs. 15, 21, and 28. In these figures the nervous system is seen from the ventral side. The outlines of the cord and ganglia have been measured from the nerve-cells, as far as these could be roughly differentiated from the surrounding tissues.¹ From fig. 15 it will be seen that the main mass of the fourth ganglion lies just in front of the penis, but many of its cells extend backwards in the region dorsal to the penis. Here they would almost seem to form a second division of the ganglion. I have not attempted to determine its structure, which differs considerably from that of the other ganglia, on account of the great size of its lateral parts. A few of its cells are distributed on the penis sheath. Past the fourth ganglion the cord diminishes rapidly, but enlarges again rather suddenly in the interior part of the caudal region. It is the second in this segment that is the largest. In the posterior region the cord divides to run into the posterior feet. At this point a number of nerve-cells are arranged, forming quite a mass. It is difficult to decide whether each of these ganglia is to be considered as representing a segment. If so, then there are three main ganglia in the segment itself, and counting the mass of cells at the termination of the cord, it would be composed of four segments. Foettinger came to the conclusion that it was one segment, formed by the partial fusion of three metameres.

In the female there are a number of differences in the configuration of the nervous system, due to the somewhat different size of the segments as compared with the male. This is most pronounced in the generative region. The absence in the female of the penis and accessory glands results in the almost complete disappearance of the cord and ganglia in the posterior part of the generative region, and throughout this portion of the body the cord and its ganglia are much less prominent than in the male. In the absence of the penis the cord retains its ventral position. In the caudal region, on

¹ In the reconstruction of the male nervous system shown in fig. 15 no allowance has been made for the dorsal curvature of the cord in the generative region.

the contrary, the cord and ganglia are much the same as in the male (fig. 15).

In *Stratiodrillus* the cord and ganglia are much the same as in *Histriobdella*. In the male the fourth ganglion is opposite the claspers. After this the cord is very much reduced where it passes dorsalwards over the penis. In *Histriobdella* this reduction is not so marked. In the caudal region also the ganglia are smaller. Haswell remarks, regarding the nervous system of the caudal region of *Stratiodrillus*, that "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" (p. 315). The nerve-cells are arranged on the ventral surface of the cord, and the lateral ganglia are much better developed in *Histriobdella*, especially those of the generative region. They send fibres into the cirri. The second ganglion would seem to be double.

Haswell has drawn attention to the fact that the nervous system in *Stratiodrillus* does not show the complete union with the body-wall tissues as does that of *Histriobdella*. I think, however, no great importance can be attached to this point. The separation shown by the nervous system in *Stratiodrillus* is due in great part to the thinness of the body-wall as compared with *Histriobdella*, and not to a more highly differentiated condition of the system itself.

It is of considerable interest to compare the nervous system of *Histriobdella* with that of the Archiannelid it resembles most, that is, *Dinophilus*. From the study of a species closely allied to *D. gyrotilatus*, Nelson (25) has determined the main structure of the central nervous system in considerable detail. In the first place there is a marked separation of the two parts of the ventral nerve-cord in the intersegmental regions, much more so than in *Histriobdella*. Unlike *Histriobdella* they do not unite to form the ganglia, but are joined by commissures, the two portions of cord remaining separated throughout their course. There

are four well-marked ganglia corresponding to the four main segments of the trunk. In addition to this, there are a few cells that probably form a fifth, corresponding with the somewhat reduced caudal segment. If we compare the reconstruction figure he gives of the nervous system with that of either the male or female *Histriobdella* given in the present paper, it will be seen that, with the exception of this greater separation of the cords, there is a remarkable resemblance in the general configuration of the nervous system of the two forms. The brain and the œsophageal commissures are much the same. In transverse sections the cords hold similar positions in the ectoderm. The ventral sinus found in the brain of *Histriobdella*, it would seem, is also present in *Dinophilus* as a small closed cavity in the brain substance itself.

In minor histological details they bear a striking resemblance to one another. The brain is clothed dorsally and laterally with a mass of nerve-cells, having the peculiar granular nuclei so characteristic of these cells in *Histriobdella*. They are similarly differentiated from the supporting tissue cells. The circum-œsophageal commissures are better developed, however, in *Dinophilus*, and pass backwards round the œsophagus just below the dorsal longitudinal muscle-strands. The centre of the brain is composed of a mass of clear fibrillar material that stains with difficulty. As in *Histriobdella*, fibres are given off by the œsophageal commissures at the point where these leave the brain. They are much bigger in the case of *Dinophilus*, and are more easily traced through consecutive sections. In *Histriobdella* there are no pre-oral commissures, and the ganglia are more circumscribed and definite than in *Dinophilus*.

As compared with the nervous system of *Protodrilus* there is a greater difference than in the case of *Dinophilus*. This is due to the lack of ganglia on the ventral cord. In *Protodrilus* the ventral cord shows no ganglionic divisions corresponding to the external segmentation. This is very

slight, being shown only by the ciliated rings. Internally it is better marked by the dissepiments and the nephridia. The two halves of the cord remain separate throughout their course, uniting at their ends in a small ganglion. Such a nervous system can hardly be compared with that of *Histriobdella*.

According to Pierantoni (26), the nerve-cells in *Protodrilus* are equally as difficult to distinguish from the surrounding tissues as in *Histriobdella*. While retaining their primitive position in the ectoderm, they send fibrils to the tentacles and the digestive system. In the ventral cord there would seem to be no localisation whatever of the nerve-cells corresponding to the segmentation.

8. SENSE-ORGANS.

Among the sense-organs of *Histriobdella* are to be classed the five tentacles of the head and the palps of the posterior legs. All these receive nerve-fibres from the central nervous system, and are armed with short, stiff, sensory hairs. The most essential of the tentacles appears to be the median one of the head. In the larva this is the first to appear, and its nerve supply in the adult would seem to be greater than that of the others. In addition to the tentacles, scattered over the cuticle of the body are a number of cells of a sensory nature that stain readily with methylene blue.

On the dorsal lateral parts of the head are the sensory pits described by Foettinger. These, as already mentioned, are very small, and placed a short distance in front of the anterior feet. Foettinger has sought to compare them with the ciliated grooves of *Archiannelids*. They measure about 14μ in their longest diameter, and are oval in outline. They are therefore much smaller than the long grooves of *Protodrilus* and *Polygordius*. In the bottom of the pit are placed a few fine sensory hairs. As described by Foettinger, the anterior edge of the pit is developed into a slight lip or ridge that is capable of being folded completely over the pit and of

obliterating it. From the way in which this lip is protruded and the pit opened when the animal is feeling its way or examining any small object it may come across in crawling on the bottom of a watch-glass, it is evident that the pit functions in some way as an organ of taste or smell. It appears to receive a set of nerve-fibres from the brain. There is no doubt that these pits correspond to the ciliated pits of the Archiannelids, despite their small size. They are present in both sexes. According to Haswell they are not present in *Stratiodrillus*.

9. THE REPRODUCTIVE SYSTEM.

The reproductive organs in the male consist of a testis, paired in its anterior part, two vesiculæ seminales, two vasa deferentia, and a median penis. Dorsal to each vesicle is the so-called granule gland (fig. 11). In relation with the penis there is a gland of unknown function, as in *Stratiodrillus*.

In the female the organs consist of a large sac or ovary filling the whole of the generative region. On its ventral surface this is furnished with a paired oviduct, armed with a large funnel, the dorsal lip of which only is ciliated. On the course of the oviducts and close to their external openings are the ampullæ or shell-glands.

