

# The Larvæ of *Polydora ciliata* Johnston and *Polydora hoplura* Claparède.

By

Douglas P. Wilson, B.Sc.,

Student Probationer at the Plymouth Laboratory.

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 With 7 Plates and 4 Figures in the Text.
 

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### I. INTRODUCTION.

THERE are numerous descriptions and figures of *Polydora* larvæ scattered through the literature dealing with Polychætes, but only in one instance, that of Leschke, has a series of reared larvæ from the egg to metamorphosis been illustrated and described. Most other workers have contented themselves with describing odd larvæ caught in the plankton, a procedure which involves grave doubts as to the species. Leschke's work on *P. ciliata*, though good on the whole, is not free from error on minor points, and his drawings are few in number and rather sketchy. It is hoped therefore that this new description of the larval development of *P. ciliata*, and that of *P. hoplura* which, so far as I am aware, is here described for

the first time, will prove of interest and value, although only the external characters are dealt with.

My best thanks are due to Dr. Allen for his helpful interest in this work, to Dr. Orton for several useful suggestions, and to the Staff generally for assistance in various matters.

## 2. METHODS.

I am indebted to Dr. Orton for the original suggestion that I might obtain the larvæ of *Polydora ciliata* Johnston from the tubes of the parents which bore in large numbers into the shells of oysters. The oysters were obtained from the estuary of the River Yealm, the soft parts removed, and the shells broken up into bits, which were examined under a lens. The shell splits between its layers, and as the burrows of the worm generally run more or less in the plane of the layers they are easily exposed along their whole lengths. It was easy to see which worms had spawned and had egg-sacs attached to the walls of their tubes, and these were then removed with the aid of a fine brush to dishes of fresh sea-water. In every case the adult was removed along with the egg-sacs and its species carefully checked. Egg-sacs obtained without the adult were rejected.

The larvæ were reared in dishes and in plunger-jars. It was found most satisfactory to use water which had been obtained from outside the Breakwater and passed through a Berkefeld filter. Nitzschia, from a culture kindly supplied by Dr. Allen, was added to this water and on this the larvæ fed. It was found important not to allow too vigorous a growth of diatoms as they then adhered to the spines of the larvæ, frequently causing the latter to stick to the glass, where they perished. Large numbers were lost in this way, and only after several trials was success obtained.

*Polydora hophura* Clap. is also found in Yealm oyster shells, although in much fewer numbers, and its larvæ were obtained and dealt with in a similar way to those of *P. ciliata*.

Larvæ were examined alive in cavity slips and all the drawings (except those of the modified chætæ of the fifth segment) were made from living active specimens able to move about freely in the cavities. This was possible on account of their tendency to head-up against the edge of the cavity on the side nearest the light and so remain in approximately the same place and position for a short time before swimming away again. While doing this all the cilia beat actively and the whole body is in a tense state of vibration and every few seconds wriggles vigorously. During the periods of comparative quietude measurements were made with a squared-net micrometer in the eyepiece, and the form of the

larva gradually built up on squared paper. The outline was then transferred to smooth white paper or bristol-board, worked up in pencil, and subsequently inked in. The original larva of each drawing, as well as others, was fixed and mounted and the drawing, as far as was possible, checked from it.

### 3. THE DEVELOPMENT OF *POLYDORA CILIATA* JOHNSTON.

#### (a) *Development within the Egg-sacs.*

A few individuals spawn in January, and worms with larvæ can be found up to about the end of October, but the spawning season appears to be at its height about March. The eggs are laid in sacs of a very thin transparent membrane, and each sac is attached to the wall of the burrow by two filaments, and is fused with its neighbour at either end so that the series forms a long string (see Text-Fig. 1). The eggs are not spawned freely to drift about on the sea-bottom as described by Leschke. It is difficult to remove an entire string without damage, but the number of sacs present in any one string appears to be about 15-20. The sacs are flattened against the outer wall of the U-shaped burrow to allow room for the worm which lies internal to them, apparently with its back against them. This can clearly be seen when an infected shell is fixed in Bouin and the calcareous matter dissolved away with acid. It is difficult to estimate exactly the number of eggs in each sac, but usually there appear to be 15-20, sometimes more, sometimes a few less. Söderström (16, p. 185) gives 70-80 as the number in each sac, but I have not seen one which approached anywhere near that figure. The number of larvæ in a complete string of sacs will thus be about three or four hundred.

Exactly how these sacs are formed is unknown. They have been specially studied in this and other Spionids by Söderström (16), who thinks that they are secreted by the nephridia through which the eggs are probably discharged.

The eggs are opaque and densely granular with yolk; by reflected light they have a pale pinkish-yellow hue. They are said to develop rapidly (Leschke, 10), but as I have been unsuccessful in keeping them alive in dishes I am unable to give times for the earliest stages. A very early stage is shown in Fig. 1, Plate I, in what is presumably lateral view. It is still very dense, and little structure can be made out. The posterior end is more transparent than the rest of the body, and there is here a broad tract of short cilia with a large dorsal gap. Anteriorly there is another broad tract of short cilia, very difficult to see, which seems to have two gaps, one dorsal and the other ventral. Possibly these are the first signs of the telotroch and prototroch respectively. It was drawn thirty-six hours after removal from the tube of the adult.

A later stage is shown in dorsal and ventral view (Plate I, Figs.

2 and 3), and several structures are now marked out. The central mass indicating the gut is still very dense and granular, but the surrounding tissues are more transparent. The larva is well rounded dorsally, less so ventrally, and the head region forms a sort of anterior ridge. The lateral eyes have appeared, the first signs of the future mouth and vestibule are seen, and the chætæ in the first pair of chæta-sacs are forming. The prototroch is formed by a single row of cilia on each side of the head. The telotroch is a single row of rather longer and stronger cilia forming a partial ring which does not extend on to the dorsal surface. Just posterior to the prototroch on the ventral surface there is on each side a finely ciliated swelling. The larva can bend its body slightly (as drawn), but it scarcely moves about yet.



TEXT-FIG. 1. Portion of a chain of egg-sacs of *Polydora ciliata* Johnston. Larvæ in process of liberation. Sketch from life.  $\times 65$ .

About twenty-four hours later the appearance is as indicated in Fig. 4, Plate I. The three primary pairs of provisional bristles are projecting from well-marked chæta-sacs and the head has undergone a big transformation. The ventral surface of the head is almost flat. In the centre the vestibule\* is forming and is well ciliated around its edges and on its roof. The gut is still very granular, and brownish by reflected light. The median pair of eyes has appeared and the eye-like chromatophore (see below) is forming. The prototroch and telotroch are as in the last stage, but stronger. The finely ciliated swellings form curious ciliated plates nearer to the middle line. The function of these remains problematical;

they disappear immediately after this stage. In one specimen I was watching they suddenly came off and stuck to the cover glass, where they disintegrated, and their owner swam away without them.

A day later the typical *Polydora* larva shape is reached (Plate I, Fig. 5). The body and the bristles are longer, and the gut, although still very

\* This could be called a mouth, but as its limits are later obscured by the development and ciliation of the cheeks Gravelly's term "vestibule," given to the fully-formed structure, is probably better, the mouth being regarded as the anterior opening of the oesophagus.

granular, has now a lumen. In addition to the prototroch and telotroch, a nototroch has appeared on the third chætigerous segment. A ventral view of the head (Plate II, Fig. 1) shows the greatly increased size of the developing vestibule, the sides of which are strongly ciliated and the roof thickly covered with fine cilia. The lateral cheeks are becoming well rounded and pigmented at their corners. The curious sensory cilia (see p. 572) are growing out. The larva is very active, and swims and wriggles about among the other larvæ in the same egg-sac.

A day or so later the larvæ are liberated into the sea and their general appearance about that time is indicated in Fig. 6, Plate I. The gut is no longer granular and is ciliated internally. The whole larva is very transparent; there is yellowish tinting on head and body and brownish pigment around the anus. The gut is greenish yellow, and is the predominating colour of the larva. The eyes are jet-black. There are two pairs of eyes, a median pair of approximately circular ones and a lateral pair situated more ventrally. The latter are roughly kidney-shape, but the shape varies considerably. I have not been able to detect a lens in these eyes, as described by Leschke. Just above the inner border of each of the lateral eyes there lies the main body of a black chromatophore whose ramifications extend over the eye region. The shape of this chromatophore is exceedingly variable, and its main body has generally been regarded as a third eye by previous workers. The ventral view of the head is similar to that drawn for a slightly later stage (Plate III, Figs. 1 and 2), and is described below (see p. 572). There are three pairs of bristle bundles. The first pair are the longest, and there are about eighteen bristles in each bundle, about nine in each of the second pair, and about six in each of the last pair. Under a high power the bristles are seen to be very finely barbed along one side. There is a sensory cilium on each side of the anus.

