The Larvæ of the British Sabellarians.

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With 9 Plates and 5 Figures in the Text.

CONTENTS

1. INTRODUCTION.

The larvæ of Sabellarians are some of the commonest of plankton organisms, and especially in the spring and summer months are present in abundance around our coasts. They have frequently been figured and described from plankton catches made in different parts of the world, but in nearly every case they have been regarded as larvæ of some form of Spionid, in spite of the fact that de Quatrefages (**18**) as long ago as 1848, Horst (**12**) in 1881, and von Drasche (**5**) in 1885 all obtained the early stages from artificial fertilisations of a species of Sabellaria. In 1914 Caullery (**3**), by comparing larvæ which he had caught in the plankton with the figures published by these three workers, and by calling attention to certain chætæ found in his oldest specimens was able to point out the chief differences between the larvæ of Spionids and those of Sabellarians. In the same year Ziegler (**21**) again obtained the early stages of *Sabellaria spinulosa* by means of artificial fertilisations, but since then no further researches on these larvæ have been made. As yet no satisfactory account of the development of any Sabellarian exists, and the present paper gives for the first time a fairly full description of the development of the external features in two species of Sabellaria, and includes the first observations which have been made on the metamorphosis and early bottom stages of these remarkable creatures. All measurements are given in the legends to the text-figures or in the explanation of the plates.

It is a pleasant duty to have to thank Dr. Allen and the members of this Laboratory for their encouragement and help in this work. Dr. Lebour and Mr. A. J. Smith have both kindly attended to my plunger jars on occasions when I have been away.

2. METHODS.

In the early spring of 1927 a number of common and familiar larvæ were picked out from plankton catches and placed in bowls of sea-water. They were then thought to be Spionid larvæ, Caullery's paper not having been seen at that time. These larvæ after some weeks metamorphosed into what was, with some surprise, recognised to be the young of a species of Sabellaria. Two species of this genus are common in the Plymouth district, one, *S. alveolata* Linnæus forming large honeycomb masses of sandy tubes attached to the rocks on the shore at Whitsand Bay, the other, *S. spinulosa* Leuckart building separate sandy tubes attached to stones and shells on the bottom of the Sound, and elsewhere below low-water mark. Living specimens of both were collected, and artificial fertilisations made. Mature individuals of both species, and especially of the former, can be obtained during the greater part of the year, and they shed their genital products as soon as they are removed from their tubes. The early larval stages are easily obtained, and it is these which have previously been described by von Drasche and others. The early larvæ were placed in plunger jars or in finger bowls. The water used was obtained well out to sea, and was passed through a Berkefeld filter to remove any organisms it contained. A few drops of a culture of Nitzschia (kindly supplied by Dr. Allen) was added to each plunger jar or bowl, and this served as food. Numerous attempts to rear the larvæ in this manner were made, and some of these were successful. On the whole those in the plunger jars did best, but in several cases excellent results were obtained in the finger bowls. In warm weather those plunger jars which stood in an aquarium tank and were cooled and protected from rapid changes of temperature by running water gave the best results. It was also found important to protect the jars from too strong a light, otherwise the diatoms became too numerous. The spines of the very young larvæ became attached to anything of a sticky nature, such as clumps of diatoms, and many larvæ often stuck to the same speck of debris, from which they were rarely able to free themselves. Older larvæ were powerful enough to pull themselves away. It is thus very important that the water should be perfectly clean. The water as a rule remained unchanged throughout each experiment.

There are two stages through which it is especially difficult to rear the larvæ. The first is the growth stage between the trochophore with nine or ten bristles in each bundle, and the considerably larger early meta-trochophore with two or three trunk segments and a telotroch. Once that stage has been passed growth continues fairly readily until the larvæ are ready for metamorphosis. They then frequently die off, sometimes first making an abortive attempt to metamorphose. It was only after numerous attempts that artificially fertilised larvæ were reared to early bottom tube-building stages.

All the drawings, except where otherwise stated, are from living larvæ, confined in cavity slips but perfectly free to move about, so that the body was not distorted in any way. Proportions were obtained with the aid of a square-net micrometer in the eyepiece, drawing in the first place on to squared paper. Larvæ were also mounted in the usual manner for the better examination of the chætæ.

3. THE DEVELOPMENT OF *SABELLARIA ALVEOLATA* LINNÆUS.

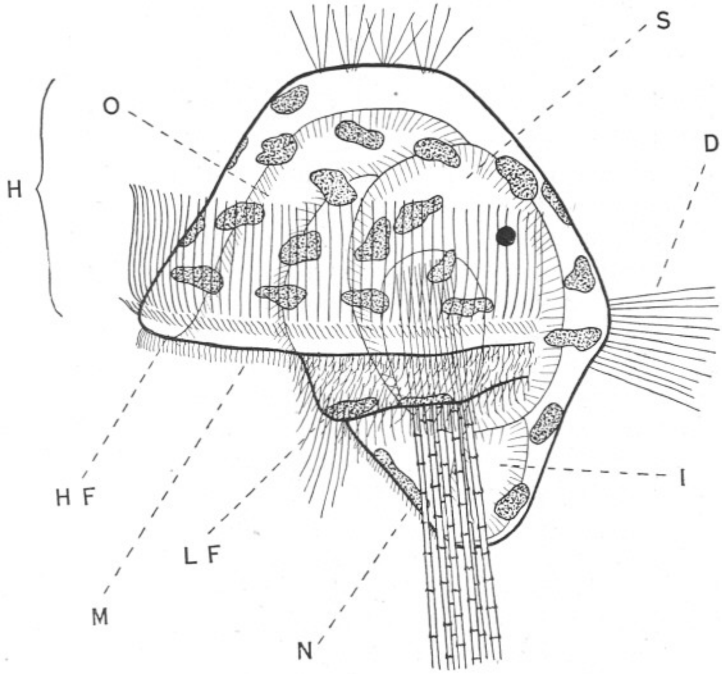
(*a*) *The pelagic stages.*

When seen in the mass by reflected light, the freshly spawned ova of this species are purplish in hue. A conspicuous germinal vesicle is present and the eggs are very irregular in shape. If not fertilised, healthy ova will remain in this condition for several hours, but if sperm be added they round up and throw off a crumpled fertilisation membrane and the germinal vesicle disappears. After a time polar bodies are extruded and segmentation commences. Eighteen or twenty hours later the embryos show the first signs of movement. Fig. 1, Plate I, is a drawing of an embryo twenty-seven hours after fertilisation. The outline is rather irregular, and the embryo is densely granular and opaque. The colour is similar to that of the freshly spawned ova. It is surrounded by the crumpled fertilisation membrane through which cilia project. Just posterior to the equator there is a complete ring of very short fine cilia, the first sign of the prototroch. At the anterior pole a few very fine long cilia form an apical tuft. The movements are rather feeble, but as the prototrochal cilia lengthen and become more powerful, the embryo begins to swim actively forwards, rotating on its longitudinal axis. The cilia of the apical tuft are usually directed forwards and twisted together. As the embryo develops its outline loses its irregularity, and, owing to a slight increase in size, it fills up the space inside the fertilisation membrane, smoothing out the wrinkles (Plate I, Fig. 2). This fertilisation membrane persists as the skin of the larva and is present up to the latest stage observed. It forms a rather close-fitting envelope separated from the "surface" of the larva by a narrow space. As this membrane is never tightly stretched, and as it is always of about the same thickness whatever the size of the larva may be, it is obvious that the original fertilisation membrane must be added to by secretion during growth. In only one culture out of many in which special attention was paid to this point, has the fertilisation membrane been observed to be actually thrown off. In this case, when a stage a little later than that shown in Fig. 2, Plate I, was reached, in many of the larvæ, but by no means in the majority, the membrane split right round in the line of the prototroch and was cast off in two pieces, one anteriorly and one posteriorly. This left the larva covered by a very delicate pellicle, and for two or three days it was possible, with a high power, to distinguish two kinds of larvæ in the bowl, those which had retained the membrane and those which had cast it off. Soon, however, it was no longer possible to do this; all the larvæ had a typical membrane round them, which must mean that either those which cast it off had all died (many of both kinds of larvæ died), or had secreted another membrane indistinguishable from the true fertilisation membrane. In either event it is highly probable that the loss of the membrane was an exceptional occurrence.

About forty-six hours after fertilisation the embryo reaches the stage shown in Fig. 2, Plate I. It is slightly elongated in an anterior posterior direction, and is opaque and granular in general appearance. With a high power the gut can be seen to be differentiating. The prototroch consists of a single row of fine cilia completely surrounding the body just behind the equator; the long apical tuft is as in the previous stage, but at the posterior end a single extremely fine cilium, which persists for some considerable time (see figures), has appeared. A slight depression in the region of the future mouth deepens a little, and fifteen hours later is as shown in side view in Fig. 4, Plate I. By that time one long and one short provisional bristle have appeared on each side (Plate I, Fig. 3) and the general colour is an unevenly distributed yellowish green by transmitted light. Otherwise there has been little change. Shortly afterwards, however, the mouth appears as a small well-ciliated invagination situated just behind the prototroch in the slight ventral depression previously mentioned. About the same time the prototroch acquires a second and posterior row of very short cilia and becomes interrupted by a gap on the dorsal surface. First one and then another bristle appears in each bundle, and the yellowish green pigment, together with specks of brown, begin to be aggregated into chromatophores. The ventral depression deepens slightly, and the prototroch is raised up on a backwardly projecting fold which runs round the ventral surface just in front of the mouth and passes up on each side, but does not extend on to the dorsal surface. A neurotroch of short cilia appears on the ventral surface, and the forwardly directed œsophagus becomes ciliated and is a conspicuous feature of the ventral view. The apical tuft loses its longest cilia but persists as tufts of short fine cilia throughout pelagic life. Thus thirty hours after the last stage it reaches the condition shown in Figs. 5 and 6, Plate I. The larva is now much less granular and more transparent than previously, but there are still a great number of oily globules in the tissues.