A. In the Male.

The testis in the male when fully developed fills the anterior and middle third of the generative region. Its extreme anterior end is separated into a right and left portion, its middle portion is fused in the median line. Behind it ends somewhat abruptly in front of the penis. The remaining posterior third of the generative region is taken up with the penis and its accessory glands. This portion is sharply divided from the anterior two thirds by the limiting membrane of the testis. This fact has not been clearly shown by Foettinger. He seems to have overlooked the well-defined

nature of the limiting membrane, and fails to show the sharp manner in which the testis is shut off from the general blasto-coelic cavity surrounding the gut. He states that the testis takes up the whole of the generative region, which is not the case, for the penis and its glands take up the posterior third as I have mentioned. The anterior paired portion of the testis is shown in section in fig. 39, while the main unpaired portion is shown in section in fig. 35. Internally the testis is filled with a number of oval bodies, the spermatidia (figs. 27 and 35). These consist of a number of nuclei with granular chromatin, arranged round the circumference of a small mass of cytoplasm. In the region close to the anterior end of the testis they form a solid mass, while in the middle they crowd its cavity as a number of oval bodies. The mature spermatozoa are found in the spaces of the testis cavity between them.

If we regard the generative region as due to the fusion of two segments, then this conclusion is supported by the arrangement of the nephridia and the ganglia. The testis itself takes up the first and largest of these, while the penis and accessory glands take up the second. The division between the testis and penis portion comes at just that point we should naturally conclude that it should from the position of the ganglia.

In the female the double nature of the generative region is not so clear as in the male, and the metamerism is masked by the extensive prolongation backwards of the ovarian sac. In the young female, however, the ovary is confined to the anterior two-thirds. The double nature of the generative region then is almost as distinct in the female as in the male.

The vesiculæ seminales are found in the posterior part of the testis, and are pear-shaped bodies with their pointed ends directed forwards. They are readily recognised on account of the large quantities of sperm with which they are always crowded. Leading into the lateral surface of each vesicle is a fine duct from the granule gland.

These are a mass of large mucus-like cells that lie against the inner surface of the cuticle of the body-wall of the generative region. They secrete a granular mucous substance which

they discharge into the vesiculæ. Each gland is composed of about twenty cells, arranged in a single layer, laterally, against the wall of the segment. They fill up the greater part of the middle third of the region. They commence anteriorly, just behind the orifice of the retracted claspers, and stretch back to a point, on a line behind the vesiculæ on either side. Dorso-ventrally they extend from the border of the dorsal longitudinal muscles round the sides of the segment to the border of the ventral bands. Their cells have a waxy appearance, and their cytoplasm, which is relatively large in amount, is very finely granular. Each cell possesses a round nucleus and a dark karyosome. On a line with the vesiculæ the dorsal cell of each group gives off a fine duct, that crosses the space of the testis cavity and runs into the ventral external surface of the vesicle of the same side. The wall of this tube is also, like the protoplasm of the cells of the gland, finely granular. About its middle there are usually two large nuclei embedded in the wall. Where the tube runs round the outer surface of the vesiculæ it is much thickened, and this appears to be due to the accumulation of drops of the gland secretion in its lumen (fig. 31).

The vesiculæ are roundish bodies with thin walls. The lateral and ventral third of their cavities is taken up with the mucous secretion derived from the granule glands. This, in sections of fixed material, projects upwards into the cavity in a mass of finger-like digitations. On the outer ventral surface of each vesicula there is a small slit. Its edges are armed with short stout cilia. It was the motion of these that Foettinger evidently mistook for the presence of a pair of excretory organs in this region. Through this slit the spermatozoa gain an entrance into the vesiculæ.

The vas deferens leads out from the posterior ventral portion of each vesicle and turns in towards the median line, and is continued as a small tube to the base of the penis. It is of considerable diameter, and forms a sac-like canal on either side. At the base of the penis the vasa deferentia of both sides meet, forming a small receptaculum seminis,

which lies between the two lateral halves of the organ. During life this is always full of very actively moving spermatozoa.

The penis is a firm, semi-solid, pear-shaped body, the pointed end being directed backwards. It is always carried retracted within the sheath. Unlike *Stratioidrilus*, it is not composed of black chitinous material similar to that of the jaws, but of some transparent substance, sufficiently rigid, however, to enable its being driven through the firm cuticle of the female in the act of copulation. It is protruded through the quadrilateral-shaped mouth of the penis-sheath by the action of the strong protractor muscles. The organ itself is composed of two lateral blades, the spermatozoa being ejected through the median canal between them during copulation.

In relation with the dorsal surface of the penis on either side, and taking up the lateral posterior corners of the generative region, are the so-called accessory glands of the penis (figs. 11 and 40). These are large vacuolated groups of cells forming oval masses running up to the dorsal surface on either side of the gut. From each gland a small duct leads down to the penis, and is inserted laterally about its middle. This opens into the canal on the penis on its ventral side. The gland-cells are divided into an anterior and posterior group. In horizontal sections the gland appears as a four-lobed structure, posterior and dorsal to the base of the penis. The anterior and smaller of these groups is composed of numerous cells, while the posterior, although larger, consists of fewer cells. The cytoplasm is granular and very vacuolar. This is shown in fig. 40, where their anterior ends come in the section on either side of the gut. In transverse section the gland will be seen to be composed of two groups of cells, one of which is much smaller and more dorsal than the other. This is wedged in against the gut on either side. Towards the posterior region of the gland the cells are somewhat larger. The largest of these contains a vacuole of considerable size. This probably acts as a receptacle for

the gland secretion. It is connected with the penis by a strand of cytoplasm that runs to its ventral side, and is continuous across the median line with a strand from a similar cell from the opposite side. Posterior and ventral to this are a number of small, darkly staining cells. They are lenticular in shape, with prominent nuclei. They fill up the corners between the large cells. The largest cell of the gland is placed about the middle or slightly towards its posterior end. The section shown in fig. 24 passes just behind its posterior border. The nuclei of the smaller cells are rod-shaped, and frequently bent in a semi-circular form. On the inner wall of the gland, close to where it abuts against the penis-sheath, are a number of darkly staining masses of nuclear material. The ends of all the gland-cells converge on the penis. When the cells are charged with secretion their nuclei are seen to be large and round, with a well-marked karyotheca. The karyoplasm is collected into a darkly staining karyosome. In the cells that have discharged their secretion, on the other hand, the nuclei are invariably long and rod-shaped, with a uniformly staining karyoplasm, and no karyosome.

In fig. 23 are represented some of the cells of the posterior group under high magnification. The cytoplasm forms a superficial layer which throws threads across the vacuolar interior of the cell. The nucleus is always situated about the middle of the cell and is of considerable size, and contains a darkly staining karyosome.

The compartment of the generative region holding the glands is sharply separated from the anterior part of the segment, which contains the testis, as already explained. This is clearly separated from the granule cells and the vesiculæ, which are within the limits of the testis proper, and enclosed by its membrane.

The region of the accessory gland is often seen distended with the accumulation of secretion within the gland. With dark ground illumination this appears opaque and whitish in colour. In the surface view of a living preparation the two

portions of the gland appear somewhat as shown in fig. 11. The anterior lobe seems distinctly separated from the posterior. The function of these glands is problematical. They doubtless pour some secretion into the canal of the penis during copulation, which assists in this act in some way.

They were first described by Haswell in *Stratiodrillus*, where they are much larger and somewhat different in appearance from those in *Histriobdella*. They seem to have been overlooked by Foettinger, although he plainly figures them in his sections. He evidently mistook them for a portion of the testis. That they are separate structures from this can be easily seen in horizontal sections. They correspond to the similar glands found in connection with the male organs in so many *Turbellaria*, as in *Proxenetes*, *Provortex*, and *Plagiostoma*.