In order to determine the stage at which the larvæ are liberated naturally, the shells from four well-infected oysters were placed in a large dish of sea-water. During the next three days larvæ were continually being given off, and as these always collected towards the surface in the corner of the dish nearest to the light they were easily removed, at intervals, with a pipette. All the larvæ so obtained were at approximately the stage just described (Plate I, Fig. 6), some being a little earlier, with the gut still slightly granular, others a little later, with the first dorsal black pigment band (see below) appearing. No earlier and no later stages than these were found. It must be noted in connection with this experiment that although I have broken up a large number of oyster shells from the Yealm estuary and examined hundreds of *Polydora* I have only found the two species, *P. ciliata* and *P. hoplura*, boring in them. At the time of the experiment (early March) the latter species had not begun

to spawn, and their larvæ in any case are easily distinguishable from those of *P. ciliata*. Text-Fig. 1 shows three egg-sacs, from two of which larvæ are escaping through ruptures in the wall, although the latter may have been caused during the removal of the sacs from the tube of the parent. One of these larvæ is drawn in Plate I, Fig. 6. It is interesting to note that once the egg-sacs have been removed to a dish enclosed larvæ do not appear able to escape, their spines stick through the membranous wall and they perish.

(b) *Structures associated with the Head.*

Attention was first called to the complex vestibule associated with the mouth in these and other Spionid larvæ by Gravely (7), who described and figured that of an advanced larva of his *Polydora* A. He also discussed its probable development, basing his conclusions in part on a figure of a trochophore which had been supposed by Claparède to be that of *Leucodora*, but which was most probably that of *Sabellaria* (see p. 587).

The early development of the vestibule in *P. ciliata* has already been noted in this paper. Commencing as quite a small hollow or opening, it rapidly enlarged backwards and deepened upwards until the condition was reached which is indicated in Fig. 1, Plate II. The steep and deep side walls are thickly covered with cilia and the roof with finer cilia. The opening can be closed by the meeting of the side "cheeks" in the middle line. Shortly after liberation, and at a stage in which the dorsal black pigment spots on the third chætigerous segment have appeared, the partially open vestibule has reached the condition represented in Fig. 1, Plate III. It has deepened still further backwards, and has also extended more forwards, and the cheeks on either side form prominent swollen pads, which, meeting in the middle line, completely close it in. The prototroch extends as a paired row of cilia running downwards and backwards over these cheeks until it meets the outermost of the strong cilia which clothe the sides of the vestibule. The latter are much more numerous than it has been possible to indicate in the figure. Anteriorly the vestibule shallows until its ciliated roof meets the ventral surface of the anterior part of the head. This part of the ventral surface immediately anterior to the vestibule appears to be exceedingly finely ciliated. Posteriorly the vestibule deepens and leads, through what is probably the true mouth, into the gut. On the fold of skin which forms the posterior ventral border of the vestibule is a patch of fine cilia, supposed by Gravely to represent a neurotroch. Fig. 2, Plate III, shows the vestibule wide open, in which condition it forms a kind of funnel directed forwards and rather downwards, through which food particles are swept as the larva swims through the water.

The head is beset with several curious stiff, strong, apparently sensory

cilia. On each side there are two very conspicuous ones just anterior to the prototroch and one strong one about the level of the lateral eye. Smaller ones occur ventral to the lateral eye region, at the anterior corners of the head, and just by the anterior end of the vestibule. The latter project inwards towards one another. On the dorsal surface there is a sensory cilium a little anterior and lateral to each median eye. Just in front of this I have, in this species, detected another very much smaller cilium (not shown in the drawings), and there may possibly be one or two other small ones elsewhere on the head which have so far eluded observation owing to the difficulty of seeing them. At the anterior extremity of the head there is a tuft of very fine cilia.

The sensory cilia, especially the three largest pairs, are usually held projecting stiffly outwards, but every now and then they bend back and beat among the prototroch. Leschke (10) appears to have observed one or two of these cilia, but Gravely apparently overlooked them, probably because they are much smaller in proportion to the size of the head, and hence less conspicuous, in the later stages he examined.

The vestibule remains more or less in the condition just described throughout larval life, but during the later stages it is rather more funnel-shaped (see Plate III, Fig. 3, and p. 574).

(c) *Development in the Plankton.*

Shortly after liberation at the stage figured in Fig. 6, Plate I, black pigment in the form of two spots, often coalesced to form an irregular band, appears on the anterior part of the third chætigerous segment in front of the nototroch. About the same time a nototroch begins to appear on the developing fourth segment, and by the second day after liberation two spots of black pigment appear in front of it also. A few days later the fourth pair of chætæ are prominent, and the fifth segment is forming (Plate I, Fig. 7). As new segments appear, in front of the telotroch, each acquires in order a nototroch, black pigment and chætæ. Fig. 2, Plate II, shows the general appearance about ten days after liberation. The dorsal parapodial lobes are now forming and are most prominent on the third and fourth chætigerous segments. There is a good deal of brown pigment in the region of the anus. A week or so later the larva is much more massive than formerly (Plate II, Fig. 3), the dorsal parapodial lobes are well developed, except that those on the second segment are not quite as far advanced as those on the following segments. At the end of each lobe are a few fine sensory cilia and one much stouter cilium; the latter are shown in the drawing of this and later stages. The black pigment now forms a double row of spots down the back. Gastrotrochs are present on the third, fifth, and seventh chætigerous segments; their cilia are longer and stronger than those of the nototrochs.

Fig. 4, Plate III, is a lateral view of a larva about a month after liberation, and several important points are to be noted. The developing tentacles form prominent swellings posterior to the prototroch and to the outside of the anterior pair of chaeta-sacs. The ventral lobes of the parapodia have appeared and chaetae of the ventral bundles are growing out. The modified chaetae of the fifth segment can now be seen, but this segment still carries dorsal bundles of provisional bristles. A black pigment spot, which was also present at somewhat earlier stages, is seen near the base of the second parapodium. At the corner of each cheek there is a very dark brown, almost black, pigment mass. This patch of pigment has been present all through the pelagic stages, but in many specimens it is light brown in colour, and in a few is absent altogether. Gastrotrochs are present on segments 7 and 10, and one is just appearing on segment 13. In some cases they are present also on segments 3 and 5. The oesophagus now reaches back to the hinder end of the third chaetigerous segment before it passes into the stomach. It is strongly ciliated.

About two weeks later, nearly six weeks after liberation, the larvae reach the stage drawn in dorsal and lateral views on Plate IV. The larva is now at the height of its larval development and is worth describing in some detail. Since the last stage a great increase in bulk has taken place. There are nineteen chaetigerous segments with well-defined boundaries and a large anal segment bearing the telotroch. The head carries a pair of long wrinkled tentacles which have wide shallow, densely ciliated grooves down their anterior ventral borders. From behind the eyes, the lateral pair of which are in a more anterior position than formerly, a high mid-dorsal ridge arises and runs back as far as the anterior border of the second segment. A slight groove runs longitudinally along each side of this ridge at the base. From close to the base of each tentacle a slight backward fold of skin forms a posteriorly projecting ridge which, running transversely inwards, meets the longitudinal groove on the corresponding side of the mid-dorsal ridge at right angles. Along each of these transverse ridges there is a row of rather long, fine, rapidly beating cilia which give a flickering appearance to this region. Gravely's figure (7, Plate 14, Fig. 2) of this region of his *Polydora A* is thus incorrect, unless this species differs markedly from *P. ciliata*, a supposition which is very unlikely. Ventrally the vestibule (Plate III, Fig. 3), when widely open, is a well-marked forwardly directed funnel, densely ciliated internally with fine cilia on the roof and longer and stouter cilia on the lateral walls and rim. Gravely figures for his *Polydora A* (7, Plate 14, Fig. 1) a single row of these stout cilia along each margin. In *P. ciliata* they are certainly not arranged in a single row; there are a great many of them on the lateral walls and rim; but whether they are arranged in regular rows or not I have been unable to determine. The prototroch has a wide

dorsal gap and runs round on each side of the head until it is difficult to distinguish from the cilia at the posterior ventral margins of the vestibule. The sensory cilia are as before, but are smaller in proportion to the size of the head. The short neurotroch is present.