About forty hours later, just over five and a half days after fertilisation, the larva reaches the stage shown in Fig. 7, Plate I. As this is the stage which has previously been specially figured by Horst, von Drasche, and Ziegler, and past which they failed to rear their larvæ, it is worth describing it in some detail. Text-Figs. 1 and 2 represent lateral and ventral views of a slightly older individual, but the only marked difference between it and the above-mentioned larva is that it possesses a few more bristles. Thus the following description, with that exception, applies to both.

The young Sabellarian has now reached what can be regarded as the fully developed Trochophore stage, and it has commenced to feed. The most striking feature is the backwardly projecting fold overhanging the mouth in front and passing round each side until it is lost as it merges into the dorsal surface. The whole of the region anterior to this fold can conveniently be referred to as the "hood." Behind this hood-fold there is on either side of the mouth a second rather similar fold or ridge which in later stages becomes more prominent. This structure will be called the "lip-fold." The diagrammatic section (Plate IX, Fig. 19) indicates the extent of the folding at this stage, while Text-Fig. 5, of the same but more highly developed structures in a larva which is probably that of Pallasia, gives a fair idea of the formation of this region in Sabellarian larvæ generally. The prototroch is carried near the edge of the hood-fold, it is complete ventrally but there is a large dorsal gap. It consists of an anterior row of long and rather strong driving cilia which form the chief swimming organ of the larva at this stage. Immediately behind a second row of shorter cilia occurs. In each of these rows the cilia are almost in single file, but as their points of attachment are not quite in line but are scattered a little, there is a slight tendency to form a very narrow band. Behind the second row there is a third line of short cilia along the edge of the hood-fold and more cilia occur in the groove formed by the hood-fold, and also on the lip-folds. On the latter the cilia are usually grouped into two or three irregular bands running parallel with the edges of the folds. These cilia can be regarded as a posterior prototroch; they are longest near the posterior edges of the lip-folds and especially at the posterior corners by the mouth. They probably form a food-collecting area, but attempts to prove this have been unsuccessful, largely on account of the minute size. The long cilia on the lip-fold corners are held more or less stiffly in the position figured and undergo vibratory movements. This distribution of the protrochal cilia is unaltered during the later pelagic stages, but in the drawings on the plates it has not been possible to indicate it very clearly owing to the relatively small size of the scale used. On the ventral surface between the mouth and the anus there is a rather deep wide groove, which is well ciliated by a broad neurotroch. The mouth leads into a ciliated œsophagus which runs forward, to open near the anterior end of the hood into a large globular stomach, also ciliated. A short ciliated intestine passes to the anus which is situated on the ventral surface close to the posterior end of the larva. On the anterior extremity of the hood, some tufts of fine apical cilia occur, while at the posterior extremity of the body a single fine cilium projects backwards. In the dorsal gap of the prototroch there is a prominent dorsal hump, and this carries a number of long fine but rather stiff cilia which occasionally vibrate. Four long provisional bristles (except in Text-Figs. 1 and 2, where there are more) project from a conspicuous chæta-sac situated on each side, and they pass out below the lip-folds. The chæta-sacs are moved by a series of muscles in such a way that they can direct the bristles in many directions. The structure of the bristles is very characteristic, they are surrounded by rings of teeth, the points of which are directed towards their distal extremities. Owing to the minute size and transparency it is extremely difficult, even with an oil-immersion, to make out the real nature of these rings. They appear to be collars arising from the bristle shaft with the free border of the collar toothed or serrated. The teeth are longer on one side of the collar than on the other (Plate IX, Fig. 11). The collars are arranged at intervals of about $8{\cdot}5\mu$, but the distance apart varies. The larva is fairly transparent and has a considerable number of oily globules in its tissues. A conspicuous feature are the fairly numerous irregular chromatophores scattered over the hood (except on the anterior-dorsal region), on the dorsal hump, on the lip-folds, at the posterior end of the body, and one along each side just lateral to the ventral groove. The chromatophores have a fairly sharp irregular outline with a greenish yellow ground-colour, over which are scattered many irregular dark brown specks. One red eye-spot has appeared on the left side in front of the place where the prototroch stops short (out of sight in Fig. 7,



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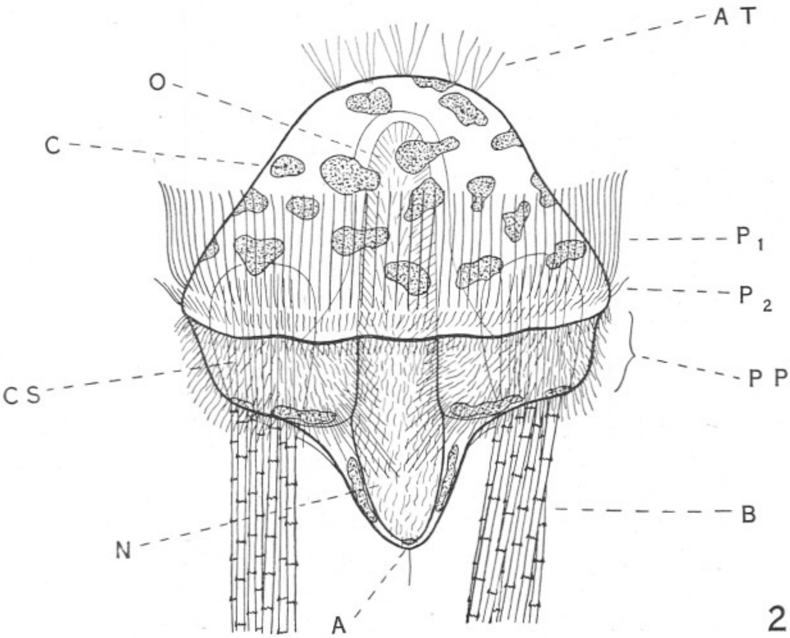

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TEXT-FIGS. 1 and 2.—Lateral and ventral views of a trochophore larva of *Sabellaria alveolata* Linnæus. From life, slightly diagrammatic, $\times 624$. Actual length (excluding bristles and apical cilia) approx. 100μ.

A, anus; AT, apical tufts of cilia; B, bristles, cut short; C, chromatophore; CS, chæta-sac; D, cilia on dorsal hump; H, hood; HF, edge of hood-fold; I, intestine; LF, edge of lip-fold; M, mouth; N, neurotroch; O, œsophagus; P_1, anterior or first row of prototroch; P_2, second row of prototroch; PP, posterior prototroch, or cilia on lip-folds; S, stomach.

Plate I). This and the eye-spots that develop later lie deeper in the tissues than do the chromatophores.

After the larva has reached the fully developed trochophore stage represented in Fig. 7, Plate I, no further differentiation of the soft tissues is apparent for some little time. The organism merely acquires more and more bristles until there are nine or ten in each bundle. During this period, which lasts for several days, sometimes about a week, the body of the larva remains the same size, or at most only becomes very slightly larger. At the end of the period it begins to grow and a constriction appears just in front of the chromatophores which are situated on each side of the ventral groove. The region behind this constriction becomes the telotrochal swelling (see p. 248 for reasons for using this term). At this period the telotroch is arising; the grasping-cilia (see p. 231) soon becoming quite prominent, but the driving cilia remain for some time fine, slender, and few in number. Meanwhile two more eye-spots have appeared, both on the right side. The second of these to develop arose posterior to and nearer the mid-dorsal line than the first. The fourth eye-spot does not develop until the larva has almost reached the stage shown in Fig. 10, Plate I, and it then appears posterior to and nearer the mid-dorsal line than the eye-spot on the left side, which was the first to appear. This curious order in the development of the eye-spots was constant in a large number of larvæ examined from different cultures, except that occasionally supernumerary ones might develop. Each eye-spot consists of numerous reddish globules (oily ?) aggregated into a cluster.