Under the heading of the male reproductive organs come the claspers. These are usually carried retracted, only being protruded when the males are impregnating the females. Under the action of strong reagents during fixation they are sometimes extended, in which case they are always seen projecting ventralwards and never laterally. Each clasper is furnished with a protractor and a retractor muscle that runs to the base of the penis, as already explained. At the base of each organ there is a large mucous cell with a large nucleus. This, in the retracted condition, occupies the anterior wall of the clasper-sheath, and is a conspicuous feature in a transverse section through the anterior region of the generative segment. In a full-grown male the cell is very large. A fine duct leads from it to the tip of the organ and pours some adhesive secretion on the surface of the clasper, similar to that poured on the surface of the feet. This cell is shown in fig. 2. The anterior lip of the orifice formed by the retraction of the organ forms a marked projection which overlaps the orifice (fig. 13). When the organ is extended this lip is obliterated, as shown in fig. 9. The gland cell then occupies the middle of the clasper. At the top of the organ there are a few short, stiff hairs. I have already mentioned that once

the male has seized the female by means of the claspers its grip is immediately rendered secure by the gland secretion, and then the male is only able to free itself from the female with difficulty. Sometimes the male can be seen being carried about by the female, making violent efforts to free itself. The claspers never seem to be used for any other purpose than that of seizing the female, and are never extended to enable the animal to hold more securely when an attempt is made to brush them off the lobster ova.

B. In the Female.

The ovary in the female holds the same position in the generative region as the testis in the male. It has a more sac-like appearance, however, and its lining membrane is thicker than in the case of the testis. In the anterior and posterior regions of the segment there is not the great thickening of the wall seen in the male. It is more uniform in thickness, and the contour of the limiting membrane throughout more distinct. In sagittal sections in the median line it appears as a long chamber lying ventral to the gut (fig. 22).

Foettinger's account of the oviduct and funnel is correct, the funnel being large and collapsible, ciliated on its dorsal side only. It projects downwards into the ventral region of the middle third of the generative segment. Its ventral lip is a short distance from the nerve-cord on either side; its dorsal lip is the longest, and almost meets that of the opposite side in the median line. The funnel is composed of a large number of flattened cells, a conspicuous one being usually seen in the edge of the dorsal lip. The cilia are remarkably stiff and short. It leads into a small, round ampulla which is usually crowded with spermatozoa. This leads into a still larger one, the walls of which are drawn out in a number of digitations. This functions as a sort of shell-gland. Its lumen is filled with a granular secretion that forms the egg-capsule. A short canal leads from the second

ampulla to the exterior. When the ovary is full of ova it is sometimes difficult to see the funnel and oviduct, as its lumen is obliterated by compression against the body-wall.

The inner surface of the ovary is closely invested with a thin layer of nucleated cells—the true coelomic epithelium. It is from this in the anterior region that the primitive ova arise. This takes place close to where the sac abuts against the end of the third segment. Here certain of the nuclei are much larger than the rest. They are the oögonial cells. They have relatively little cytoplasm and large, transparent nuclei. A considerable number of them are seen at this point in different stages of development. The fact that the oögonia arise from a small, circumscribed portion of the anterior end of the ovary, and not from its epithelial surface in general, recalls the condition described by Nelson (25) in *Dinophilus conklini*, which differs from the other species of this group, *D. vorticoides*, *D. tæniatus*, and *D. gigas*, in that only a small portion of the ovary likewise gives rise to the oögonial cells. It is evident that the epithelium of the middle and posterior portions of the ovarian cavity play no part in their formation. As they pass backwards and become the primary oöcytes, the epithelium of this part of the cavity throws out processes that attach themselves to the growing oöcytes, folding up round them and forming a supporting matrix crowded with small nuclei. They furnish them with the material for their growth, but beyond this take no part in their formation. As the oöcyte grows these follicle cells diminish rapidly in size, and their nuclei undergo degeneration, becoming long and granular. They appear to have something to do with the formation of the yolk-granules, but how this is accomplished is not plain. These arise in situ, as nothing similar to them can be distinguished in the follicle cells, which are always clear and transparent. At the time of their formation the granules are also clear and transparent, and only acquire their dark appearance after they have been formed some time. For this reason the small oöcytes, although highly granular, are almost as transparent as the

oögonial cells. By the time the oöcytes reach the middle of the generative region they turn dark brown in colour. In a few days they increase greatly in size. Their outline becomes regular, and the superficial layer of their cytoplasm seems to stain much more intensely than the deeper portion. Their nuclei become large, round, and transparent, and are readily distinguishable in the living animal. There appears to be no yolk-nucleus present, but the germinal nucleus goes through a number of changes during the formation of the deutoplasm, that probably has to do with the great elaboration of this material.

The mature eggs are found in the posterior region, where they take up the greater part of the ovarian chamber. They measure from 80–200 μ in their longest diameter, according to the size of the female. They are oval in shape and somewhat flattened. They are highly granular, the granules being very uniform in size.

Unlike *Stratioidrilus*, there may be a number of ripe eggs within the chamber at one time, although one usually predominates in size over the others. In the violent movements of the animal small fragments of the egg are sometimes broken off by compression against the gut, or from friction against the other eggs of the cavity. These are seen to move about the cavity quite freely, and, by some peculiar cohesive process, are capable of joining up with the egg again. This can be seen taking place under the microscope. The fragments have a membrane of their own, and may be seen lying against the egg from which they have separated. The membrane between them breaks down, and they flow together rapidly.

Normally the ripe ovum is almost divided in two portions by its compression against the gut. When a ripe ovum is discharged its place is immediately taken by the next in size. I have never actually observed the female in the act of depositing her eggs; as I have mentioned, this takes place usually at night. From the fact that the funnel in the female is well forward at the generative region and the ripe ova are

sometimes far back at the caudal end of the ovary, they have to move some considerable distance forward before they can find exit through the oviducts. In passing through the second ampulla the egg is surrounded by its capsule, which binds it firmly to the membranes of the lobster's ova, or the hairs of the carapace surface of the branchial chamber.

I have already drawn attention to the fact that the oöcyte commences to prepare for the first maturation division and the extrusion of the polar bodies when it has acquired only a portion of its yolk material. It is noteworthy that only one of the oöcytes undergoes this change at a time. It is the most advanced and the largest. While the amphiaster is seen in this egg, I have never observed it in any of the younger ones, although some of these to all external appearances are as large and as mature as the one in which it has appeared.

As the oöcyte prepares for maturation its staining reaction changes. Up till this time the superficial layer of its cytoplasm stains darkly, while the deeper portions surrounding the nucleus do not take the stain. With the appearance of the maturation spindle the staining reaction of the cytoplasm becomes uniform throughout the cell.

The first sign of approaching maturation is announced by the changes undergone by the nucleus. It is distinguishable in the living egg as a clear spot in the middle of the dark granular cytoplasm. By a number of changes, which I have not followed in detail, the chromosomes form, the germinal vesicle breaks down, and the amphiaster of the first polar body forms. This at the moment it appears is very small, but grows rapidly with the growth of the egg. From the time it appears to the time it reaches its full dimensions it at least trebles its length, while the egg grows considerably in size. From measurements made of the length of the central spindle, from centrosome to centrosome, and the diameter of the egg in its longest axis, it was found that from the time the central spindle was clearly visible to the time it ceased to grow it trebled its length, while the egg a little more than doubled

its longest diameter. The spindle seems to grow with the egg. The size of the amphiaser is always proportional to that of the ovum. In the large female, where the eggs are almost double the size of those of the small ones, the spindle is correspondingly larger. The size of the spindle is apparently determined by that of the cell.

In *Limulus*, according to Munson (23), the growing centre of the egg is the vitaline body. This, in the early stages, presents all the appearances and features of the centrosome and sphere, and, in fact, is the centrosome of the dividing oögonia. In later stages it remains as the definite centrosome in the cytoplasm. Thus it appears as the primitive basis or centre of growth of the cytoplasm, building this in part from the granules supplied by the follicle-cells. In *Histriobdella* growth does not seem confined to the region near the amphiasers, but seems to take place generally throughout the cytoplasm of the egg. No yolk-nucleus or vitaline body is present. In sections of fixed eggs the cytoplasmic material in the immediate vicinity of the spindle is markedly less dense than in the peripheral region of the ovum. In some sections the middle of the ovum appears as a space, in the middle of which is the spindle with its chromosomes.