The parapodia are well developed, the ventral lobes are present, and there are several chætæ in the ventral bundles. The ventral bundles of the first six segments are composed of sabre-shaped bristles, those of the seventh and succeeding segments carry hooded crochets in addition to these. The actual numbers of these bristles in the ventral bundles are correctly illustrated for the specimen from which the drawing on Plate IV was made. With the exception of the fifth segment the dorsal bundles are well provided with long provisional bristles, but among these shorter dorsal bristles of the adult type (about six each in most bundles) have appeared, except on the first segment. The provisional dorsal bristles of the first segment are the longest and number about fifteen in each bundle, those of the following segments about half that number. The ventral lobes of the first pair of parapodia are turned upwards instead of downwards, as are those on the succeeding segments. Colourless branchiæ are present on segments 7 to 12.

The fifth segment is now much modified. The provisional bristles have been lost, while the strong specialised bristles, each, except the first pair, with a strong lateral tooth, are very conspicuous. Four pairs of these project outwards, their curved tips being directed rather upwards and backwards. They are moved about and thrust outwards as the larva wriggles. Behind two other pairs are developing. These strong bristles are accompanied by a few small winged chætæ and by a fairly thick bristle lying between the first and second specialised bristle on each side. Text Fig. 3 shows a group of the specialised bristles from one side of another larva of approximately the same age.

The third and all succeeding segments carry nototrochs. Gastrotrochs are present on segments 3, 5, 7, 10, 13, 15, and 17. Those on 3 and 5 have shorter cilia than the others. There is frequently great irregularity in the development of the gastrotrochs; one larva of twenty chætigerous segments had them developed as follows: None on segments 3 and 5, one on segment 7, partial ones on segments 8 and 9, normal ones on segments 10, 13, and 15, a partial one on segment 16, and fully developed ones on segments 17 and 18. The nototrochs were normal.

The large anal segment carries the powerful telotroch, the cilia of which are longer and stronger than those of the prototroch. The dorsal gap is relatively smaller than before. The presence of this gap was remarked by Gravely (?) to be a characteristic feature of the larvæ of *Spionidæ* and *Polydoridæ*.

The pigmentation is of special interest. The eyes, and the pair of

eye-like chromatophores which ramify around them, are black. The spot at the corner of each cheek is usually very dark brown or black, sometimes it is much paler or absent altogether. There is a patch of irregular black pigment at the anterior base of most of the parapodia (see side view, Plate IV). This is especially well marked anteriorly, where it often appears to coalesce with the dorsal pigment bands. In dorsal view black pigment appears as a series of irregular bars on the anterior borders of segments 3-8, the posterior bars being longest. On segment 9 in place of bars there is a much ramified stellate spot on each side of the middle line, and similar spots occur on all the posterior segments, gradually becoming smaller as they are situated farther back. The ramifications of the spots may extend on to the segment in front. There are a few spots of black pigment on the anal segment.

The irregular anterior bars and the stellate spots are each a single chromatophore. These chromatophores undergo expansion and contraction; they may expand so that almost the whole of the dorsal surface appears to be covered by a very finely ramified net of black pigment, or they may contract to irregular black bars or spots without ramifications. The drawing shows an intermediate condition. The chromatophores of the earlier larvæ also possessed this faculty. It is thus important to note that the shape and degree of ramification of the pigment spots in *Polydora* larvæ form no basis for the discussion of specific differences, although some writers have tended to use them for that purpose. Moreover, the change from bars to stellate spots may not be as sudden as is here illustrated, or it may take place on the segment in front or the segment behind, or the pigmentation may be otherwise irregular, some spots may be missing, or supernumerary ones present.

The general body colour is brownish and the larva is fairly transparent. There are two rings of stippled dark brown pigment on the anal segment, one in front of the telotroch, the other behind. The œsophagus is slightly sinuous and now extends back to about the posterior border of the sixth segment before enlarging to form the "stomach." The gut then gradually narrows to the anus; it is faintly indicated in the dorsal view on Plate IV. The anal segment is notched on the dorsal surface; this is the first indication of the dorsal notch of the future anal cup. On each side of the notch there is a sensory cilium; these cilia have been present throughout the pelagic existence. The ventral surface of the larva is slightly hollowed to form a wide shallow trough.

I have unfortunately been unable to induce my larvæ to metamorphose. Pieces of broken oyster shell were supplied, but none of the larvæ settled down, but died off after growing one or two more segments. Probably metamorphosis is almost identical with that in *P. hoplura*, which is described on page 583.

*(d) Swimming Movements and the Grasping-cilia.*

So far little mention has been made of the movements of the larvæ. They are strongly positively phototropic, and the early stages especially will swim across a dish towards a source of light in an almost straight line. The body is stretched out, the spines closely laid along the sides, and the vestibule usually opened widely. They swim forwards, often on their backs, frequently slowly rotating on their longitudinal axes. Sometimes they swim in circles about one place. When irritated, as when they bump up against some object, the body is rapidly curled round ventrally, bringing the anal segment against the now closed vestibule, the spines at the same time being erected so as to point in all directions. The later stages sometimes swim by lateral wriggles, but they also still swim by means of their cilia with the body stretched out and the spines laid along the sides.

Close inspection of the living larva reveals a most interesting series of cilia in connection with the method of swimming. At each end of every nototroch there is a short longitudinal row of cilia that project outwards. These cilia do not beat regularly along with the other cilia, but have a sort of trembling movement, and always remain more or less curled. Their function is to curl round and take hold of the bristles when the latter are laid along the sides of the body in swimming. So far as I am aware cilia with this function have not been described before, and I therefore propose to call them "grasping-cilia." I first noticed cilia of this kind on the telotroch of *Sabellaria* larvæ (a paper on which will subsequently be published), where they are large and strong, and during swimming are used to grasp the ends of the long provisional chætæ which arise from a pair of large chæta-sacs situated in the head region. They do not occur on the telotroch of *Polydora*, nor in *Sabellaria* on the nototrochs that develop just before metamorphosis.

The presence of these cilia raises anew the old question concerning the function of the long provisional bristles. These bristles have usually had two functions assigned to them, that of suspension organs and that of protection. It is possible that they fulfil both those functions, but in addition another possibility suggests itself. Owing to the manner in which the bristles are laid along the sides of the body, the bundles in front overlapping the bundles behind, and then all these held in by the grasping-cilia curling round them, apparently fairly tightly, an increased rigidity of the whole body must result. This increased rigidity will increase the driving efficiency of the cilia, and of the swimming as a whole. The bristles are also held in to the stream-line with less exertion than would be entailed if the grasping-cilia were absent.

Some, at least, of the bristles always project dorsally beyond the

telotroch, and the tips of those of opposite sides meet or are crossed behind. These bristles pass through the dorsal gap in the telotroch and thus possibly explain the presence of that gap, for even if the telotroch were a complete ring the beating of the most dorsally situated cilia would be hindered or prevented altogether by the presence of the bristles close above them. Gravely (7) has suggested that the dorsal gap in the prototroch is correlated with the ventral gap caused by the presence of the vestibule.

The nototrochs are formed (as they are in the adults) by short rows of cilia placed end to end with slight gaps between them. These gaps are faintly indicated in the drawings, they are rather more conspicuous in *P. hoplura*. The first nototroch in the larvæ just liberated from the egg-sac has two such rows, the latest larva drawn has six in each nototroch. The cilia of each row are longest in the middle and shortest at the ends. The gastrotrochs are formed in a similar manner, and the prototroch and telotroch can also be seen to be formed of rows of cilia placed end to end without gaps between them.

#### 4. THE DEVELOPMENT OF *POLYDORA HOPLURA* CLAPARÈDE.

##### (a) *Development within the Egg-sacs.*

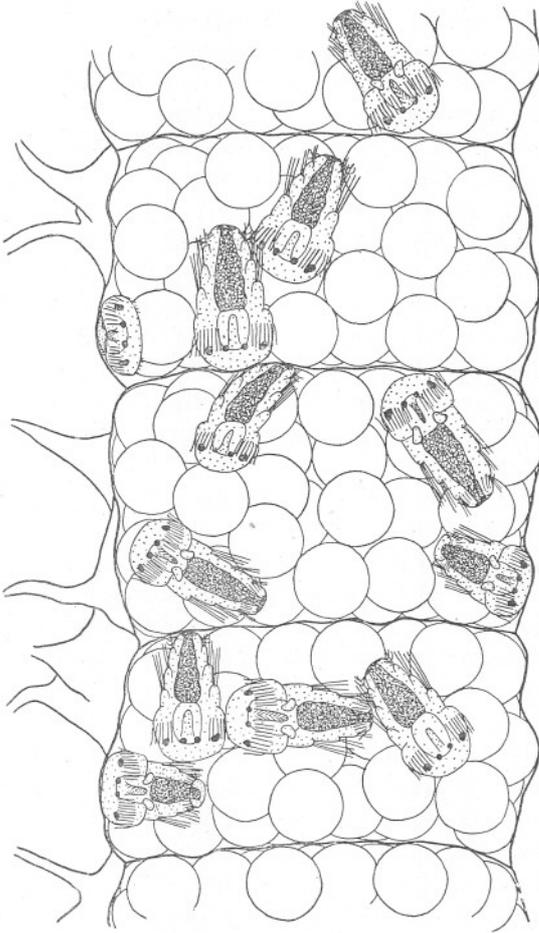
*Polydora hoplura* is a much larger species than the foregoing, and there are never more than a few individuals in any one oyster shell. The breeding season commences much later than in *P. ciliata*, and does not last as long. In oysters from the River Yealm they started to spawn in 1927 about the end of June, and all had finished by the end of October.