The larva drawn in Figs. 8 and 9, Plate I, was twenty days old, and it is definitely a metatrochophore. The telotrochal swelling and two or three trunk segments are marked out, but the limits of the segments are rather indistinct. The telotroch is present, but at this stage possesses a ventral gap, through which the neurotroch passes to the anus. There are three eye-spots, one on the left and two on the right side. Each bristle-bundle contains fifteen to seventeen bristles, one or two of them being quite short. In other details the creature closely resembles the trochophore, except that it is larger and the hood and lip-folds are more prominent. Growth continues and new trunk segments appear in front of the telotrochal swelling. A six-weeks'-old larva is shown in Figs. 10 and 11, Plate I, but many larvæ by this time are much more advanced. There is a great variation in the rate of growth of individual larvæ from the same culture, and reared in the same bowl or plunger jar. At the stage shown in these drawings, irregular pigment bands are present on the dorsal anterior part of some of the trunk segments, and they extend round the sides of the body to about as far as the borders of the wide ventral trough in which the neurotroch lies. These pigment bands ordinarily have a black appearance, but they are really composed of a large number of very dark brown granules crowded together. Four red eye-spots are present in the positions indicated. The chromatophores have the same appearance as before, but they are confined to the hood, lips, dorsal hump, and the telotrochal swelling. On the hood they form a more or less regular line in front of the prototroch; elsewhere they are more scattered, but are absent from the anterior-dorsal area and from an area on each side just lateral to the eye-spots. The telotroch has either a ventral gap, or its cilia in that region are indistinguishable from the neurotrochal cilia which pass through it. In the ventral view the telotrochal swelling is represented as being turned slightly forwards; it is characterised by a number of clear vesicular-like "cells" that are present in addition to the chromatophores, which are rather darker than those on the hood. The larva is fairly transparent and very active.

Fig. 1, Plate II, shows in lateral view a larva from the same culture and plunger jar as the last, but only two days older. It was one of the more advanced larvæ referred to above. The trunk is much bigger in proportion to the hood than formerly. The three parathoracic segments are clearly defined, but as yet bear no parapodia. Behind them the first three abdominal segments have appeared; these bear slight lateral lobes, the first appearance of the dorsal uncinigerous processes of the parapodia. Between the parathoracic segments and the hood is a region more or less undifferentiated which will subsequently form into the two anterior thoracic segments of the adult. The most striking new feature, however, is the development of a pair of tentacles, one on each side of the dorsal hump at the place where the hood-fold edge merges into the dorsal surface. The attachment is almost in line with the end of the prototrochal row. These tentacles subsequently form the structures in the adult which are referred to as palps by many authors (e.g. Fauvel, **6**). Just ventral to each chæta-sac two small lobes have arisen, the largest of which will grow out into what may be called the ventral cirrus. The neurotroch is still a broad band of fine cilia, but cannot be seen in lateral view owing to the shallow trough in which it lies.

Another larva from the same culture, drawn seven days later, is shown in Fig. 2, Plate II. The dorsal parapodial lobes of the parathoracic segments have appeared, and each has two short bristles projecting from it. The uncinigerous lobes of the abdominal parapodia are larger, and now possess a number of uncini (Plate IX, Fig. 18); the first pair have four or five each, the second pair two each, and the third pair one each. The second pair of these uncinigerous lobes is situated more ventrally than the first and third pair. An important new feature is the appearance of a few special chætæ among the bases of the long provisional bristles. These chætæ will subsequently form some of the first crown chætæ of the metamorphosed larva. Three kinds are present, one each of two sorts of bristles and a few paleæ of a curious broad flattened form (Plate IX, Figs. 13, 14, and 12). The tentacles are longer and are thickly ciliated on their ventral surfaces, but the cilia are not yet very active. They are not contractile (or very slightly so) and are held stiffly in the position shown. The cirrus ventral to the chæta-sac is quite long; on it are a number of sensory cilia. The great chæta-sacs are passing backwards into a more posterior position. A horseshoe-shaped area around the posterior border of the mouth is becoming glandular; it is the first appearance of the building organ. The ciliation is the same as described for younger larvæ except that there is no ventral gap in the telotroch. The driving cilia of the telotroch are longest at the dorsal ends of the row next to the grasping-cilia, and they gradually decrease in size and power as they approach the mid-ventral position.

The larva shown in Fig. 3, Plate II, was seven and a half weeks old, but was from another culture reared in the autumn of 1927, the larvæ of the previous drawings having been reared in the spring, but all died before this stage was reached. In its main features this larva is very similar to the preceding stage, but the body is more massive and the parapodia more distinct. Each dorsal bundle of the parathoracic parapodia consists of two prominent spear-headed bristles (Plate IX, Fig. 16) and two finer bristles (Plate IX, Fig. 17) which do not project much. In addition the third pair each has a long slender barbed bristle. Ventral bundles have also appeared on these segments, and have two fine bristles to a bundle. These cannot be seen in dorsal view, but are shown in Fig. 2, Plate III, which is a ventral view of a slightly later stage. The uncinigerous lobes of the first pair carry about ten uncini each, the second pair about five and the third pair about four. The numbers, however, vary considerably and need not be the same on either side. There are about thirty-five provisional bristles in each of the great bundles, and among them there are twelve to fourteen primary crown paleæ of the flattened type (Plate IX, Fig. 12) as well as the two short pointed bristles (Plate IX, Figs. 13 and 14) which were present in the previous stage. Owing to the greater growth of the body in comparison with the hood, the mouth and lip-folds are now well exposed. The building organ has increased in size, and the rudimentary parapodia of the two anterior thoracic segments are appearing. Fig. 2, Plate III, gives a good idea of the ventral surface of the anterior end, but in this drawing the structures are a little more advanced. There has been no change in the general ciliation except that the first signs of a nototroch are present on the first parathoracic segment. The tentacles are of considerable length, and are thickly ciliated ventrally. Chromatophores similar to those on the hood are present on their dorsal surfaces. The anus is situated on the apex of a slight cone. The larva is rather opaque, the general body-colour being brownish. The chromatophores are darker brown than formerly, particularly those on the telotrochal swelling. The eye-spots have also become darker.

The larva has now reached the end of its pelagic development, but before describing the metamorphosis it will be well to consider the swimming movements.

(b) *Swimming movements and the "grasping-cilia."*

Sabellarian larvæ do not show a very active reaction towards light, but they do tend to keep on the side of the bowl or dish furthest from the window whenever the light is strong. This is most noticeable with the earlier stages after they have got one or more of their eye-spots. Polydora larvæ, under similar conditions, will be found on the side of the bowl nearest to the light (see Wilson, **20**, p. 577). They swim with the hood anterior to the direction of movement, and when watched in a plunger jar they will be seen, as a rule, to keep themselves orientated so that the hood is uppermost, i.e. in the position in which the figures are drawn. But they frequently depart from this upright position to swim in any direction, often moving along with the body placed horizontally. While swimming the two bundles of provisional bristles are kept close to the sides and the distal tips of the bundles meet one another above and behind the telotrochal swelling. The bristles pass through the dorsal gap in the telotroch and are held by the "grasping-cilia." The telotroch passes up the sides of the swelling on to the dorsal surface, and there the row of cilia turns abruptly forwards to form a longitudinal row on each side of a large dorsal gap. The cilia of these longitudinal rows project laterally and rather dorsally. They always remain more or less curved at their extremities, and although they undergo vibratory movements, they never actually beat. Their function is to curl round and grasp the long provisional bristles while the larva is swimming. Cilia with a similar function are present at the ends of the nototrochs—but not on the telotroch—of Polydora, and have already been described (Wilson, **20**, p. 577). In Sabellaria these cilia are much stronger and more conspicuous. Their function is probably twofold: (1) they help the larva's progress by holding in the bristles to the stream-line, and (2) their action must give increased rigidity to the larva as a whole and to the telotrochal swelling in particular, thus increasing the efficiency of the telotroch as a driving organ. In the later stages the driving cilia of the telotroch are longer and stronger than those of the prototroch, and possibly finally supersede the latter as a swimming organ. Under such circumstances anything which helps to make the soft body of the larva rigid will be to its advantage. The correctness of this interpretation appears to be supported by the appearance, during the later stages, of the single long barbed bristle from each of the parapodia of the third parathoracic segments. These appear at a time when owing to the growth of the body the telotrochal swelling has been carried so far back that the grasping cilia can only just reach the tips of the provisional bristles. The two long bristles from the third parathoracic segment project further back than they do and are also held by the grasping-cilia. This will give rigidity to the body at a new point. In the latest stages, just before metamorphosis, it frequently happens that the long ringed bristles no longer reach as far back as the grasping-cilia unless the larva contracts its body. Fig. 3, Plate II, shows the body slightly contracted; it is frequently more stretched in the swimming larva, and then the grasping-cilia can only take hold of the barbed bristles from the third parathoracic segment. These bristles are lost during metamorphosis. It is interesting to recall the fact that in the development of the telotroch the grasping-cilia develop faster than the driving-cilia and are used for grasping the bristles while the latter are still fine and weak.