The ovum goes through a portion of maturation during the time it is still adding material to its cytoplasm. While the achromatic threads of the amphiaser can be readily seen in the living egg, the chromosomes cannot be detected without staining. At the end of the prophase eight chromosomes are found in the equatorial plate of the spindle.

The astral rays are much less definite than the strands of the central spindle. While the former seem in the living egg as if due to the arrangement of the yolk-granules in definite lines, the latter appear as actual threads running between the granules themselves. In speaking of the astral rays Wilson (32) says: "A careful study of their relation to the meshwork in the Echinoderm, and in many other forms (especially in *Nereis*, *Thalassema*, *Lamellidoris*, and *Asterias*), leaves no doubt in my opinion that they are actual

fibrillæ, that thread their way among the crowded alveolar spheres. In my best preparations the astral rays appear like wires bending to and fro among the alveoli" (p. 13). "From a study of *Toxopneustes* one would be led to the conclusion that they arise in rows of granules or microsomes, held together by the continuous substance" (p. 15). These words exactly describe the appearance of the astral rays in the living egg of *Histriobdella*.

Towards the centre of the astral figures the rays appear as continuous fibres, while peripherally they break up into rows of granules. I believe in both the asters and the central spindle the granules do not build up the achromatic figure, but are merely incidental to it. This is borne out by the fact that they are less numerous within it than in the surrounding cytoplasm. For this reason the area of the amphiaser in the living egg is always the most transparent. The archoplasm can be distinctly seen as a clear substance running between the microsomes.

The less dense nature of the astral rays, as compared with the fibres of the spindle, has been clearly demonstrated recently by Lillie (19) on centrifugalised eggs, where the egg-granules are readily driven through the substance of the astral rays, while they are stopped and forced to go round that of the spindle.

The chromosomes in *Histriobdella* are arranged round the periphery of the equatorial plate. Each chromosome lies directly against one of the spindle-fibres. These run from one centrosome to the other without any break in their continuity. It is obvious that the chromosomes have no proper mantle-fibres, and that the number of fibres composing the spindle is in excess of that of the chromosomes. In sections the number of fibres can be counted. There are twenty, while there are only eight chromosomes.

The centrosome itself is not distinguishable as a distinct point or granule in the living egg, but its position is indicated by a small area where the fibres of the astral rays and those of the spindle all converge on one another. No sphere can be distinguished.

In the early stages, during the formation of the central spindle, its fibres in part appear to arise outside the area of the nucleus. In one instance I was able to distinguish the spindle-fibres beyond the still evident remains of the nuclear wall. The centrosome clearly arises beyond the limits of the nucleus, and from the reticulum of the cytoplasm, and its presence can be clearly detected before the dissolution of the nuclear wall.

Much has been written on the origin of the spindle and the centrosomes as to whether they are of nuclear or cytoplasmic origin. It has been established that the spindle-fibres may arise from either. In the case of the mantle-fibres they arise almost invariably from the nucleus, while the spindle substance proper arises from the cytoplasm, as has been shown by Meves (22) in *Salamandra*, Calkins (3) and Ishikawa (17) in *Noctiluca*, Flemming and Heidenhain (14) in leucocytes. In cases where no central spindle is present the astral rays seem to arise from the cytoplasm, as in a number of plants, some worms, as *Thalassema*, according to Griffin (11), and in a number of Annelids as described by Mead (21). In other cases from the nucleus, according to Flemming (7), Rückert (27), Wilson (33), and Korschelt (18).

According to Watase (31) the centre of the aster is merely the point where the greatest number of cytoplasmic filaments meet, the centrosome thus produced giving rise in turn to the spindle filaments. Thus the spindle-fibres originate from the centre of the aster, and not from the nucleus. This is clearly shown in the case he instances of the blastomeres of *Loligo*, where the nucleus remains a clear area in the middle of the central spindle. There is a short period in the formation of the spindle in *Histiobdella* when almost the same conditions are shown. Again, the observations on eggs that have been artificially fertilised by salt solutions clearly point to the origin of the spindle quite independent of the nucleus. According to Wilson (34) all degrees exist between the asters that lie remote from the nucleus and of undoubted cytoplasmic origin, and those close beside it.

When the amphiaster attains the prophase, it remains in this stage until the egg is fertilised and deposited in the sea-water. If this does not take place, or if the conditions for egg-laying are unfavourable, it apparently remains in this state indefinitely, not making any further progress.

In one instance I was able to keep a large female under observation for the greater part of a week with the amphiaster of its largest egg in the prophase. At the end of this time the fibres of the central spindle and the astral rays were as distinct as at first, and showed no evidence of dissolution. It is evidently contact with the sea-water that is necessary to cause the completion of maturation and the extrusion of the polar body.

The spindle is of considerable size, measuring from 50–60 μ from centrosome to centrosome. It can be readily seen in the living egg with the aid of a good hand-lens. As the animal moves and the egg outline is changed by compression against the body-wall, it does not change the position of its main axis with regard to that of the egg. According to Hertwig's well-known law, as the result of the interaction of the nucleus and protoplasm the spindle comes to lie in such a position that its longitudinal axis corresponds with the axis that passes through the greatest protoplasmic mass. In figs. 18–20 are shown the position of the amphiasters in the egg as it has undergone change. The axis of the spindle, it will be seen, does not always correspond with that of the main axis of the egg, but on the whole it lies very close to this, and the cytoplasm always shows a tendency to group itself symmetrically about the spindle. I have made a number of observations that seemed to show that the form of the egg does not greatly affect the direction of the spindle-axis.

In fig. 32 is shown the egg when it has undergone considerable pressure in its long axis through contraction of the animal. The spindle shows no appreciable shortening as the result of this pressure. In fig. 18 the egg shows the commencement of two furrows running into the cytoplasm, due to compression against the gut. In fig. 32 a small portion

has been broken off the posterior end. This subsequently joined up with the egg again.

No polar body is given off by the egg while it remains within the cavity of the ovary. I have had a female under observation for several days, and have been able to follow the growth and maturation of a particular egg from the first without seeing the formation of any polar body taking place.

I have mentioned that the male is often seen to fertilise the female while she is without eggs and still immature and in the larval state. In these females the sperm can be seen working their way through the tissues and finally collecting in the oviduct. I believe this invariably takes place. Whether the sperm, once in the oviducts, retain their vitality till the female reaches maturity and bears eggs I have been unable to determine. It would seem that it is immaterial whether this does or does not take place. The female is usually fertilised over and over again before she reaches maturity and bears eggs, so that fertilisation is probably effected by the last supply of sperm she may happen to receive. It is clear that the presence or absence of ova in the female play no part as a factor in fertilisation.

No matter where the sperm are injected into the body of the female—and the male exercises no choice in this respect—they seem to collect ultimately in the ampullæ of the oviducts. It would seem as if some substance in this situation exerted a chemotactic influence over their movements, causing them to collect here from all parts of the body.

The sperm are frequently seen in the blastocœlic cavity in small masses beneath the gut. In this situation they are still shut off from the cavity of the ovary and the eggs.

In the anterior end of the ovary, crowded among the small oögonial cells, are frequently seen small masses of sperm. These appear to have undergone considerable change and to have partially lost their tails. It is probable that these sperm have gained access to the ovary by way of the oviducts. It is remarkable, however, that in the posterior region of the ovarian cavity no sperm are seen free among the ova, but they

would seem to be confined to its anterior region. Fertilisation takes place within the ovarian chamber, as a large oblong sperm-nucleus is always found in the ovarian egg, in which the amphiaster has appeared. This always lies at some distance from the spindle and close to the egg-membrane, while the spindle is centrally placed. I have been unable to determine at just what stage in the growth of the ovarian egg fertilisation takes place. As the egg is seen to increase considerably in size after the amphiaster has appeared, and as the sperm nucleus is always found in the ovum when this is present, it is possible that the egg is fertilised at a stage in which the yolk-granules are first beginning to appear. The fusion of the pro-nuclei takes place only after the polar body is extruded, and this takes place when the egg has been deposited in the sea-water.