The egg-sacs (Text-Fig. 2) are much larger than in *P. ciliata*, and when freshly spawned the contents have a deep bright yellow colour by reflected light. The sacs are similar in structure to those of *P. ciliata*. I have been unable to obtain a complete undamaged string and count the sacs, but they are several times more numerous than in the smaller species; there appear to be about fifty to each individual worm.

The general appearance of the sacs is shown in Text-Fig. 2. In each there are a few larvæ, and what appear at first sight to be a large number of segmenting ova. The latter (Plate V, Fig. 1) are roughly spherical, and are surrounded by a definite membrane, and are very opaque on account of the dense yolk they contain. They are, in fact, yolk masses. When crushed under a cover glass they break up into a great number of oily globules of all sizes. The tight packing of these globules inside the membrane causes them to assume hexagonal and other shapes and to appear at first sight like the cells of a segmenting ovum. Sections have failed to reveal the presence of nuclei in these yolk masses, nor can nuclei be seen in the living ones. The yolk masses always present the same

appearance whatever the stage of the larvæ may be. The larvæ in any one string are always at the same stage.

By carefully slitting open with fine needles and emptying twelve sacs counts varying from thirty-four to ninety-four yolk masses and from one



TEXT-FIG. 2. Portion of a chain of egg-sacs of *Polydora hoplura* Claparède, showing early larvæ and yolk-masses. Sketch from life.  $\times 65$ .

to six larvæ per sac were obtained. These gave an average of sixty yolk masses and three larvæ per sac. All these sacs were from the same portion of a long string.

The yolk masses form the food of the larvæ. Instead of becoming planktonic at a stage with three pairs of bristle-bundles, as in *P. ciliata*,

the larvæ remain within the protecting burrow of the parent amid a plentiful supply of food until a very late stage, thus shortening pelagic life to a few days, possibly to a few hours in some cases.

That the larvæ actually feed on these yolk masses there is no reasonable doubt. Their guts are seen to be full of yolky globules which have exactly the same appearance as those of a crushed yolk mass. The yolk masses, too, are fewer in number the older the larvæ found in a sac, until finally large well-developed larvæ, such as that drawn on Plate VII, are found along with only one or two yolk masses or with none at all.

A similar condition of things has been described by Söderström (16) for *Pygospio elegans*, and he has also found very late larvæ of *Polydora natrix* Söder. in egg-sacs which contained also a mushy mass that he supposed to be their food. Mesnil (12, p. 225) many years ago observed what appears to have been a very similar state of affairs for *Polydora polybranchia*. Mesnil and Caullery (13) have also described an analogous case in *Spio filicornis* O. F. Müller, in which they distinguish two kinds of spawn. One which they call A gives rise to larvæ that become pelagic at a stage with three pairs of bristle-bundles; in the other, which they call B, some of the larvæ feed on undeveloped ova and larvæ arrested in their development.

Although the larvæ of *Polydora hoplura* thus feed on special food material provided for them by their parents they are quite able to lead a pelagic existence, and if removed at the stage with three chætigerous segments can be reared in plunger jars on Nitzschia. Larvæ so reared appear to be identical with those developing in the egg-sacs in the normal way. In the plunger jar they took about six weeks to reach the stage at which they metamorphose. How long they take to develop under normal conditions it has been impossible to determine. Egg-sacs, once they have been removed from the burrows, soon putrify.

In spite of the striking difference in the mode of life the larvæ of *P. hoplura* are similar in all important respects to those of *P. ciliata* and the development follows the same general course. The early larvæ are, however, considerably larger. Fig. 2, Plate V, shows in ventral view an early larva in which the vestibule is forming and in which the pair of problematical ciliated ventral plates are prominent. The sensory cilia and the nototroch on the third chætigerous segment are just appearing, but the prototroch and telotroch with their usual dorsal gaps are well developed. Both pairs of eyes are present. The gut is still very full of granular yolk material. The sensory cilia on each side of the anus are rather long. The larva is quite active, and swims and wriggles among the surrounding yolk masses.

The stage with three chætigerous segments is shown in Fig. 3, Plate V. In all important respects it closely resembles the corresponding stage in

*P. ciliata*, but it is larger, the sensory cilia are more prominent and there is a spot of black pigment on each side between the first and second pair of bristle bundles that did not occur in the smaller species, and the pigment around the anus is also much blacker.

A ventral view of the head of a little older larva is shown in Fig. 1, Plate VI. The vestibule is partially open and its structure is essentially the same as that already described for *P. ciliata*. There is, however, no pigment on the corners of the cheeks and no fine cilia on the ventral surface of the head in front of the vestibule. The sensory cilia are almost the same as in *P. ciliata*, but there are some minor differences in the region ventral to the lateral eyes. These differences are clearly seen when the corresponding drawings are compared.

Development proceeds in all essentials as in the former species. Fig. 4, Plate V, shows a larva with several segments in which the dorsal lobes of the parapodia with their apical sensory cilia are quite distinct. In this species at this stage the lobes of the first and second pair are as distinct as those immediately following. Just behind the eyes, in the dorsal gap of the prototroch, the first signs of the future dorsal ridge and the long fine cilia on each side can be seen. These could also be seen from very early stages in *P. ciliata*, but they were very indistinct and difficult to detect and have not been indicated in the drawings of that species. Gastrotrochs are present on segments 3 and 5. The body is slightly trough-shaped ventrally. Another black spot has appeared on each side of the second chætigerous segment; it is situated below and behind the one present in the last stage and cannot be seen in dorsal view.

A lateral view of the stage in which the tentacles are budding out as small swellings is shown in Fig. 3, Plate VI. This stage is very similar to the corresponding stage in *P. ciliata*, and is about the same size. Some individuals, as is the one drawn, are now actually smaller than corresponding *P. ciliata* larvæ. The ventral lobes and chætæ are appearing on most of the parapodia, but not on the first pair. The two black spots on the side just in front of the second pair distinguish the larva from that of *P. ciliata*, where there is only one. There is also a very dark, almost black, patch of pigment above the anus. An important difference is that there are still no signs of the modified chætæ of the fifth segment, these do not appear until a little later in development, later than they do in *P. ciliata*.

The larva drawn on Plate VII was one of a number found quite free in the tube of the parent, not enclosed in sacs, and no yolk masses were seen with them. Most probably they were just about to be liberated into the plankton. This larva is so similar in its structure to the corresponding stage in *P. ciliata* that a separate description is unnecessary. There is a slight difference in the general appearance, and this is sufficiently indicated in the figure. The fifth segment is not yet much modified, due

to the later appearance of the strong specialised chætæ in this species. Three of these chætæ here project on each side, and a fourth is developing behind them. The first has no lateral spur, the others have two spurs each, a strong one on one side and a smaller one on the other side. Lying between the first and second chætæ there is a fairly thick bristle, and a few winged bristles accompany them. The specialised chætæ of one side of a specimen at a rather earlier stage are shown in Text-Fig. 4. The long provisional dorsal chætæ of the other segments appear to have already started to fall out as there are now only two or three of them in most bundles. Dorsal bristles of the adult type are fairly long and numerous. The ventral bundles are all provided with sabre-shaped chætæ, and the seventh and succeeding segments with hooded crotchets as well. Six pairs of colourless branchiæ, ciliated on their inner surfaces, are present on segments seven to twelve. Pigmentation is very similar to that of *P. ciliata* with the addition of a pair of small lateral spots on the sides of each segment above the parapodia. These spots commence on about the eighth segment. In a side view black pigment on the anterior part of the base of the parapodia, arranged in a similar manner to that in *P. ciliata*, can be seen. Gastrotrochs are present on segments 3, 5, 7, 10, 13, 15, and 17, those on 3 and 5 having the shortest cilia.