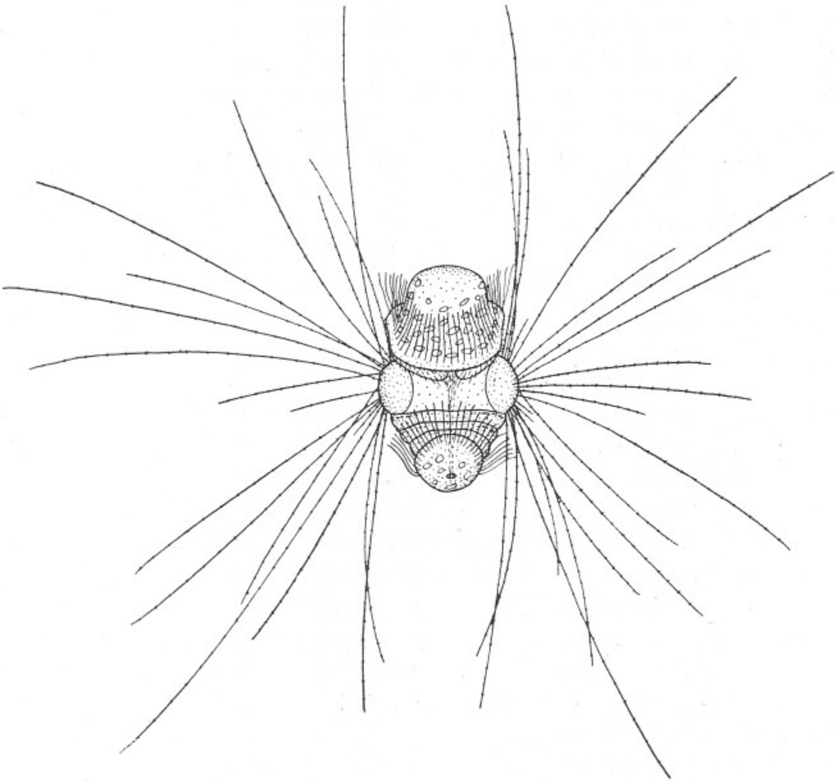
While swimming, a larva will every now and then suddenly flex the body ventrally so as to bring the telotrochal swelling close to the hood in the region of the mouth. At the same time the bristles are spread to point in all directions (Text-Fig. 3). This occurs when it bumps up against anything or is otherwise irritated. Tiny fishes have been seen to take larvæ into their mouths and immediately spit them out again with their spines erect. Some of these larvæ were afterwards examined; they appeared to be uninjured. This power of spreading the spines is acquired about the stage shown in Fig. 6, Plate I. The spines may also have a suspensory function, but this is difficult to prove. The larvæ frequently swim for long periods without erecting them and rarely have been seen to keep them spread for long, and then only while they were continually being irritated.

In all the figures, for the sake of clearness, the spines have been drawn in the partially erect condition. In Fig. 7, Plate V, the grasping-cilia are shown partially in action.

(c) *Metamorphosis and the early bottom stages.*

The duration of pelagic life varies within wide limits. Reared larvæ take from six weeks to three months from the time of fertilisation before they are ready to metamorphose. It is likely that the shorter period most nearly represents the time taken in the sea.

After a larva has reached the stage drawn in Fig. 3, Plate II, it shows an increasing tendency to crawl about on the bottom. This it does head downwards by applying the mouth to the substratum, on which the lips are spread out and flattened, the building organ being pushed back and stretched aside to allow of their full protrusion, so that their ciliated surfaces, which are normally just inside the mouth opening, come into contact with the ground. The tentacles are turned outwards and forwards so that their ciliated surfaces also come into contact with the substratum. They are not, however, kept pressed against it, but are repeatedly raised up a little and put down again in a manner suggestive of feeling. In this way the larva glides forwards, the tentacles preceding and possibly testing the ground over which it travels. The hold is



TEXT-FIG. 3.—Ventral view of a formalin-preserved Sabellaria larva showing bristles erect. $\times 156$. This is the position assumed when the larva is irritated and is characteristic of the larvæ as seen in preserved tow-nettings.

tenacious, a larva can resist quite strong squirts of water, and if it is clinging to the inside of a pipette is very difficult to dislodge. After crawling about for some time a larva may suddenly take to swimming again, settling down later on.

The change in habits is accompanied by changes in structure. The hood commences to shrink and the lips and mouth are exposed more and more fully (Plate III, Fig. 2). The building organ is enlarging rapidly, and the first two thoracic segments begin to be defined by the growth of their parapodial rudiments. The body lengthens and the telotrochal swelling is flexed somewhat ventrally, while the cone bearing the anus grows out into a long process which turns forwards ventrally to form the characteristic caudal region of the adult. Ventral bristles appear on the abdominal segments and more nototrochs develop dorsally. Meanwhile great changes have been taking place in the head region. The hood has continued to shrink and the prototrochal cilia gradually disappear although some may persist for some time. The tentacles are in process of turning forwards permanently, and are becoming very contractile and wrinkled. In some cases a secondary tentacle is growing out on each side close to the anterior lateral corner of the mouth. These are probably the first filaments of what is sometimes called the palp (e.g. Benham, Camb. Nat. Hist., Vol. II). They are indicated as showing through the transparent tentacles in Fig. 1, Plate III, and are clearly shown, but are more highly developed in Plate IV. The great chæta-sacs have become fully exposed and have rotated a little so as to bring the ventral cirri into a lateral position. A second cirrus is present on the border of each chæta-sac close to the inner ventral corners. These secondary cirri were present as small swellings in the larva drawn in Fig. 3, Plate II, but they were then hidden between the bristle bundles and the back of the larva. The latter has now the appearance shown in Fig. 1, Plate III, and the long provisional bristles are rapidly falling out. The great chæta-sacs and the associated tissues turn upwards and forwards, at the same time shedding any provisional bristles which may remain. They finally take up a position projecting forwards and rather dorsally, and thus come to form the peduncular crown of the adult. These observations of the metamorphosis thus confirm the assumptions of descriptive morphologists that " les deux gros pédoncules operculaires représentent très probablement les rames dorsales fusionnées des deux premiers pièds rejetés en avant du prostomium " (Fauvel, **6**, p. 205).

The time taken to metamorphose varies, but appears to be normally about two days ; it is often longer.

The specimen represented in ventral view in Plate IV was just over seven weeks old, and had probably metamorphosed a week or ten days previously. It was living in a little tube of mucus and debris on the bottom of the plunger jar. As this is, unfortunately, the most advanced stage to which the larvæ have been reared, it will be well to describe it in some detail. The peduncles project forwards and rather dorsally. On each twelve to fourteen primary crown paleæ (Plate IX, Fig. 12) are arranged in a circular row spread out fanwise from the centre. The circle is interrupted by a large gap on the side immediately facing the opposite peduncle. This is similar to the arrangement of the crown paleæ of the adult. Inside the curve of the row and close to the gap are situated the two pointed bristles previously mentioned. These are shown in Figs. 13 and 14, Plate IX, the former being placed immediately lateral to the latter. Another pointed and curved bristle (Plate IX, Fig. 15) has appeared on the inner side of each peduncle below the level of the crown paleæ. The two cirri are prominent and probably represent the first of the numerous papillæ which in the adult form a row just below and outside the outer row of crown chætæ. In a median position, just ventral to the gap between the peduncles, is a strongly ciliated conical process, formed in front of the eye-spots during the shrinkage of the hood. The four eye-spots are still present, but the anterior pair (indicated in Plate IV) are closer together than in the larva. The eye-spots are almost black with a reddish tinge. The tentacles project forwards and outwards; they are strongly wrinkled and contractile, and have thickly ciliated ventral surfaces. Along their edges there is on every wrinkle a pair of specially stout cilia, and there are a number of these cilia on the tip. Just ventral to their place of attachment a dark brown swelling represents the remains of the hood. The brown pigment is a concentration of the brown specks of the chromatophores, the latter having shared in the general shrinkage of the hood. The prototroch disappeared long ago. The lip-folds form prominent ciliated lateral lips. Close to the anterior lateral corners of the mouth are a pair of wrinkled "tentacles" ciliated on their anterior surfaces in a similar way to that in which the ventral surfaces of the tentacles are ciliated. These "tentacles" are probably the first of the many filiform tentacles, sometimes referred to as the palps (Benham, *loc. cit.*), which are such a conspicuous feature of the ventral region of the head in the adult. Posterior to the mouth is the large glandular horse-shoe-shaped building organ. This is finely ciliated, especially on its anterior border and in the deep groove between it and the lateral lips. At each anterior lateral corner of this structure is a short process with sensory cilia and two fine capillary bristles, the rudimentary parapodia of the first thoracic segment. A short distance behind these a second similar pair of projections with one fine capillary bristle each represent the second thoracic segment. Then follow the three parathoracic segments with four bristles, two prominent and two inconspicuous (Plate IX, Figs. 16 and 17) in each dorsal bundle, and with two fine capillary bristles in each ventral bundle. The first three pairs of uncinigerous dorsal processes are prominent. The first pair are considerably broader in a dorso-ventral direction than the posterior two pairs, and they have about ten to twelve uncini (Plate IX, Fig. 18) each. The second pair possess five or six uncini each and the third pair four or five. The numbers of uncini vary considerably. In the drawing the ligaments attached to the uncini are indicated. Ventral to each uncinigerous process is a single long fine bristle representing the ventral bundle of the parapodium. Behind the third pair of processes two slight swellings will probably develop into the fourth pair. Posteriorly the body curves forwards ventrally and is continued as the caudal appendage, on the extremity of which the anus opens. Close to the base of the caudal appendage and on the inner surface of the bend there is a small swelling which contains a mass of dark brown pigment. This is the shrunken remains of the telotrochal swelling.

A certain amount of black pigment—really composed of dark brown granules—still remains, especially on the dorsal surface. The worm on the whole is rather opaque, and the segment limits, particularly those of the abdominal segments, are not very visible. Nototrochs are present close to the posterior borders of the segments, and also on the head, the arrangement being the same as that shown for a more advanced individual of *S. spinulosa* in Fig. 1, Plate VIII. There is also a neurotroch in a shallow ventral groove.