In *Stratiodrillus* Haswell has observed the fertilisation of the egg taking place within the ovarian cavity.

In *Dinophilus tæniatus*, according to Harmer (12), the same conditions hold regarding impregnation and fertilisation as in *Histriobdella*. The penis is inserted anywhere under the skin, the act of copulation taking place repeatedly with the same female. He says, "the act of copulation has no relation to the maturity of the ova of the female, nor is it prevented by the fact that the female has already received an ample supply of spermatozoa by a preceding operation" (p. 13). The spermatozoa can be seen collected in small masses beneath the gut. Fertilisation is therefore internal. The polar bodies are given off apparently when the eggs reach the exterior, or shortly after they are deposited in the sea-water.

In the ripe egg, after the amphiaster of the first polar body has been formed in this manner, a remarkable occurrence can be brought about, which demonstrates most clearly the semi-solid nature of the spindle itself. In compressing the cover-glass on a preparation of a living parasite I happened in several instances to rupture the body-wall in the vicinity of the ovum. The egg-envelope was also broken

at the same point. The yolk-granules then rapidly poured through the opening into the sea-water, and carried the amphiaster with them. It held together as a semi-solid body, and could be seen turning over and over as it was pushed along by the granules. Once in the water outside the body the granules tended to disperse, while the amphiaster remained with its immediate surrounding granules, apparently a solid body. It remained like this for several minutes until it finally dissolved and disintegrated. I have tried to represent this taking place in fig. 8. The asters go first, while the central spindle still remains intact. This seems to show that the substance of the spindle is of firmer texture than that of the asters and centrosphere; and this is borne out, as I have mentioned, by the actual appearance of the archoplasmic substance of the asters as compared with the sharp, definite structure of the spindle. The yolk-granules adhere and seem almost a part of the archoplasmic substance of both asters and spindle, the amphiaster really appearing as a mass of brown yolk-granules held together by the thread-like archoplasmic substance. As the spindle begins to dissolve the yolk-granules can be seen being liberated from the transparent substance of the archoplasm and moving away in the sea-water. In fact the whole process of the dissolution of the amphiaster, as seen under an oil-immersion lens, is similar to that of some gelatinous substance slowly dissolved by the action of sea-water. That the spindle has some considerable rigidity is borne out by the fact that it keeps its shape, and can be seen rolling over and over as it is drawn along in the sea-water. It shows no tendency at first to flatten under the pressure of the cover-glass. This is always considerable, although its corners are supported as much as possible by wax feet, as the capillary attraction invariably draws the cover-glass down somewhat in the middle. It is not till the spindle has begun to dissolve that this rigidity is lost, when it undergoes flattening. It at the same time becomes more transparent, the archoplasmic threads appearing as if actually undergoing dissolution by the sea-water, leaving the dark

yolk-granules behind them arranged in positions that had previously been held by the archoplasm. There is a short period during which the spindle almost remains alone, the asters having completely disappeared from either end. It is at this time that the spindle can be seen to roll over as it is pushed farther and farther away from the point of rupture in the body-wall by the escape from the egg of fresh cytoplasm.

In a number of experiments I subsequently ascertained that this rupture of the egg and extrusion of the spindle will not occur if the egg is far back in the body-cavity. The body-wall ruptures at its thinnest part, which is well forward in the generative region. If the egg has to move forward some considerable distance under pressure, before it can begin to flow through the rupture the amphiaser is usually broken and destroyed. It takes place most satisfactorily when the egg is only a short distance from the point of rupture of the body-wall. It can only be observed to occur when the amphiaser itself is fully mature. When not fully formed it dissolves immediately any movement of the yolk-granules takes place. Unless, moreover, the rupture in the body-wall is fairly large, the amphiaser is usually broken in the act of being forced through, being destroyed by the granules pushing it through from behind.

In one instance the central spindle had the appearance of being composed of a mass of distinct threads, some of which on one side of the spindle had been injured and broken, the yolk-granules appearing as small grains entangled in these fibres.

I think this observation clearly demonstrates the truth of a suggestion that has been put forward, that the achromatic threads and amphiasers are firm structures, or at least more rigid than the reticulum of the cytoplasm. Gardiner (10), in his paper on the egg of *Polychærus caudatus*, states (p. 89), "That the amphiaser is much more rigid than the surrounding cytoplasm is shown by two instructive preparations which were the result of accident. Ova containing

amphiasters in the stage now under discussion were ruptured just before the worm containing them was placed in Hermann's fluid. The cytoplasm had flowed or been pressed out of the ovum, carrying with it the amphiaster. In both cases the cytoplasmic network had been completely bent and twisted into a confused snarl. The achromatic rays were somewhat, but not nearly so much distorted, but the centrospheres were almost unchanged. From this I infer that the amphiaster and the rays are, on the whole, much more rigid than the cytoplasmic network or the cytoplasm from which they are formed." Evidently the same thing took place in this instance as I have observed in *Histriobdella*, where the large size of the spindle and the granular nature of the egg renders the various steps in the process clearly visible under the microscope.

By pricking the egg-membrane of *Allolobophora*, Foot and Strobell (9) have been able to get the egg contents on the slide, and there photograph it after fixation. "By this method the germinal vesicle, and sometimes even the spindle, flow out of the egg-membrane intact" (p. 201). Some excellent photographs are shown of these in figs. 125-130 of this paper. In *Allolobophora*, as in *Histriobdella*, the early stages of the first maturation division are gone through by the egg while it is still within the receptacula ovarum.

10. CONCLUSION AND SUMMARY.

Harmer (12) was the first to point out that *Histriobdella* was more closely related to *Dinophilus* than to any other Archiannelid, although Pierantoni (26), in his recent monograph, has placed *Histriobdella* and *Dinophilus* as an appendix to the Polygordidæ (including *Protodrilus*). Schimkewitsch (28) has contended that *Dinophilus* is closely related to the Rotifers, and Haswell (13) has put forward a similar claim for *Histriobdella*. In *Histriobdella* it is certain that the parasitic mode of life has resulted in a peculiar specialisation, which, combined with its direct mode

of development, renders its relationship hard to determine, and hides the primitive characteristics of its organisation. That the Rotifers themselves are likewise a highly specialised class of somewhat uncertain affinities is an opinion that is gaining ground, since so much doubt has been thrown on their supposed relation to the Annelid trochophore. The work of Wesenberg-Lund (20) has shown that the most simple and trochophore-like of the Rotifers are probably the most highly specialised and the farthest removed from the Annelids. Yet the clearly segmented plan of both *Dinophilus* and *Histriobdella*, it must be admitted, is essentially similar to that of a Chætopod. This, combined with the clearly Polychæt nature of egg-segmentation in *Dinophilus*, is sufficient to place these forms in direct connection with the Annelids, quite apart from either *Protodrilus* or *Polygordius*.

Under the heading of the various organs I have already gone into a more or less detailed comparison of *Histriobdella* with *Dinophilus*, so that it is only necessary to review the subject here from a more general standpoint. In both forms the animal consists of a distinct head and trunk, the latter composed of relatively few segments. In both the nervous system consists of a well-defined brain or neuropile, and a double ventral nerve-cord, with metamerically arranged ganglia. In *Dinophilus* these are formed by transverse commissures, while in *Histriobdella* the two parts of the cord unite directly to form the ganglia. The external segmentation corresponds with that of the nervous system. *Dinophilus* does not possess the feet, cirri, or tentacles that so clearly mark segmentation in *Histriobdella*. But the metamerism is less definitely shown by the ciliated bands, mucus glands, and the ring-like constriction of the body into a series of segments. On the other hand the nephridia show a more metamerically placed arrangement than they do in *Histriobdella*. In both (with the exception of *Stratiodrillus*) the nephridia open to the exterior in the segment following that in which they arise, as in Annelids. In *Histriobdella* the muscular system shows a very high

degree of development, and for this reason can hardly be compared with that of *Dinophilus*; in both, however, the main musculature consists in a series of longitudinal ventro-lateral and dorso-lateral muscles. The alimentary canal shows the same divisions, although differing considerably in the relative proportion of its parts. The strong chitinous jaws are wanting in *Dinophilus*. In each the cavity surrounding the gut is a primitive blastocele with no definite epithelial lining. This cavity sends prolongations into the head. The equivalent of the coelom in both is represented by the cavity of the reproductive glands. In the male these consist of a more or less paired testis, vesiculæ, vas deferens, and median penis, and in the female a large ovarian cavity, paired or unpaired, with oviducts.