The vestibule of this specimen is illustrated in Fig. 2, Plate VI. Its structure is mainly the same as in the other species, but the opening is directed rather more downwards.

In order to determine the stage at which the larvæ are liberated in the normal way, a similar experiment to that performed for *P. ciliata* was carried out for the present species. The shells of two dozen oysters were placed in large glass dishes of sea-water, and in a few hours a good number of larvæ had been given off and had gathered against the glass on the side nearest to the light. While the majority of these were rather earlier than the stage just described, and a few had not yet even started to grow their tentacles, a good proportion of them were quite as advanced. This big variation in the stage at which the larvæ were liberated may have been due to the disturbance involved in the removal of the oysters from their native estuary, or because some broods are possibly not as plentifully supplied with yolk masses as others, and are released as soon as the food-yolk has been all used up. We have seen that the larvæ are quite capable of leading a pelagic existence from very early stages (see p. 580).

#### (b) *Development in the Plankton.*

If the above-mentioned experiment gives a true picture of the normal release of the larvæ, it will be seen that the length of time a larva spends in the plankton will depend on the stage of development at which it is

liberated. In some cases possibly only a few hours elapses before the larvæ settle down and metamorphose, in others probably as long as two weeks is passed in the plankton before the larvæ are ready to infect fresh oysters. Larvæ placed in a plunger-jar and in finger-bowls, and supplied with broken pieces of oyster shell sterilised by boiling, took from a few days to two or three weeks to settle down. But in any case the pelagic life is much shorter than in *P. ciliata*, and the larvæ are protected during the greater part of their development.

(c) *Settling-down and Metamorphosis.*

A few larvæ from the same brood as that drawn on Plate VII were, four days after removal from the burrow of the parent, placed in a shallow dish containing sterilised broken pieces of oyster shell and their movements followed with low powers of the microscope. The larvæ often still swam by means of their cilia and with the body stretched out straight, the spines being laid along the sides and held by the grasping-cilia. On alighting on a piece of shell larvæ would start to crawl about over its surface in the usual Polychæte manner. While thus crawling they adhere very tenaciously, apparently by a secretion of mucus, and are very difficult to dislodge by squirting water at them. They can also cling very firmly to the sides of a pipette. As they wander about, often for comparatively long distances and for a long time, they carry the tentacles stretched obliquely forwards and outwards. They now appear to be no longer affected by light, but should they, as often happens, suddenly take to swimming again, they usually move towards the light. As they crawl about they explore any small hole or cavity they come across, and do not hesitate to crawl in between the overlapping layers of periostracum. Holes and pits do not seem to be explored so much with the tentacles as with the head and lips. If not satisfied they move away again, often crawling backwards for a time.

Only in one case was I able to observe a larva actually settle down. This one came across a small concavity in the chalky layer which was overhung by a projecting shelf of hard shell. After exploring it for several minutes, and once or twice almost crawling away again, it wedged the middle part of its body under the projecting shelf which was too small to cover it completely, and then moved restlessly about, turning round to face the opposite direction several times. Soon it had secreted a quantity of transparent mucus, which more or less covered it up, and in this mucus a number of its longer bristles were lost. At times it appeared to be exerting the region of the fifth segment below the shelf in a position which was out of sight. Occasionally, when it crawled forwards so that this segment could be seen, it pressed the points of the strong modified

bristles against the chalk and jerked them sharply backwards and upwards. It did not however do very much of this, and after about an hour of restless wriggling quieted down. By the next day the mucous coat was a little thicker, and entangled in it were particles of the chalky layer of the shell and other debris. The tentacles had lengthened and become slenderer, and were waved about after the manner of the adult. The fore-part of the body was often stretched well out of one end of the mucous-tube which was still shorter than the body. Four days later the tentacles were still longer, about as long as the worm itself, and the snout had a pronounced forward prolongation. The lateral eyes had been carried forwards and brought closer together, and were much anterior to the median pair. The anal cup was well formed. Eight days after it had first settled down this specimen was removed and carefully examined. In general appearance it resembled the adult except for coloration and in only having 22 segments. It was, however, unmistakably a *P. hoplura*. The forward elongation of the snout, the lengthening of the tentacles, and formation of the anal cup have already been mentioned. The dorsal ridge extended back almost to the posterior border of the second chæti-gerous segment. The sensory cilia had gone, so had the prototroch, telotroch, gastrotrochs, and the nototrochs anterior to the seventh segment as well as those on the most posterior segments. Nototrochs were present only on the middle segments of the body, and were most pronounced on those bearing branchiæ. There were no signs of grasping cilia. The sensory cilia at the ends of the dorsal and ventral parapodial lobes had gone. The long provisional bristles had been lost. The last four segments had in each dorsal bundle one strong curved bristle of the kind characteristic of this species. The ventral bundles of the seventh and succeeding segments carried only hooded crotchets, the sabre-shaped bristles found among them in the larva had gone. The fifth segment had become more prominent. There were still only six pairs of branchiæ, but these had grown much longer and more strap-like, the fourth and fifth pairs being the longest, the sixth pair the shortest. Each had a row of strong and fairly long cilia on the inner or dorsal surface. Nearly all the black pigment had disappeared, there being only a few specks here and there. The eye-like chromatophores had gone. The body-wall was very transparent and almost colourless. The œsophagus extended back to about the ninth segment before passing into the stomach, which was brown owing to its contents.

Larvæ liberated in a natural manner, from infected oyster shells placed in dishes, were put into a plunger-jar together with broken pieces of oyster shell which had been boiled. Within about a fortnight all the larvæ had either died off or settled down on these pieces and there metamorphosed. Most of those that settled chose the cracks along freshly broken edges,

but others had got in between the overlapping layers of periostracum that are found round the edge of an oyster shell. Each young *Polydora* had collected debris and formed a tube. In some cases these tubes were almost straight and ran along the length of the crack in which the larva had settled; in others the ends projected and from first one and then the other the tentacles were waved about in the usual manner. Three months later the pieces were examined and some of the worms removed. They had penetrated very little if any further into the shell, and the largest one seen had only 30 chætigerous segments. Most of them had six pairs of branchiæ, the second to the fifth pair being the longest, the sixth pair the smallest, but a few had only five pairs, in which case the fifth pair was the shortest. The specialised bristles of the fifth segment all had lateral teeth, the first pair without lateral teeth, the rather thick bristle found in the larva having disappeared. Three months later still, when the pieces of shell were split open, a few of the young worms were lying in distinct grooves in the brown horny layers, but on the whole they did not appear to have penetrated very far. The seventh pair of branchiæ was appearing in most cases, and the sixth pair was now as long as the first, but in others the sixth pair was only just putting in an appearance. The largest individual seen had 35 chætigerous segments, and the ninth pair of branchiæ was developing. Probably in the sea growth is much faster than this.

(d) *Comparison with P. ciliata.*

Although there still remain several species of British *Polydora* whose larval developments have yet to be worked out, it may nevertheless be of value to plankton workers to state briefly those characters by which *P. hoplura* larvæ can most easily be distinguished from those of *P. ciliata*. They can be tabulated as follows:—

*P. CILIATA.*

1. Released at a stage with three pairs of bristle-bundles.
2. Majority of larvæ of all stages after formation of vestibule have a mass of pigment, often dark brown, at the corners of the cheeks.
3. No lateral black spots between first and second pair of bristle bundles in early stages. Later a pair of spots, corresponding to the later ones of *P. hoplura*, appears.
4. A little brown pigment in the anal region in early stages. Later a few black spots may appear.
5. In latest stages two rows of black chromatophores down the back.

*P. HOPLURA.*

1. Usually not released until after the appearance of the tentacles.
2. Never have any dark pigment at the corners of the cheeks.
3. From 3 chætigerous segments stage onwards there is a pair of lateral black spots between first and second pair of bristle bundles. Later another pair of spots appears below and rather behind this pair.
4. Considerable quantity of black pigment in the region of the anus at all stages.
5. In latest stages four rows of black chromatophores down the posterior half of the back. Spots of outer rows small.

These are the best characters by which to distinguish the two species, especially as the pigment is preserved fairly well in alcohol and in formalin. It must be emphasised, however, that the pigment is liable to great variation, thus the cheek spots in *P. ciliata* may be absent altogether, and the rows of spots on the back may, in both species, become irregular owing to the absence of some spots or the presence of supernumerary ones. But by taking account of all the characters mentioned, it is almost always possible to separate these two species one from the other.



TEXT-FIG. 3.

Modified chaetae of the fifth segment of a late *Polydora ciliata* larva. Traced with a drawing eyepiece.  $\times 264$ .



TEXT-FIG. 4.