The gut is divided into several regions. In the parathoracic segments the rather thick wall contains a fair number of small oily globules. On either side is a large gland, probably the thoracic gland shown in the figure of a young individual in McIntosh (**16**), p. 28, Fig. 139. A clear portion with only very few small globules in the walls follows, and this portion close to the posterior end of the first abdominal segment leads into a part where the walls are crowded with many closely packed large oily globules, in which condition the gut continues to the anus. This latter portion is indicated in Plate IV. It is a very conspicuous feature of the young worm and indeed of the later larval stages where it is situated further forward and may be present as early as the larva shown in Fig. 10, Plate I. This characteristic appearance has been omitted in the earlier drawings for the sake of clearness.

During the later stages much individual variation respecting the relative times of appearance of the different organs occurs. This is well seen in the development of the caudal appendage, for while in some individuals (as in Fig. 1, Plate III) it is quite large before the crown paleæ have been directed forwards, in others it does not develop until some time after the head region has fully metamorphosed. In such cases the telotroch persists although the worm is living in a tube. Again, the palps or tentacular filaments at the anterior lateral corners of the mouth in some cases appear quite early (as in Fig. 1, Plate III), in others very much later. All grades of intermediate conditions are found. Other organs show similar variation, although perhaps in lesser degree.

(d) *The building of the first sandy tube.*

The young worms after metamorphosis were frequently, but by no means always, found to be living in tubes of mucus on the bottom of the bowl or plunger jar in which they had been reared. To the sides of these tubes debris of various sorts was attached, especially masses of living diatoms and the cast-off provisional bristles. The tubes could be detached with a pipette and then if the larvæ were supplied with fine sand they would readily build in dishes or cavity-slips, while being watched through the microscope. All larvæ with mucus tubes were able to build tubes of sand grains, the mucus tube forming a foundation. All larvæ which were without mucus tubes, either because they had been removed from them or because, apparently, they had not made them, were unable to construct sandy tubes. They would attempt to do so, but they only succeeded in cementing grains into an irregular mass, even though they were kept amid sand for several days and in some cases were supplied with pieces of sterilised oyster shell—plentifully sprinkled with sand—which might serve as an irregularly creviced substratum on which to build. Some larvæ which metamorphosed in a dish containing sand also failed to construct either a mucus or a sandy tube. The explanation of this is not apparent.

To return to the worms with mucus tubes. As soon as sand grains are supplied, some are seized by the tentacles and conveyed to the mouth. The ciliated ventral surface of a tentacle is applied to a grain and immediately it is caused to travel towards the base. The grain is moved along by the cilia, on which it appears to be balanced or held, and it probably does not come into direct contact with the surface epithelium at all. The special strong cilia arranged in pairs along each side of the tentacle appear to play an important rôle in transporting particles. A grain is not seized by a tentacle curling round it, indeed the tentacles are never sharply bent. If the worm be lying back downwards in its tube (which in these observed instances was always horizontal) the tip of a tentacle will be inserted under a particle which will then travel along with its weight supported by the cilia. This is illustrated in Fig. 2, Plate VIII. If, on the other hand, the worm be lying back upwards the tip of the tentacle will be placed on top of the particle and it will slide over the substratum. It is uncertain as to whether one tentacle alone can actually lift a particle, but the two together applied on either side can do so and are sometimes so employed, if the particle be a big one. The "palps," if long enough, also assist in the collection of building material. In one of these ways grains arrive one at a time, to be held in the mouth by the lips. The first few are cemented round the edge of the mucus tube and then others are cemented to them. While holding a grain in its mouth, the worm moves backwards in its tube so as to bring it into contact with the tube edge. It then moves forwards a little and turns the grain slightly, and then moves back once more. This backward and forward motion continues for a time, the worm continually twisting and turning the grain, trying it in different positions and at different places on the tube edge. If finally the grain more or less fits, possibly if it jams a little among those already fixed, it is cemented into place. But if after a few attempts it does not fit, it is discarded and another tried. Some worms will in this way discard several grains for every one fitted, others are more persistent in trying each particle. One larva in particular discarded very few grains; it would try each again and again all round the tube edge, turning it between every attempt, so that nearly every particle tried was finally fitted in somewhere. A particle appears to be cemented into position by the building organ, which is passed a few times over the place of contact on the inside of the tube. This rubbing of the building organ over the place of contact was seen every time a particle was fixed. Possibly the latter is also coated with some sort of cement while it is being turned about in the mouth. Fig. 2, Plate VIII, is a drawing of an actual tube. The mucus tube is covered with irregular clusters of diatoms and other debris, among which some of the larval provisional bristles are visible. The worm is shown in the act of collecting sand grains with its tentacles and one grain is held in the mouth.

The sandy tube is usually built rather slowly, the worm taking frequent rests. In one case, about thirty grains were fitted in four and a half hours, and by the next day the tube was more than twice as long. In another case—that of the particularly persistent larva mentioned above—a tube of about forty-five sand grains was constructed in two hours, while another individual during the same time fitted about thirty grains. The last tube was roughly as long as the body of the worm excluding the tentacles. On the whole, the building operation impresses the observer as a rather clumsy proceeding; certain operations are performed more or less persistently, and it appears to be a mere matter of chance as to whether any particular particle is fitted or not.

4. THE DEVELOPMENT OF *SABELLARIA SPINULOSA* LEUCKART.

(a) *The pelagic stages.*

The development of this species follows so very closely in almost all its details the development of the preceding species that a separate full description is unnecessary. Only those points, therefore, in which it differs in any way from *S. alveolata* will be dealt with in this account.

The drawings (Plates V to VIII) will serve as a further source of information.

The ova of *S. spinulosa* are on the whole slightly smaller than those of *S. alveolata*. In both species, however, variation in size occurs. They are of a pale pinkish colour, when seen in the mass by reflected light. Figs. 1 and 2, Plate V, show in dorsal and lateral views an actively swimming larva thirty-one hours old. Twenty-four hours later (Plate V, Figs. 3 and 4) the hood-fold is becoming prominent, the dorsal gap in the prototroch has formed and four provisional bristles are present in each bundle. The larva is still very granular, but the pigment is already grouping itself into chromatophores which are just like those of *S. alveolata*. The fully developed trochophore stage is represented in ventral view in Fig. 5, Plate V. It cannot be distinguished from that of the preceding species and it develops its bristles and eye-spots in just the same way. Fig. 6, Plate V, shows an early metatrochophore three weeks old. If it be compared with the corresponding stage of *S. alveolata* (Plate I, Fig. 9), a slight difference will be noticed in the form of the trunk and especially in the way in which the telotrochal swelling is marked off from the rest of the body. This difference appears, on the whole, to be constant, but considerable variation exists and it is of no practical service in separating the larvæ of a mixed culture. It is, moreover, difficult to observe in active larvæ and it disappears when the larvæ are fixed. It might be thought that the bristles would show some distinction, but none has been detected. Figs. 7 and 8, Plate V, show in lateral and ventral views a larva two months old. This stage is usually reached much earlier, but in both species the time taken by different individuals of the same culture under apparently identical conditions (i.e. in the same bowl or plunger jar) varies very greatly without any visible effect on the structure. In the lateral view the grasping cilia are represented as holding some of the bristles. The tentacles are just budding out a little posterior to the end of the anterior row of prototrochal cilia.

The larva shown in Fig. 1, Plate VI, was from the same culture and plunger jar as the one just described, but it was only one day older. It was a particularly fine large specimen. At this stage it is approaching the end of its pelagic existence, and the primary chætæ of the crown are already well developed among the bases of the provisional bristles. These chætæ differ markedly from those of *S. alveolata*, and once they have appeared larvæ of the two species are separated with ease. The paleæ (Plate IX, Fig. 1) which correspond to the broad flattened forms of *S. alveolata* are here longer and narrower and are strongly toothed along the margins. They are not flattened, but are rounded into a trough-like shape. The drawing is from a rather flattened specimen. In addition to ten or eleven of these in each bundle two pointed bristles (Plate IX, Figs. 6 and 7) are also present. The parathoracic parapodia have four bristles, two prominent (Plate IX, Fig. 8) and two inconspicuous (Plate IX, Fig. 9) in each dorsal bundle, while each of the third pair have also a long barbed bristle, of similar function to that of the other species. On these segments the ventral bundles, consisting of two fine bristles each, have appeared. The abdominal parapodia consist of the dorsal uncinigerous lobes only. Each of the first pair of lobes has about eight uncini (Plate IX, Fig. 10), the second pair about four, and the third pair about three, the actual numbers varying as in *S. alveolata.*

(b) *Metamorphosis and the early bottom stages.*

Development of the larva continues a little further until it is ready to metamorphose at a stage in development closely corresponding to that at which *S. alveolata* metamorphoses. Fig. 1, Plate VII, shows the ventral aspect of a larva in which the hood is just commencing to shrink back. This and all succeeding drawings (except Fig. 2, Plate VII) are from larvæ picked out of the plankton at a late stage and which metamorphosed in finger bowls, but all (except Fig. 2, Plate VI, and Fig. 1, Plate VIII) have afterwards been carefully checked on larvæ reared from the egg. In any case, there is not the least doubt as to the species, the crown paleæ being absolutely distinctive.