With Annelids *Dinophilus* shows a closer relationship than *Histriobdella*, mainly due to its less direct development. In fact the development of *Dinophilus* brings it into line with that large group of animals such as the Polychætæ, Echiuridæ, Gephyrea, Lamellibranchs, and the Gasteropoda, in having the ectoderm arising from the first three quartettes, mesoderm from the left posterior cell of the fourth quartette (4 D.), and the endoderm from the remaining cells. In the derivation of a large part of the ectoderm of the trunk from the posterior cell of the second quartette the resemblance to the Polychæt Annelids is most pronounced. This is further enforced in the origin of the bilateral cleavages in the cross cells and in the products of 2 D. "The transition from the spiral type of cleavage to the more specialised bilateral type occurs in precisely the same directions as in the Polychæts. Moreover the second bilateral divisions of the cells of the posterior arms of the cross continue this resemblance. All these characters, if such they may be called, when viewed as a whole point in no uncertain way to the descent from the Annelid stem, and at a point not far from that at which the Polychæta arose" (Nelson, p. 728).

The weight of our evidence, furnished by recent work on the morphology and embryology of *Dinophilus*, is strongly

in favour, therefore, of a close relationship with Annelids. The general ciliation, the caudal appendage, ciliated rings, nervous system, general configuration of the head, trunk, and alimentary canal are what are found in a number of Annelids, and most clearly in such a form as *Ophyotrocha*. Nelson (25) has even suggested that the pre-oral nerve commissures can be satisfactorily explained by deriving them from the nerve-ring of the Trochopore. He comes to the conclusion: "On the whole, *Dinophilus* can best be considered as a very young Polychæt worm, retaining some of its larval features, with setæ and parapodia undeveloped, and whose peritoneum and cœlom have been transformed into a generative organ" (p. 135).

The relationships of *Histriobdella* to *Polygordius* and *Protodrilus* have been gone into fully by Foettinger (8), Harmer (12), and Haswell (13), so I need not repeat their arguments for this relationship here. It seems to me, from the Archiannelid point of view, it is important to determine what features of *Histriobdella* are primitive, and what have been derived from its peculiar mode of life. Eisig (5) has gone so far as to suggest that in *Histriobdella* we have to do with a highly modified, possibly degenerate animal, and not an Archiannelid at all. If *Histriobdella* is a degenerate form then it must be a degenerate Chætopod as Haswell (13) has pointed out. "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 characters of the segmentation became lost, a special set of locomotor organs with an elaborate musculature became evolved." "This view appears to me to involve difficulties so great that they render the degeneration theory extremely improbable, and it seems to me 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" (p. 327).

Apart from any degeneration I agree with Haswell (13) that the relationship of *Histriobdella* with *Polygordius* "is extremely remote, and not such as to justify their inclusion in the same class." The absence in *Histriobdella* of a blood-vascular system, a distinct prostomium and peristomium, the presence of mouth opening well forward in the head, chitinous jaws, and complicated generative apparatus in the male, paired limbs, and mucous glands, clearly separate it from *Polygordius* and *Protodrilus*, placing it quite apart from these forms. With the Rotifers, on the other hand the relationship is undoubtedly more pronounced. Haswell has pointed out that all the main features of *Histriobdella* can be traced to this class, although in general features the resemblance is greater perhaps with the *Gastrorichia* than with the Rotifers proper. The chitinous jaws of *Histriobdella* can be readily homologised with the mastix of Rotifers. In the absence of solenocytes and the general similarity of the nephridia of *Histriobdella* to the flame-cell type nephridia of Rotifers, we have a further resemblance. In both the cuticle is firm and shows a tendency to contract into ring-like folds. In both, also, the generative organs, especially in the male, can be reduced to the same plan.

In *Paraseison* we have a Rotifer not unlike *Histriobdella* in many of its features. The body is elongated and worm-like, with a distinct head bearing the mouth at its anterior extremity. In the middle of a very rudimentary coronal disc which bears no ciliated apparatus are four small bundles of hairs, placed in two pairs. Behind the mouth are found the orifices of two glands, similar to those found on the anterior feet of *Histriobdella*. On the top of the head is a small tubercle representing the dorsal median tentacle of *Histriobdella*. There is a narrow œsophagus, which leads into a large cylindrical stomach. There is no gut, and the stomach, which is not ciliated, is definitely closed. But this condition has plainly been evolved within the limits of the genus, as it is not characteristic of other Rotifers. It is

noteworthy that *Paraseison*, like *Histriobdella*, is parasitic, being found on the gills of the Crustacean *Nebalia*. It is undoubtedly with such forms as *Paraseison* among the Rotifers that *Histriobdella* must be compared. The greatest objection to the comparison of *Histriobdella* with the Rotifer is encountered in regard to the nervous system. This in *Histriobdella* is already so elaborated, and of that type found among the higher Annelids, as to be hardly comparable to the diffuse, and less differentiated, and centralised system of Rotifers.

I cannot agree with Haswell that Zelinka's (36) discovery of a sub-œsophageal ganglion in *Callidina* and *Discopus* renders this comparison more easy. A further difficulty is found in the absence of any true metamerism in the Rotifers. This difficulty is possibly not so great when we consider the arrangement of the transverse muscle-cells in such a rotifer as *Discopus synaptæ*. Leaving aside any comparison, therefore, of the nervous system, it nevertheless remains a fact that *Histriobdella* undoubtedly resembles the Rotifers more closely than any other group of animals.

If *Histriobdella* is related to the Rotifers it becomes necessary to determine the relationship of *Dinophilus* to the same class. Schinkewitsch (28) was the first to point out the similarity of the caudal appendage in *Dinophilus* to the foot of the Rotifer. In *Dinophilus*, as in the Rotifer, this is used in attaching the animal. In both forms there is a marked sexual dimorphism. But as Nelson (25) has pointed out, the caudal appendage in *Dinophilus* resembles more that of some of the polytrochal annelid larvæ than the foot of the Rotatoria, and the sexual dimorphism can have arisen within the genus, as it is found in other groups of the Annelida besides the Rotifers. One striking difference between the Rotifers and *Dinophilus* is the apparent total absence of a definite mesoblast in the Rotifers, while it is clearly present in *Dinophilus*, where it has the same cell-origin as in Polychæts. In Rotifers the mesoblast would seem to be represented by the germ-cells alone, and it is

necessary to suppose that the Rotifers separated from the main stem of the Annelida at a stage earlier than that of the formation of a definite mesoderm, while *Dinophilus* arose only after the cœlo-mesoblast had definitely appeared. On the whole, *Dinophilus* is not so closely allied to the Rotifers as *Histriobdella*. Unfortunately our lack of information with regard to the development of the cœlo-mesoblast in *Histriobdella* prevents our forming any opinion as to how much it resembles the Rotifers in this respect.

It is remarkable with regard to the Rotifers that, despite their wide distribution and their great number of species, so comparatively few marine forms should be known. What has become of these if they have ever existed? Are forms like *Belatro* and *Hemidasys* (Claparède, 4), *Turbanella* (Schultz, 29), or the *Echinoderes* (Zelinka, 37) to be looked upon as the modified descendants of a marine branch of these animals? Here we have a marked metamerism coupled with the main features that characterise both *Histriobdella* and the Rotifers. It is possible that it is with some of these somewhat obscure groups that the relationship of *Histriobdella* really lies.