Modified chaetae of the fifth segment of a late *Polydora hoplura* larva. Viewed somewhat from the convex sides of the curved tips. Traced with a drawing eyepiece.  $\times 264$ .

The latest stages can also be distinguished by the difference in the shape of the specialised chaetae of the fifth segment. In *P. hoplura* there is a small secondary spur on the second and succeeding chaetae which is absent in *P. ciliata*. (Compare Text-Figs. 3 and 4.)

##### 5. PREVIOUS RECORDS OF POLYDORA LARVAE.

The first writer to figure a *Polydora* larva was Örsted (14), who in his "Conspectus" of 1843 gives a sketch (Plate VI, Fig. 96) of one he found along with adult examples of *Leucodorum ciliatum* Johns. He shows three pairs of bristle-bundles and four eye-spots, and I have little doubt that this was actually a *Polydora ciliata* larva. Twenty years later Claparède (4) published a beautifully illustrated account of the development of *Leucodora ciliata*, but, as has been pointed out first by Agassiz (1) and then by later writers, and by Claparède himself in conjunction with Mecznirow (5), this is probably not *Polydora*. Gravely, however, thinks that it may be (6, p. 51). Claparède and Mecznirow (5) figured a larva they then supposed was that of *Polydora*, but this also has been shown by various writers to belong not to that genus but most probably to *Pectinaria*. Agassiz (1) figures and describes, from specimens obtained from the plankton and kept in confinement, the development of an undoubted *Polydora* larva from a stage in which the tentacles were just appearing to a late stage after metamorphosis. Whitelegge (17) found the ova and larvæ of a species of *Polydora* attached alongside the adults to the walls of their burrows in oyster shells at Newcastle, in New South

Wales. He believed the species to be *Polydora ciliata* Johns, but his figure of the egg-sacs resembles more closely that given by Söderström (16) for *Polydora ligni* Webster. His original figures of the larvæ are too poor to discuss. Andrews (2) figured and described the egg-sacs and early larvæ of his *Polydora commensalis*. Leschke (10) appears to have been the first to rear the larvæ of *P. ciliata* from the egg to metamorphosis. Apart from minor errors and some slight differences from my account, the chief of which have already been pointed out, his account is good as far as it goes, but his figures are few and poor. Gravely (6) described and figured different stages of *Polydora* larvæ picked out from the plankton at Port Erin; he considered they belonged to two species that he called A and B, neither of which appear to correspond with either of the two species described in this paper. The larvæ he described as the metatrochophores of *Polydora* (6, p. 46), following Claparède's figures (4, Plate VII, Figs. 4 and 5) were certainly not *Polydora*, but were very probably *Sabellaria* larvæ, as I shall have occasion to show in a future paper. Gravely (7) was the first to draw special attention to the complicated vestibule of these larvæ, and his figure of this has already been discussed. It must be remembered, however, that his species was probably a different one from either of mine. He bases a suggestion as to the way in which he supposed the vestibule to originate in development, partly on the trochophore figured by Claparède, as that of *Polydora*, and he repeats the latter's figure (7, Text-Fig. 3A), but, as has already been mentioned, this is not *Polydora* but is very likely *Sabellaria*. Söderström (16) has published a long account of the egg-sacs of the Spionidæ, to which the reader is referred for an account of his theory as to their formation, and for other interesting information. Of general interest is Gravier's fascinating paper (8) on the spawning and incubation of *Polychætes*.

In addition to these most important references to *Polydora* larvæ, there are a number of odd figures scattered through the literature. De Saint-Joseph (15, Plate III, Fig. 73), Mesnil (12, Plate XIV, Figs. 7 and 8), McIntosh (11, Plate XCIII, Figs. 6 and 7), Häcker (9, Taf. II, Figs. 16-18), Carazzi (3, Taf. II, Fig. 16), and one or two others, all figure one or more *Polydora* larvæ, usually from specimens caught in the plankton. Carazzi states that his larva is *P. hoplura*. I consider, however, that until the developments of several more species have been worked out it is futile to discuss them.

## 6. SUMMARY.

1. The developments of *Polydora ciliata* Johns. and *Polydora hoplura* Clap. are described from the egg to a very late planktonic stage in the case of the former, and to young metamorphosed individuals in the case of the latter. Only external characters are described.

2. In both species the eggs are laid in egg-sacs attached to the wall of the parent's burrow.

3. The larvæ of *P. ciliata* are released at a stage with three chætigerous segments and lead a long planktonic life.

4. The larvæ of *P. hoplura* are provided with special food in the form of yolk-masses; they undergo most of their development while in the protecting burrow of their parent; are released at a very late stage, and have only a short planktonic life.

5. The larvæ of both species have a complicated vestibule surrounding the mouth, and are provided with special sensory cilia on the head.

6. The larvæ are provided with a special kind of cilia, situated at the ends of every nototroch, which are used to take hold of the long provisional bristles in swimming. This suggests that one of the functions of the long bristles is that, in conjunction with these grasping-cilia, they increase the rigidity of the swimming larva, and hence the efficiency of its driving cilia.

7. Previous references to *Polydora* larvæ are briefly discussed.

## 7. REFERENCES.

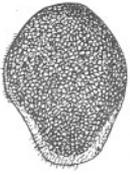
1. AGASSIZ, A. 1866. On the Young Stages of a Few Annelids. Ann. Lyceum Nat. Hist., New York. Vol. VIII.
2. ANDREWS, E. A. 1891. A Commensal Annelid. Amer. Nat., Vol. XXV.
3. CARAZZI, D. 1893. Revisione del genere *Polydora* Bosc. e cenni su due specie che vivono sulle ostriche. Mitt. Zool. Sta. Neapel. Bd. XI.
4. CLAPARÈDE, A. R. E. 1863. Beobachtungen über Anatomie und Entwicklungsgeschichte Wirbelloser Thiere.
5. CLAPARÈDE, E., and MECZNIKOW, E. 1868. Beiträge zur Kenntniss der Entwicklungsgeschichte der Chætopoden. Zeit. wiss. Zool. Bd. XIX.
6. GRAVELY, F. H. 1909. Polychæt Larvæ. L.M.B.C. Memoir XIX.

7. GRAVELY, F. H. 1909. Studies on Polychæt Larvæ. Quar. Jour. Micro. Sci., Vol. 53.
8. GRAVIER, C. 1923. La Ponte et l'Incubation chez les Annélides Polychètes. Ann. des Sc. Nat. Zool., 10<sup>e</sup> série. T. VI.
9. HÄCKER, V. 1898. Die pelagischen Polychæten- und Achætenlarven der Plankton-Expedition. Erg. der Plankton-Exped. der Humboldt-Stiftung. Bd. II, H.d.
10. LESCHKE, M. 1903. Beiträge zur Kenntniss der pelagischen Polychætenlarven der Kieler Förhrde. Wiss. Meer. Kiel. Bd. VII.
11. MCINTOSH, W. C. 1915. A Monograph of the British Marine Annelids. Vol. III.
12. MESNIL, F. 1896. Études de Morphologie Externe chez les Annélides. 1. Les Spionidiens des Côtes de la Manche. Bull. Sc. de la France et de la Belgique. T. XXIX.
13. MESNIL, F., and CAULLERY, M. 1917. Un nouveau type de dimorphisme évolutif chez une Annélide Polychète (*Spio Martinensis* Mes.). Compt. Rend. de l'Acad. des Sci. T. 165.
14. ÖRSTED, A. S. 1843. Annulatorum Danicorum Conspectus.
15. SAINT-JOSEPH, Baron de. 1894. Les Annélides Polychètes des Côtes de Dinard. Ann. Sc. Nat. Zool. 7<sup>e</sup> série. T. XVII.
16. SÖDERSTRÖM, A. 1920. Studien über die Polychætenfamilie Spionidæ.
17. WHITELEGGE, T. 1890. Report on the Worm Disease affecting the Oysters on the Coast of New South Wales. Records of the Australian Museum, Vol. I.

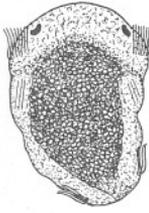
## PLATE I.

Larvæ of *Polydora ciliata* Johnston. All drawings from life  $\times 156$ .