Fig. 2, Plate VII, is a dorsal view of the anterior region of a metamorphosing larva reared from the egg and over four months old. The great chæta-sacs are turning forwards. This process has almost been completed in the specimen drawn in Fig. 3 on the same plate. In the latter specimen the telotrochal swelling is flexed ventrally and the anus is on the apex of a slight cone. In some individuals at this stage the caudal appendage may be quite long. The prototroch has gone, but the telotroch remains, although its cilia are disappearing. The worm had a mucus tube which was attached to the bottom of the bowl. This is the most advanced stage to which this species has been reared from the egg. The single specimen reared as far as this was nearly fifteen weeks old.

Later stages have been obtained by rearing larvæ from the plankton. Fig. 2, Plate VI, is a ventral view of the head region of such a stage. The " palps " are only just arising, but as in *S. alveolata* there is considerable variation in the time of appearance. The hood has shrunk to very small proportions and is represented by a darkly pigmented patch anterior to the mouth. Above it is the ciliated anterior conical projection or " snout."

A dorsal view of the most advanced specimen obtained is shown in Fig. 1, Plate VIII. It is especially interesting in that the primary crown paleæ have been replaced by a secondary set. The new paleæ of the outer row have the appearance shown in Fig. 2, Plate IX, and they resemble somewhat the adult paleæ of the same row. There are six of these paleæ on the left and eight on the right side, but the crown was slightly damaged by clogging masses of diatoms when the specimen was obtained, and some may have fallen out. Inside the outer row other paleæ are present. These are three in number (Plate IX, Figs. 3, 4, and 5) and they are rather like the paleæ of the inner two rows of the adult. Unfortunately, owing to the way in which the crown was damaged, their actual positions in the crown are uncertain. A curved bristle is present in the inner side of each peduncle, as in *S. alveolata*. The parathoracic parapodia contain about five bristles in each dorsal bundle. The first pair of abdominal uncinigerous processes have about twenty uncini each, the second pair about eleven each, and the third pair five or six each. The number of chætæ in the ventral bundles of all segments is doubtful, but there are most probably two or three bristles in each ventral bundle of the parathoracic segments and one bristle in each ventral abdominal bundle. A pair of small swellings (only one is visible in the drawing), just anterior to the shrinking telotrochal swelling, may possibly be the developing fourth pair of uncinigerous processes, but if so, they are in a rather different position from the similar swellings in *S. alveolata*. A nototroch is present close to the posterior border of each segment, and a short one exists between the two pairs of eye-spots. As in the allied species, after metamorphosis, the anterior pair of these are closer together and situated more ventrally than the posterior pair.

Two young worms were obtained in which each peduncle of the crown carried one or two paleæ of the secondary type (Plate IX, Fig. 2). These were situated at the dorsal end of the curved outer row, the remainder of the paleæ in the row all being of the primary type (Plate IX, Fig. 1). We may perhaps conclude from this that the primary paleæ fall out and are replaced in regular sequence starting from the dorsal end of the curved row.

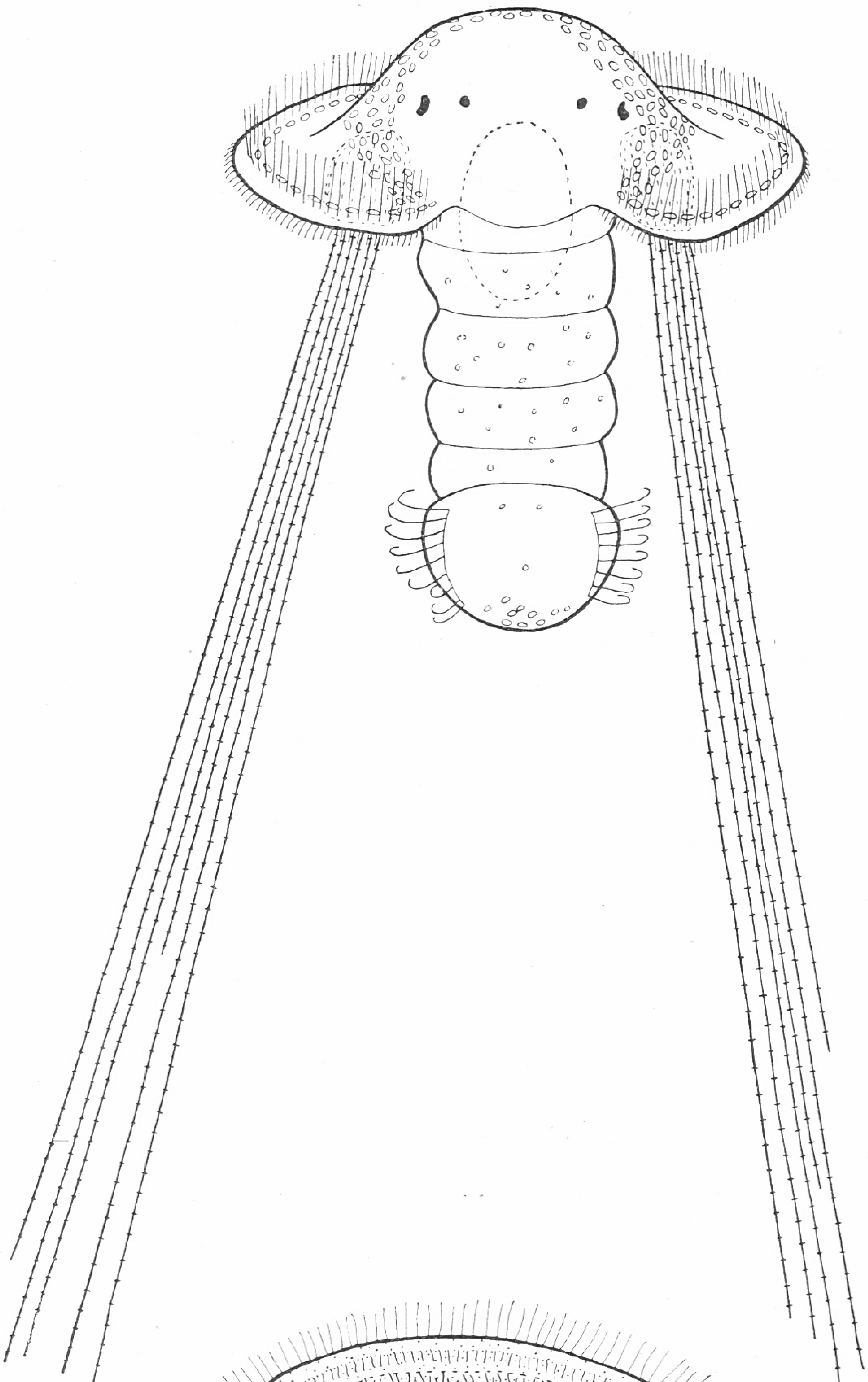
The building operations of this species have not been observed.

5. THE LARVA OF *PALLASIA MURATA* ALLEN.

Besides the two species of Sabellaria, the larvæ of which have just been described, one other Sabellarian has been recorded for the British Isles. This is the rare *Pallasia murata*, which has been described by Allen (**1**) as occurring in the neighbourhood of Plymouth, and of which only a very few specimens have been obtained, although the empty tubes are moderately common. Very little is known concerning the larval stages, but Caullery describes and figures (**3**, p. 172, and Fig. 3) a larva which he found in the plankton at Wimereux and which almost certainly belongs to this genus and most probably to the species also. It was in an advanced stage of development with primary crown chætæ at the base of the dorsal part of each bundle of provisional bristles. One of these chætæ was a strong hook resembling closely the hook present on the dorsal surface of each peduncle of the adult Pallasia. Close by each chæta-sac were about ten tentacular cirri, probably the papillæ which form a row along the external margin of each adult peduncle, and corresponding to similar papillæ in Sabellaria, in which only two are found by each chæta-sac in the later pelagic and early bottom stages. Four parathoracic segments were present, a feature in which Pallasia differs markedly from Sabellaria, where there are only three. The larva had also nine pairs of uncinigerous processes instead of only three as in Sabellaria larvæ. The anal cone, corresponding to the telotrochal swelling in Sabellaria, is of special interest in that, posterior to the telotroch, it presented fine transverse constrictions which may represent segments that will form the caudal appendage. There can be little doubt, after a consideration of these points, that this larva was indeed the larva of Pallasia, as Caullery demonstrated. It may be that his earlier larvæ also belong to the same genus, but this is at present impossible to decide. The pigment on the back, which in the Sabellaria larvæ described in this paper was very dark brown, or black in general appearance, is referred to by Caullery as "violacé" in both his early larvæ and in his Pallasia larva. This may or may not prove to be a distinction between the two genera.

Towards the end of February, 1927, at the very beginning of the present observations, and while engaged in picking out from the plankton Sabellaria larvæ which were at that time thought to be some form of Spionid, a single larva of the same type, but of a strikingly different general appearance, was obtained. Rough sketches of the dorsal aspect and of the mouth region in ventral view of this larva were made at the time and are reproduced in Text-Figs. 4 and 5. The larva was not observed in any great detail in case prolonged confinement in a cavity-slip should kill it, for it was hoped to rear it to a stage at which the genus, at least, could be determined. Unfortunately these hopes were not realised, and the larva subsequently died without further development. Since then the searching of many plankton catches has failed to yield another specimen. These rough sketches, however, have now a special interest, for it is very probable that this is the larva of *Pallasia murata* Allen. That assumption is based on the fact that *P. murata* is the only species of Sabellarian besides *S. alveolata* and *S. spinulosa* which has been recorded from anywhere reasonably close to the British Isles, and it is known to occur on grounds close to where this particular and distinctly Sabellarian larva was caught.