In conclusion, it may be stated that our present knowledge does not warrant us farther than to conclude that *Histriobdella* is a highly specialised form, retaining many Rotiferan features, and that it is to be grouped with *Dinophilus* as a primitive Annulate, but not directly related to *Polygordius* and *Protodrilus*.

SUMMARY.

(1) *Histriobdella homari* is a normal inhabitant of the branchial chamber of the European lobster. It is found in equal numbers throughout the year, on both the male and female.

(2) The anterior feet of the head, unlike those of *Stratiodrillus*, are non-retractile.

(3) There are four pairs of nephridia in both sexes. They are closed, and are of the primitive flame-cell type similar to

those of Rotifers. Unlike those of *Dinophilus*, they bear no solenocytes.

(4) There is a pair of salivary glands in connection with the mouth.

(5) There are fewer teeth in the jaw-apparatus than Foettinger has represented.

(6) The ventral nerve-cord is composed of two portions, which separate in the intersegmental to unite in the segmental regions, in prominent ganglia. The metamerism of the nervous system corresponds with that of the external form.

(7) In the male there is a complicated generative apparatus. It is similar in all respects to that of the male generative apparatus in *Stratiodrillus*.

(8) Fertilisation takes place internally. The largest egg is usually seen in the prophase stage of the first maturation division. The amphiaser and the spindle can be seen to pass out through the body-wall with the cytoplasm, when the egg is ruptured by pressure. It remains for some seconds intact in the sea-water surrounded with yolk-granules.

(9) In the equatorial plate there are eight chromosomes in the first maturation division.

(10) *Histriobdella* is to be placed close to *Dinophilus*. It retains many Rotiferan features, and is more closely connected with this group than *Dinophilus*. *Histriobdella* and *Dinophilus* show distant relationship with *Polygordius* and *Protodrillus*, but cannot be classed with them as true Archiannelids.

LITERATURE.

1. Van Beneden, J. P.—“Note sur une larve d'annélide d'une forme tout particuliere, rapportée avec doute aux Serpules,” ‘Bull. Acad. Roy. Belgique,’ tome xx, 2nd pte., 1853, p. 69.
2. ——— “Histoire naturelle d'un animal nouveau, désigné sous le nom d'*Histriobdella*,” ‘Bull. Acad. Roy. de Belgique,’ 2nd serie, tome v, 1858, p. 270.

3. Calkins, G. N.—“Mitosis in *Notiluca miliaris* and its Bearing on the Nuclear Relations of the Protozoa and Metazoa,” ‘Journ. of Morph.,’ vol. xv, 1899, p. 711.
4. Claparède, E.—“Observations sur les Rotateurs,” ‘Annals de Sci. Nat. Zool.,’ V ser., t. viii, 1867, p. 5.
5. Eisig, H.—“Die Entwicklungsgeschichte der Capitelliden,” ‘Mitt. a. d. Zool. Stat. Neapel,’ Bd. xiii, 1898, p. 1.
6. Flemming, W.—‘Zellsubstance Kern, und Zellteilung,’ Leipzig, 1882.
7. ——— “Zur Mechanik der Zelltheilung,” ‘Arch. f. Mik. Anat.,’ vol. xlv, 1895, p. 696.
8. Foettinger, A.—“Recherches sur l’organisation de *Histriobdella homari*,” ‘Arch. de Biol.,’ vol. v, 1884, p. 435.
9. Foot, K., and Strobell, E. C.—“Prophases and Metaphase of the First Maturation Spindle of *Allolobophora fætida*,” ‘Amer. Journ. Anat.,’ vol. iv, 1905, p. 199.
10. Gardiner, E. G.—“The Growth of the Ovum, Formation of the Polar Bodies, and the Fertilisation in *Polychærus caudatus*,” ‘Journ. of Morph.,’ vol. xv, 1898, p. 73.
11. Griffin, B. B.—“Studies on the Maturation, Fertilisation, and Cleavage of *Thalassema* and *Zirphæa*,” ‘Journ. of Morph.,’ vol. xv, 1899, p. 583.
12. Harmer, S. F.—“Notes on the Anatomy of *Dinophilus*,” ‘Journ. of Marine Biol. Assoc.,’ N.S., vol. i, 1889, p. 1.
13. Haswell, William A.—“On a New *Histriobdellid*,” ‘Quart. Journ. Micr. Sci.,’ vol. 43, 1900, p. 299.
14. Heidenhain, M.—“Neue Untersuchungen über die Centralkörper und ihre Beziehungen zum Kern und Zellenprotoplasma,” ‘Arch. f. Mik. Anat.,’ Bd. xliii, 1894, p. 423.
15. Hempelmann, F.—“Zur Morphologie von *Polygordius lacteus* Schn. und *P. triestinus*,” ‘Zeit. f. wiss. Zool.,’ vol. lxxxiv, 1906, p. 527.
16. Hermann, F.—“Beitrag zur Lehre von der Entstehung der karyokinetischen Spindel,” ‘Arch. f. Mik. Anat.,’ Bd. xxxvii, 1891, p. 569.
17. Ishikawa, C.—“Studies on Reproductive Elements: II, *Notiluca miliaris*,” ‘Journ. Coll. Sci. Imp. Univ. Japan,’ vol. vi, 1894, p. 297.
18. Korschelt, E.—“Ueber Kernteilung, Eireifung und Befruchtung bei *Ophryotrocha puerilis*,” ‘Zeit. Wiss. Zool.,’ Bd. lx, 1895, p. 543.

19. Lillie, Frank B.—“Karyokinetic Figures of Centrifuged Eggs,” ‘Biological Bull.,’ vol. xvii, 1909, p. 101.
20. Lund, C. Wesenberg.—“Danmarks Rotifera: I, Grundtraekkene i Rotiferernes Okologi,” ‘Morfologi og Systemstik,’ Kobenhavn, 1899.
21. Mead, A. D.—“The Origin of the Egg Centrosomes,” ‘Journ. of Morph.,’ vol. xii, 1897, p. 391.
22. Meves, F.—“Über eine Metamorphose der Attractionsphäre in den Spermatogonien von Salamandra maculosa,” ‘Arch. f. Mik. Anat.,’ Bd. xlv, 1894, p. 119.
23. Munson, J. P.—“The Ovarian Egg of Limulus: A Contribution to the Problem of the Centrosome and Yolk Nucleus,” ‘Journ. of Morph.,’ vol. xv, 1898, p. 111.
24. Nelson, J. A.—“The Early Development of Dinophilus,” ‘Proc. Acad. Nat. Sci. Phil.,’ 1904, p. 687.
25. ———— “The Morphology of Dinophilus Conklini n. sp.,” ‘Proc. Acad. Nat. Sci. Phil.,’ 1907, p. 82.
26. Pierantoni, U.—“Protodrilus,” ‘Fauna und Flora des Golfes von Naple,’ 31 Monographie, 1908.
27. Rückert, J.—“Zur Eireifung bei Copopoden,” ‘Anat. Heft,’ Bd. iv, 1894, p. 261.
28. Schimkewitsch, W.—“Zur Kenntniss des Baues und der Entwicklung des Dinophilus vom Weissen Meere,” ‘Zeit. f. Wiss. Zool.,’ Bd. lix, 1895, p. 46.
29. Schultze, M.—“Über Chætonotus und Ichthydium Ehrb. und eine neue verwandte Gattung Turbanella,” ‘Arch. f. Anat. u. Phys.,’ Jahrg. 1853, p. 241.
30. Shearer, C.—“On the Structure of the Nephridia of Dinophilus,” ‘Quart. Journ. Micr. Sci.,’ vol. 50, 1906, p. 517.
31. Watasé, S.—“Homology of the Centrosome,” ‘Journ. of Morph.,’ vol. viii, 1893, p. 433.
32. Wilson, E. B.—“On Protoplasmic Structure in the Eggs of Echinoderms and some other Animals,” ‘Journ. of Morph.,’ vol. xv (Suppl.), 1899, p. 1.
33. ———— ‘The Cell,’ New York, 1900.
34. ———— “Experimental Studies in Cytology: I,” ‘Arch. f. Entwickl.,’ vol. xii, 1901, p. 529.