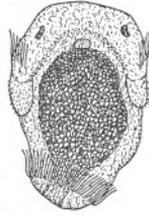
- FIG. 1. Early embryo from egg-sac. View of left side. Actual length approx.  $135 \mu$  (see page 569).
- FIG. 2. Later stage from egg-sac. Dorsal view. Actual length approx.  $173 \mu$  (see page 570).
- FIG. 3. Ventral view of the same larva as shown in Fig. 2.
- FIG. 4. Early larva 24 hours older than the one shown in Figs. 2 and 3. Ventral view. Actual length approx.  $200 \mu$  (see page 570).
- FIG. 5. Larva from egg-sac 24 hours older than the one shown in Fig. 4. Dorsal view. Actual length approx.  $231 \mu$  (see page 570.)
- FIG. 6. Stage at which the larvæ are liberated from the egg-sac. A day or so older than the larva shown in Fig. 5. Dorsal view. Actual length approx.  $256 \mu$  (see page 571).
- FIG. 7. Larva with four chætigerous segments, two nototrochs, and two pairs of dorsal black pigment spots. A few days after liberation from egg-sac. Dorsal view. Actual length approx.  $300 \mu$  (see page 573).



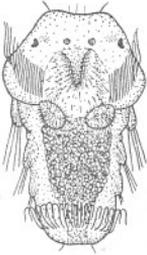
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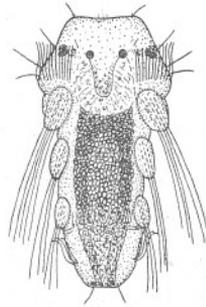
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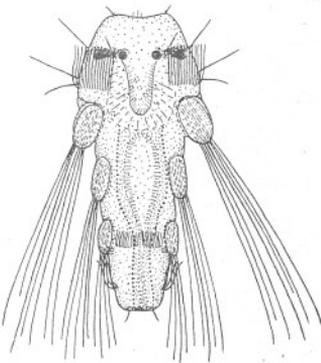
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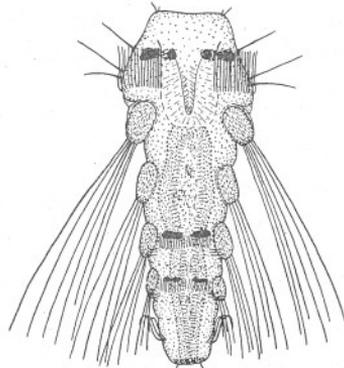
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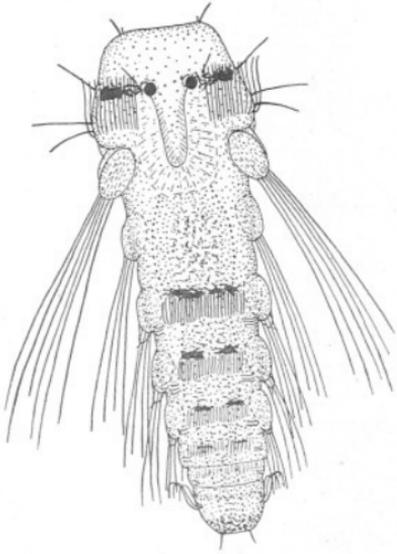


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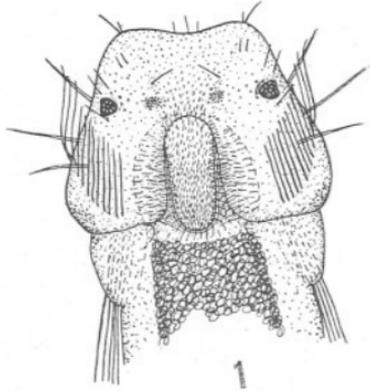
## PLATE II.

Larvæ of *Polydora ciliata* Johnston. All drawings from life.

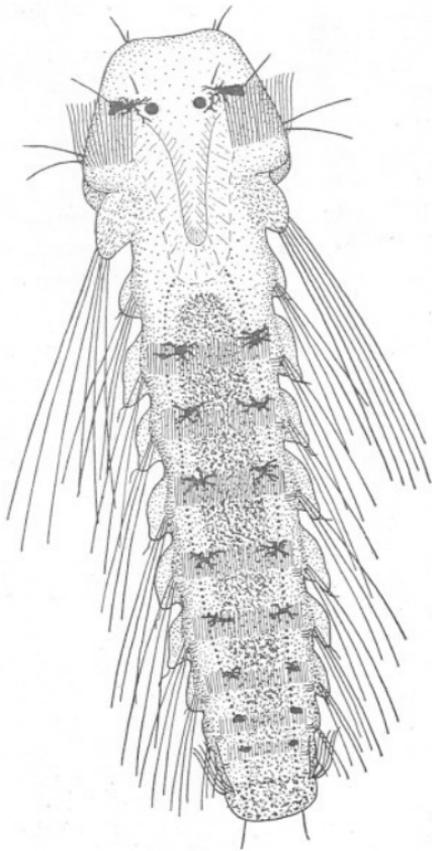
- FIG. 1. Ventral view of head of same larva as shown in Plate I, Fig. 5. Developing vestibule open.  $\times 312$  (see pages 571 and 572).
- FIG. 2. Larva about 10 days after liberation from egg-sac. Dorsal view.  $\times 156$ . Actual length approx.  $394 \mu$  (see page 573).
- FIG. 3. Larva about a week later. Dorsal view.  $\times 156$ . Actual length approx.  $605 \mu$  (see page 573).



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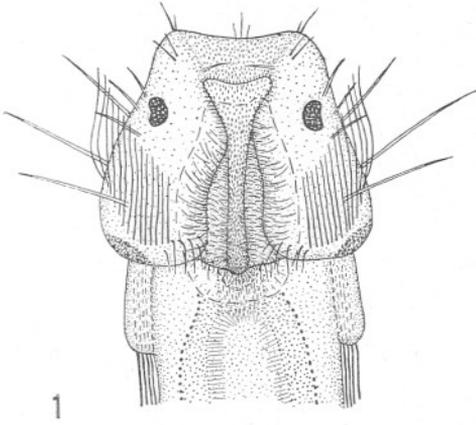


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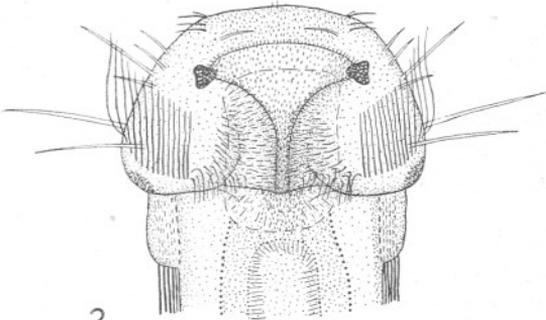
## PLATE III.

Larvæ of *Polydora ciliata* Johnston. All drawings from life.

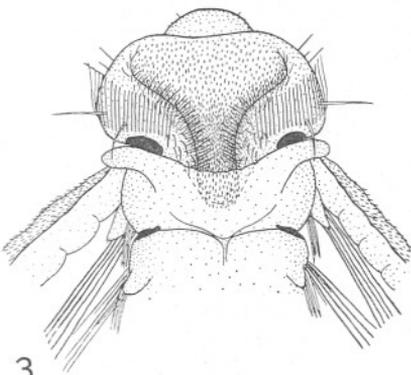
- FIG. 1. Ventral view of the head of a larva shortly after liberation from the egg-sac. Vestibule partially open. The position of the lateral eyes is indicated.  $\times 312$  (see page 572).
- FIG. 2. Ventral view of the head of a larva at the same stage showing the vestibule wide open.  $\times 312$  (see page 572).
- FIG. 3. Ventral view of the head of the larva drawn in dorsal and lateral views on Plate IV. Vestibule wide open.  $\times 156$  (see page 574).
- FIG. 4. Lateral view of a larva about one month after liberation from the egg-sac.  $\times 156$ . Actual length approx.  $770 \mu$  (see page 574).