The larva was much bigger than the corresponding stage of Sabellaria, and the provisional bristles were longer and straighter. The hood and



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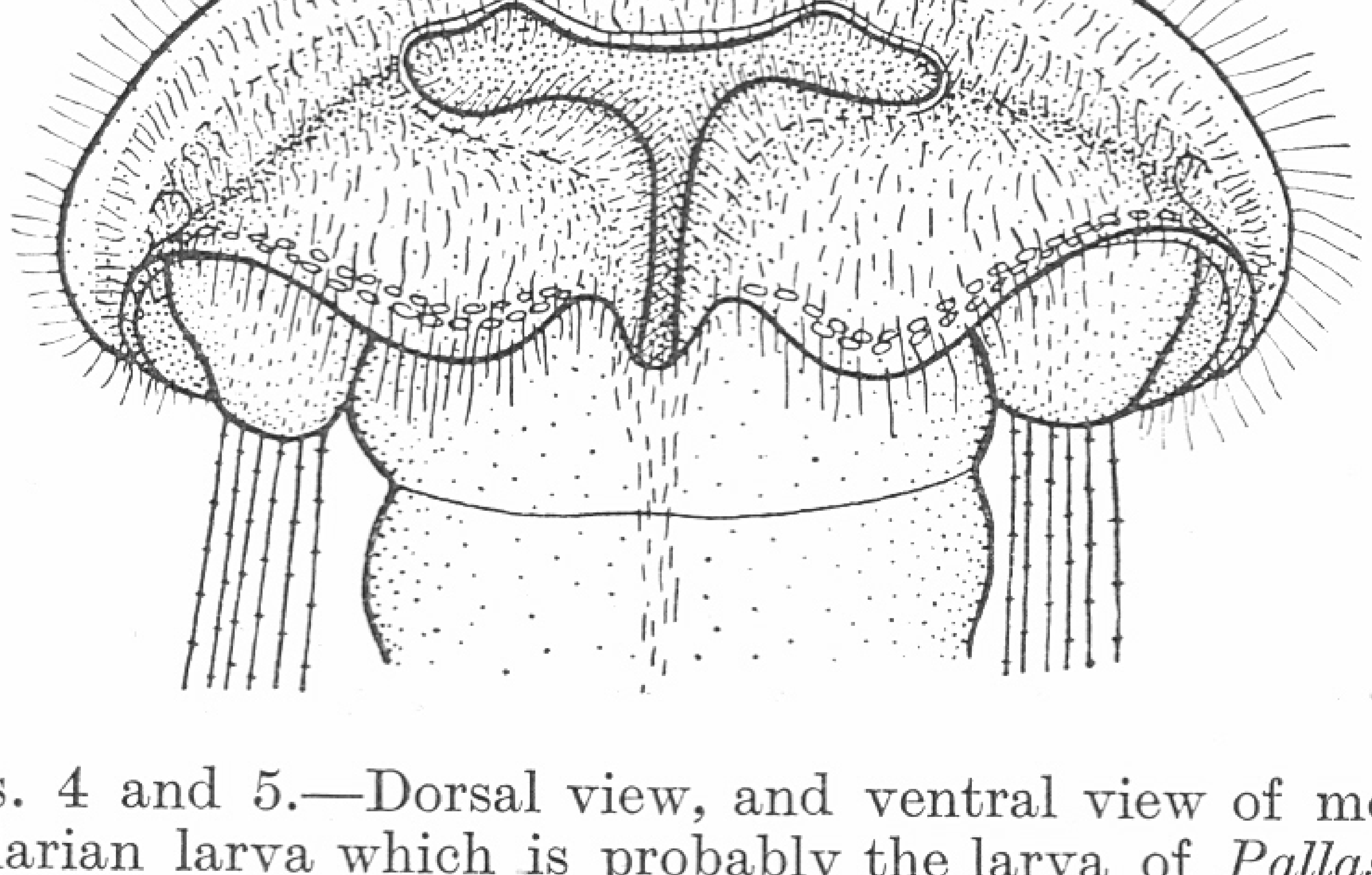

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TEXT-FIGS. 4 and 5.—Dorsal view, and ventral view of mouth region, of a Sabellarian larva which is probably the larva of *Pallasia murata* Allen. Sketch from life $\times 156$. Actual length (excluding bristles) approx. 410μ.

lip-folds were more highly developed than they are in Sabellaria, but in their essential structure they were the same. Chromatophores of a beautiful pale green colour were scattered over certain regions of the hood and arranged in a row just anterior to the prototroch. Two pairs of eye-spots were present. The ciliation appears to have been the same as in Sabellaria. The manner in which the telotroch is drawn is interesting; the cilia shown are obviously grasping-cilia. No driving cilia are represented although it is highly probable that some were present. This drawing was made before the grasping-cilia in Sabellaria had been observed and at the time their function was certainly unsuspected.

In two points this larva can be compared with Caullery's latest stage. Thus the extra development of the hood-fold is indicated in his drawings (**3**, Fig. 3). Secondly, Caullery writes of the chromatophores as being yellow in colour, but the colour may change with age, as it does to some extent in Sabellaria, where the chromatophores gradually become darker brown when viewed as a whole.

6. KEY TO THE BRITISH SABELLARIAN LARVÆ.

It is now possible to construct a tentative key which will enable plankton workers to distinguish the later pelagic stages of the three British species of Sabellarians.

1. Provisional bristles less than 400μ long. Hood-fold fairly prominent. Chromatophores brown or yellow in general appearance..........2
   Provisional bristles approx. 760μ long. Hood-fold very prominent. Chromatophores a beautiful pale green colour or possibly yellow in the later stages..3
2. Primary crown chætæ, which appear among the bases of the provisional bristles during the later stages, very broad and flat, very slightly toothed (Plate IX, Fig. 12).................*S. alveolata*
   Primary crown chætæ long, slightly trough-shaped, of moderate width and very strongly toothed along both edges (Plate IX, Fig. 1) *S. spinulosa*.
3. In addition, during later stages, a strong hook by the base of each bundle of provisional bristles; four parathoracic segments and more than three pairs of uncinigerous lobes................*Pallasia murata*.

It is at present impossible to separate the early stages of the two species of Sabellaria.

7. PREVIOUS RECORDS OF SABELLARIAN LARVÆ.

De Quatrefages appears to have been the first to record the eggs and larvæ of Sabellaria. In 1847 he published a short paper (**17**) dealing mainly with fertilisation and the fertilisation membrane, followed in the next year by a longer paper (**18**) discussing those subjects in great detail, and containing also an account and figures of the segmentation and the early larvæ of a species of Sabellaria. He figures the prototroch as a wide band of cilia, which was entirely lost in his latest stage with four bristles on each side. At this stage his larvæ died. In 1850 he published another paper (**19**), describing various experiments on the artificial fertilisation of Sabellarian ova. No further work on this subject was published until 1881 when Horst (**12**) described his researches on the early development of *S. alveolata*. A short extract (**13**) of this paper was brought out about the same time. A plate of figures accompanied the longer paper, most of them concerned with the segmentation stages, in which Horst disagrees with the account given by de Quatrefages. A figure of the trochophore is also given on this plate with the chromatophores shown in colour. The colouring is quite good. He has, however, failed to distinguish the hood-fold from the lip-fold; they are shown as if they were fused into one. The strong forward arching of the prototroch over the mouth does not exist in a free-swimming larva, but might be caused by pressure beneath a cover-glass. In 1885 von Drasche (**5**) described the segmentation and early stages of *S. spinulosa*. His figure of the trochophore is also coloured, but, while he illustrates the greenish yellow ground colour of the chromatophores quite faithfully, in only two of them does he show the brown specks. A single eye-spot is shown, but is placed on the right side instead of on the left. During the present research this single eye-spot which appears first has never been seen on the right side, but always on the left. Several prototrochal rows of cilia are drawn with the cilia in the posterior rows about as long as in the anterior row. He does not seem to have realised the presence of the hood-fold, and the lip-folds are drawn to appear as though they pass below instead of above the provisional bristles. It is also interesting to note that he states that the fertilisation membrane (" Eimembran ") is lost and does not form the cuticle of the larva. Nothing further was known until 1914, when Ziegler published another account (**21**) of the segmentation and early larvæ of *S. spinulosa*. He gives figures of the trochophore stage with six bristles in each bundle, in which he indicates the hood-fold. In the same year Caullery published his valuable paper (**3**), pointing out the chief characters of Sabellarian, as distinct from Spionid larvæ. This paper has already been frequently referred to. Since that time no further work on Sabellarian larvæ has been published, except that McIntosh has given some outline figures (**15**, Plate XCIV) of larvæ which probably belong to this group. Unfortunately there appears to have been some confusion in the numbering of this plate. Figs. 8 and 9 are probably Sabellarian larvæ; the former is stated to be a Spionid larva, while Fig. 9 is not referred to. Figs. 10 and 11 are stated to be probably Sabellarian larvæ; the former is certainly not, but the latter may be. There is no Fig. 11*a*. Some of this numbering was corrected in a later volume (**16**, p. 5).