35. Zelinka, C.—“Die Gastrotrichen,” ‘Zeit. f. Wiss. Zool.,’ Bd. xlix, 1890, p. 209.
36. ——— “Studien über Raderthiere,” ‘Zeit. f. Wiss. Zool.,’ xliv, p. 396, Bd. xlvii, p. 353, Bd. liii, p. 1, 1885–1892.
37. ——— “Über Echinoderes,” ‘Verh. d. deutschen Zool. Gesell.,’ 4th Jahressam., 1894, p. 46.

EXPLANATION OF PLATES 17—20.

Illustrating Mr. Cresswell Shearer’s paper “On the Anatomy of *Histriobdella Homari*.”

LETTERING.

ac. Accessory glands of the male reproductive apparatus. *an.* Anal aperture. *ap. p.* Appendage of the posterior leg. *blc.* Blastocœlic cavity. *bl. m.* Muscular organs of jaws. *br.* Bridle piece of jaws. *brn.* brain. *cd. g. 1–cd. g. 3.* Ganglia of the caudal region. *cl.* Clasper. *cl. p.* Ciliated pit of the head. *cœ.* Cœlom. *cœ. ep.* Cœlomic epithelium. *com.* Nerve commissures. *f.* Fulcrum of jaws. *fol.* Follicle cells. *fgl.* Flagella of the nephridial canals. *g. 1–g. 5.* Ganglia of the ventral nerve-cord. *gl. cl.* Gland-cell of clasper. *gr. g.* Granule gland. *int.* Intestine. *int. 2.* Intestine, posterior part. *j.* Jaws. *j. 1.* Upper ramus of jaws. *j. 2.* Lower ramus of jaws. *l. a.* Anterior legs or feet. *l. p.* Posterior legs. *m.* Mouth. *m. d.* Dorsal longitudinal muscles. *m. d. p.* Median duct of the penis. *m. gl.* Salivary glands of the mouth. *m. ob.* Oblique muscles. *m. v.* Ventral longitudinal muscles. *n. c.* Ventral nerve-cord. *neph. 1–neph. 4.* Nephridia. *neph. c.* Nephridial canals. *neph. h.* Head of the nephridium. *neph. o.* Opening of the nephridial canal on the external surface. *neph. s.* Spaces on the course of the nephridial canals. *æs.* Œsophagus. *o. im.* Immature ova. *or. p.* Orifice of the penis sheath. *ov.* Ovary. *ovd.* Oviduct. *p.* Penis. *r.* Ramus of upper jaw. *sprn.* Spermatidia. *spc.* Spermatocyte. *st.* Stomach. *t. 1.* Median tentacle. *t. 2* and *t. 3.* Lateral tentacles. *te.* Testis. *th.* Teeth. *v. def.* Vas deferens. *ves.* Vesicula seminalis. *vn. c.* Ventral nerve-cord. *vit.* Vitellarium or shell-gland.

PLATE 17.

Fig. 1.—Female *Histriobdella* with eggs. The largest egg shows the presence of a maturation amphiaser $\times 300$.

Fig. 2.—Clasper extended.

Fig. 3.—Third and fourth nephridium in the female. This and all the subsequent figures of the nephridia have been drawn from living preparations impregnated with methyl-blue; 2 mm. oil-imm., comp. ocs. 4 and 6. $\times 500$ and $\times 1000$.

Fig. 4.—Third nephridium in the male.

Fig. 5.—Third nephridium in the male.

Fig. 6.—Second nephridium in the male.

Fig. 7.—Male *Histriobdella* with claspers retracted. $\times 300$.

PLATE 18.

Fig. 8.—Rupture of an egg through the body-wall in a living preparation by compression of the cover-glass. The first maturation amphiaser is seen outside the body-wall in the sea-water. $\times 300$.

Fig. 9.—Male with claspers extended. $\times 300$.

Fig. 10.—Third and fourth nephridium in the male. $\times 800$.

Fig. 11.—Generative segment in the male. Taken from a living preparation, showing the reproductive organs.

Fig. 12.—Fourth nephridium in the male. $\times 800$.

Fig. 13.—Fourth nephridium in the male. Segment contracted. $\times 800$.

Fig. 14.—Second nephridium in the female. $\times 800$.

PLATE 19.

Fig. 15.—Reconstruction of the nervous system in the male, showing the dorsal curve taken by the ventral nerve-cord in the region of the penis. Lateral view. $\times 300$.

Fig. 16.—Young in egg-capsule.

Fig. 17.—Young in egg-capsule. Earlier stage than that shown in fig. 16.

Fig. 18.—Oöcyte with first maturation amphiaser. This, with the subsequent figures, 19, 20, 26, and 32, are all drawn from the same egg-cell. They show the changes of shape assumed by the egg in the movements of the animal. They were drawn at intervals of from ten to twenty minutes.

Fig. 19.—Oöcyte, same as that shown in fig. 18, drawn twenty minutes later.

Fig. 20.—Oöcyte, same as that of fig. 19, fifteen minutes later.

Fig. 21.—Reconstruction of the nervous system in the female. The brain surface is measured from the ganglion cells and not from the fibrous core. Ventral view. $\times 300$.

Fig. 22.—Sagittal section in the female showing the sac-like nature of the ovarian cavity.

Fig. 23.—A cell of the accessory gland of the male.

Fig. 24.—Transverse section in the male in the region of the penis. $\times 400$.

Fig. 25.—Eggs attached to the membranes of the lobster "berry."

Fig. 26.—Oöcyte twenty minutes after that shown in fig. 20.

Fig. 27.—Spermatidia.

Fig. 28.—Reconstruction of the nervous system of the male. Ventral view. $\times 300$.

Fig. 29.—Longitudinal section of the wall of the intestine in the posterior region.

Fig. 30.—Young, a short time after hatching. $\times 300$.

Fig. 31.—Section through the generative region in the male showing the granule glands.

Fig. 32.—Oöcyte twenty minutes later than fig. 26.

PLATE 20.

Fig. 33.—Transverse section in the male through the region of the vesiculæ seminales.

Fig. 34.—The same. In a region a little posterior to the last.

Fig. 35.—Transverse section through the middle of the generative region in the male.

Fig. 36.—Chitinous jaws.

Fig. 37.—Horizontal section in the male.

Fig. 38.—Transverse section through the middle of the second segment.

Fig. 39.—Transverse section through the anterior region of the generative segment in the male, showing the divided nature of the anterior portion of the testis.

Fig. 40.—Transverse section through the posterior region of the generative segment in the male.

Fig. 41.—Transverse section through the dorsal region of the body-wall in the caudal segment, showing the insertion of the oblique muscle-fibres.

Fig. 42.—Horizontal section through the region of the first segment in the male, showing the head of the first nephridium.

Fig. 43.—Transverse section through the neck region.

Fig. 44.—Transverse section through the caudal region, showing the oblique muscles.



Shearer, Cresswell. 1910. "Memoirs: On the Anatomy of Histriobdella Homari." *Quarterly journal of microscopical science* 55, 287–359.

View This Item Online: <https://www.biodiversitylibrary.org/item/49303>

Permalink: <https://www.biodiversitylibrary.org/partpdf/201121>

Holding Institution

American Museum of Natural History Library

Sponsored by

Biodiversity Heritage Library

Copyright & Reuse

Copyright Status: Public domain. The BHL considers that this work is no longer under copyright protection.

Rights: <https://www.biodiversitylibrary.org/permissions/>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.