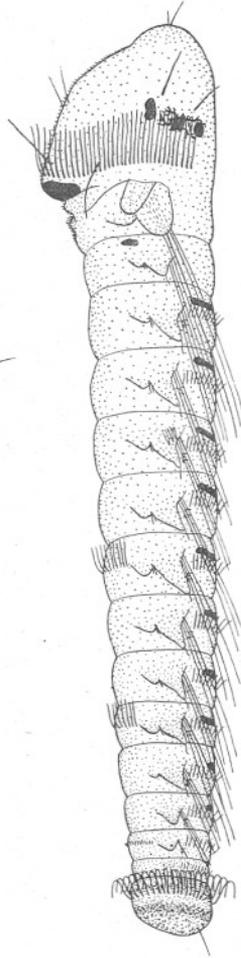
1



2



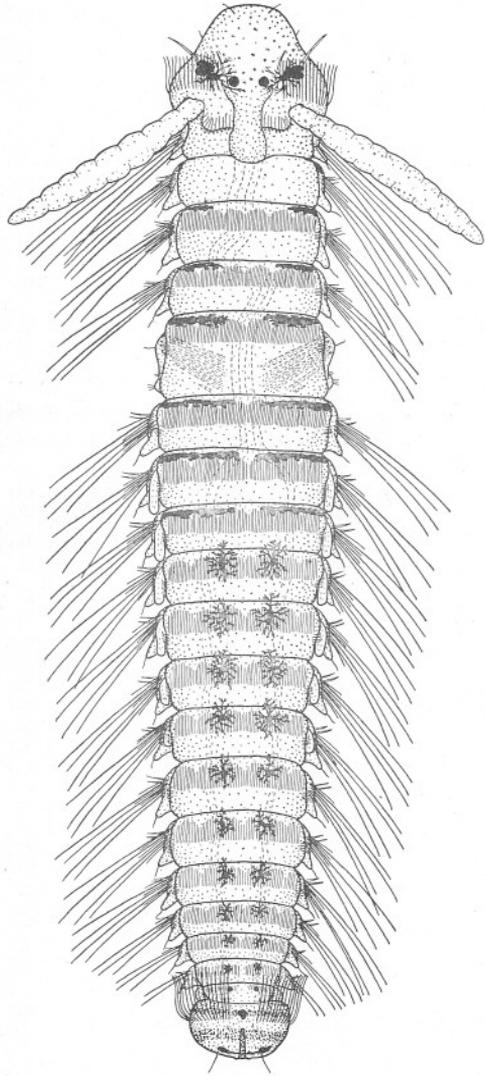
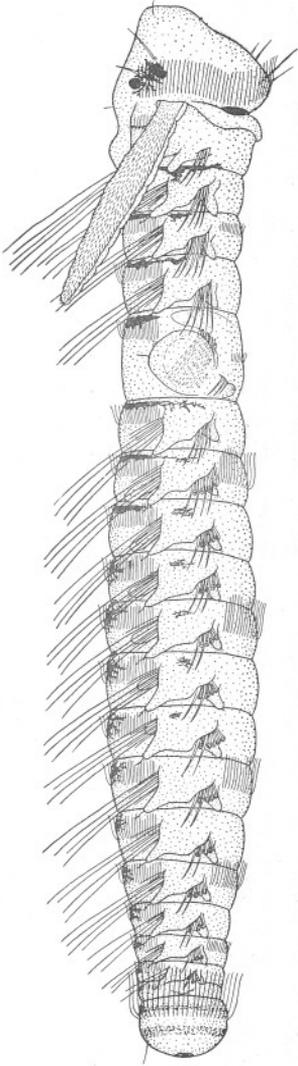
3



4

## PLATE IV.

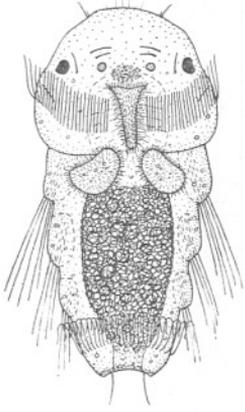
Dorsal and lateral views of a larva of *Polydora ciliata* Johnston about six weeks after liberation from the egg-sac. From life  $\times 104$ . [Actual length approx.  $1340 \mu$  (see pages 574-576).



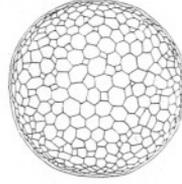
## PLATE V.

Larvæ of *Polydora hoplura* Claparède. All drawings from life  $\times 156$ .

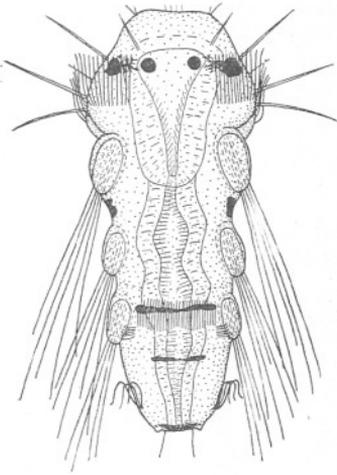
- FIG. 1. Yolk mass from egg-sac. Actual diameter approx.  $140 \mu$  (see page 578).  
FIG. 2. Early larva from egg-sac. Ventral view. Actual length approx.  $305 \mu$  (see page 580).  
FIG. 3. Larva with three chaetigerous segments from egg-sac. Dorsal view. Actual length approx.  $355 \mu$  (see page 580).  
FIG. 4. Later larva from egg-sac. Dorsal view. Actual length approx.  $500 \mu$  (see page 581).



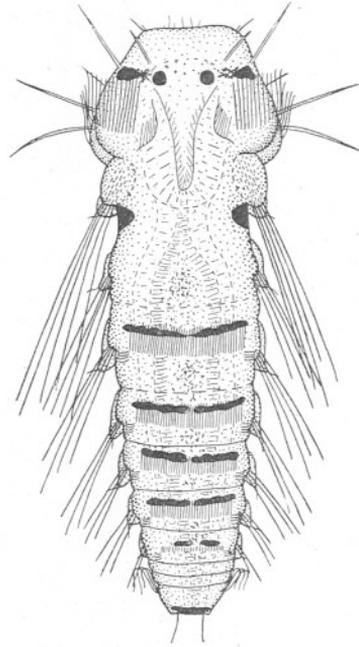
2



1



3

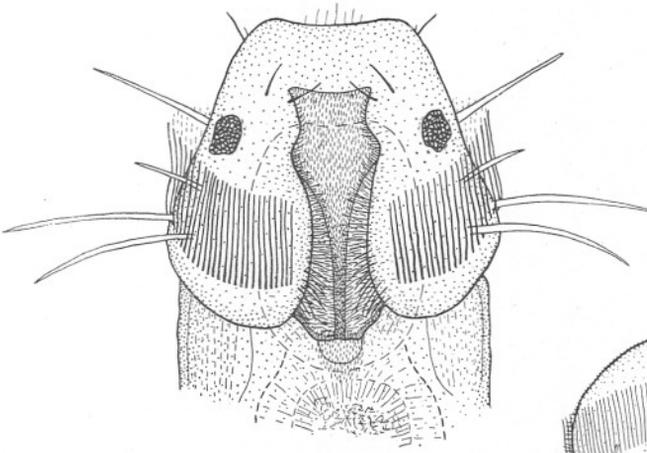


4

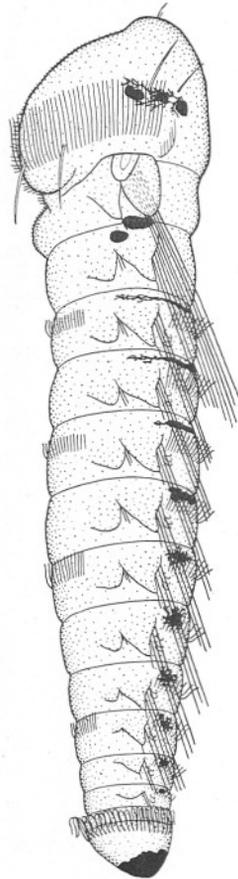
## PLATE VI.

Larvæ of *Polydora hoplura* Claparède. All drawings from life.

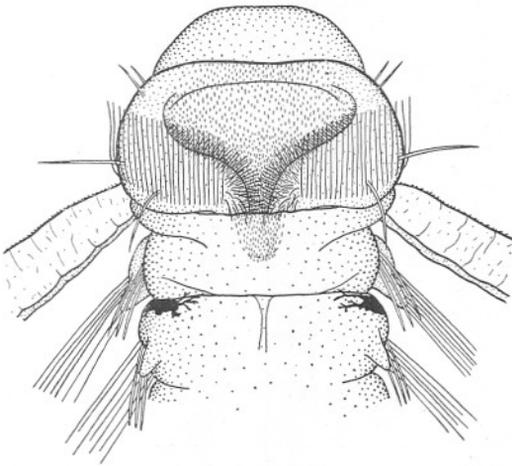
- FIG. 1. Ventral view of head of a larva a little older than that shown in Plate V, Fig. 3. Vestibule partially open. The position of the lateral eyes is indicated.  $\times 312$  (see page 581).
- FIG. 2. Ventral view of the head of the larva drawn in dorsal view on Plate VII. Vestibule wide open.  $\times 156$  (see page 582).
- FIG. 3. Lateral view of a fairly late larva from egg-sac.  $\times 156$ . Actual length approx.  $720 \mu$  (see page 581).



1



3



2

## PLATE VII.

Dorsal view of a larva of *Polydora hoplura* Claparède, which, with others, was found free in the burrow of the parent. From life.  $\times 104$ . Actual length approx.  $1670 \mu$  (see page 581).