In addition to the foregoing publications where Sabellarian larvæ are referred to as such there exist a number of papers containing figures of larvæ which almost certainly belong to the Sabellariidæ, although they are usually described as some form of Spionid. Busch, as early as 1851, figures these larvæ (**2**, Taf. VII, Figs. 5–8), which he obtained off Heligoland, the Orkneys, Cadiz, Malaga, and Trieste, but he does not name them. Fewkes (**7**) gives three figures (Plate II, Figs. 1–3), and describes them under the name of Spio sp. without giving any reasons for attributing them to that genus. He obtained his larvæ at Newport, U.S.A. Häcker also described and figured (**11**, p. 16, Taf. II, Figs. 14 and 15) similar larvæ from the west coast of Africa, and likewise called them Spio. Caullery has already suggested that the larvæ of these three authors were really Sabellarians. Both Fewkes and Häcker refer to a paper by Leuckart and Pagenstecher (**14**) who give figures of different stages of a larva which, without bringing forward any real evidence, they had referred to Spio in the following words: "Es handelt sich hier ohne Zweifel um eine *Spio*, deren Charaktere sich jedoch nicht so weit ausbildeten, dass sie eine Artunterscheidung mit Bestimmtheit gestattet hätten." They believed the species might be *Spio crenaticornis* on account of the similarity of the tentacle wrinkles of that species and those of their latest larva, and also because *S. crenaticornis* was common in Heligoland where their larvæ were obtained. Their figures (Taf. XXIII, except Fig. 1), however, show the Sabellarian characters; even a few primary crown paleæ are indicated among the provisional bristles of their oldest stage. In the latter, it is true that five pairs of parathoracic parapodial bristle bundles are shown and no abdominal uncinigerous lobes, but the other characters, including the general shape, are so certainly Sabellarian that this can be regarded as an error of observation. Thus the responsibility of being the first to attribute Sabellaria larvæ caught in the tow-net to the genus Spio appears to rest with these joint authors and their identification was later accepted by both Fewkes and Häcker.

Claparède's early Leucodora (Polydora) larvæ (**4**, Taf. VII, Figs. 4–5) were also very probably trochophores of Sabellaria, at a stage when they had got nine or ten bristles in each bundle and before the trunk region had begun to be definitely segmented. As was pointed out in a previous paper (Wilson, **20**) Gravely (**9**, p. 46), accepting these figures and also Fig. 6 on the same plate as the larvæ of Polydora, described as metatrochophores of that genus some larvæ which he had found on several occasions in the July plankton at Port Erin. His description of these metatrochophores (which were only examined in the fixed contracted condition), so far as it goes, corresponds very well, except for one point, with Sabellaria larvæ, and not at all to Claparède's Fig. 6, Taf. VII, as Gravely himself seems to have realised. The point in which the description does not correspond is in the length of the provisional bristles, which are stated to be 850μ long, which would make them longer than the bristles of Pallasia. These bristles are described as ringed, but it is not stated that the rings (collars) were toothed. In another paper Gravely repeats Claparède's figure (**10**, Text-Fig. 3a), and uses it in a discussion on the probable mode of development of the vestibule in Polydora. If, as is highly probable, this larva is really Sabellaria, then the notch shown in the prototrochal rim in the neighbourhood of the mouth would indicate the lip-folds. The ciliated œsophagus is represented as running in an anterior direction just as it does in Sabellaria larvæ. In any case this larva and Gravely's metatrochophores are certainly not Polydora. The same remark applies to the metatrochophore figured by Flattely (**8**, Fig. 1) who, following Gravely's description, called it Polydora. The figure shows the Sabellarian characters.

8. NOTE ON THE CAUDAL APPENDAGE OF SABELLARIA.

Comparatively little appears to be known of the internal structure of the caudal appendage. This smooth achætous posterior region is usually stated to be "unsegmented." Externally at all events that does, indeed, appear to be the case, but sections reveal the presence of a number of transverse septa, fifty or sixty in number, in the adult *S. alveolata*. The gut is fused to the dorsal and lateral body-walls of the appendage, but on the ventral side the two are separated by a space. The septa cross this space at regular intervals. The space is further divided by a median longitudinal mesentery which runs down the whole length of the appendage. These septa, the well-developed blood vessels associated with them, and the caudal appendage generally, were observed by the late Mr. Arnold T. Watson, whose original notes of an extensive series of observations, spread over many years, on the anatomy of the British species of this genus, I have been privileged to consult through the kindness of Mrs. Watson and Professor Fauvel. If these septa delimit true segments, and there appears to be no reason to suppose that they do not, then the caudal appendage is really a segmented structure composed of fifty or sixty segments. In development it arises from the posterior part of what has been termed the telotrochal swelling. It appears that it is from the region immediately anterior to this swelling that new chætigerous segments are produced, and that the greater part of the swelling shrinks away when the pelagic life is over. The telotrochal swelling, as a whole, cannot therefore be properly termed a pygidium, and it is for this reason that the former term has been used here.

Sections have been cut of the caudal appendage at the stage when it was growing out during metamorphosis, but the scarcity of material has rendered it impossible to give an account of the development of the internal structures.

9. SUMMARY.

1. *Sabellaria alveolata* Linnæus has been reared for the first time from the egg through the pelagic stages and metamorphosis to early bottom stages. The chief features in the development of the external characters are described and special attention is drawn to the existence of peculiar grasping-cilia on the telotroch. The manner in which the young worm builds its first tube of sand grains is also described.

2. *Sabellaria spinulosa* Leuckart has similarly been reared for the first time from the egg to early bottom stages. Its development is very similar to that of the preceding species, but during the later pelagic life the two can easily be separated, as the primary paleæ of the crown, which appear among the long provisional bristles of the first pair of parapodia, show a marked specific difference. The early stages cannot be distinguished.

3. A larva which is probably that of the rare *Pallasia murata* Allen is described.

4. A tentative key to the British Sabellarian Larvæ is drawn up.

5. The observations of previous workers are discussed. It is shown that Sabellarian larvæ have frequently been described as the larvæ of Spio or of Polydora, in spite of the fact that the early stages of Sabellaria had been obtained more than once from artificial fertilisations. Caullery was the first to point out the error, and he is fully confirmed in this paper.

6. It is shown that the caudal appendage of a full-grown *Sabellaria alveolata* possesses internally a series of fifty or sixty transverse septa.

10. APPENDIX.

The following is an original note, by the late Mr. Arnold T. Watson, which is of special interest in that it describes early bottom stages of *Sabellaria alveolata* only a little more advanced than the latest stage to which I have been able to rear my worms. The note is dated October 16th, 1915, and apparently refers to a mass of tubes and living worms of this species which were received at Sheffield from Seascale on October 7th.

" The mass received is in a very healthy condition and in parts was encrusted with numerous very young specimens—some slightly older than others. In all young specimens a median ciliated process arises between the two opercular lobes. In the youngest it was clearly seen arising separately a short distance behind the upper lip, and the membrane joining the lobes was further still from the back of the upper lip. In older ones the ciliated process seems adhering to the membrane. There is at this stage (when the worm would be about 1·1 mm. long and have three tentacles at each side in addition to the two central tentacles) an " eye-spot " at each side of the central ciliated process and through the dorsal face two other larger eye-spots—situated nearer the mouth—can be clearly seen. When the worm bends its peristomial lobes to form a right-angle with its body both sets of eye-spots can be seen in top view forming a square. The papillæ external to the paleæ (about three or four on each side) are much longer in proportion than in the adults, and some of them (possibly all) are tipped with " tactile (?) hairs." The young Sabellarians in situ are difficult to see ; as in this specimen the lobes look like black specks and correspond closely with adjoining black sand-grains.

" A young specimen about 1·1 mm. long when extended alive has two tentacles on each side of the peristomial lobes (in addition to the two long median tentacles) and three cirri just below the paleæ, viz. : one long one at the dorsal edge and one at the ventral end of the crescent and one intermediate between the two—each with ' tactile hairs.' Two dorsal eye-spots about the level of start of long tentacles. The median ciliated process is very evident but difficult to tell whether it was above or under the membrane."

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PLATE I.

Larvæ of *Sabellaria alveolata* Linnæus. All drawings from life $\times$ 156. All measurements exclude apical cilia and bristles.

FIG. 1.—Free-swimming embryo 27 hours after fertilisation. Actual length approx. 95μ (see page 223).

FIG. 2.—Embryo 46 hours after fertilisation. Actual length approx. 95μ (see page 224).

FIG. 3.—Embryo 61 hours after fertilisation. Actual length approx. 100μ (see page 224).

FIG. 4.—View of right side of the same larva as shown in Fig. 3.

FIG. 5.—Larva 91 hours old. View of left side. Actual length approx. 100μ (see page 225).

FIG. 6.—Ventral view of the same larva as shown in Fig. 5.

FIG. 7.—Larva about five and a half days old. View of left side from a slightly ventral position. Actual length approx. 100μ (see page 225).

FIG. 8.—Larva about twenty days old. View of right side. Actual length approx. 165μ (see page 228).

FIG. 9.—Ventral view of the same larva as shown in Fig. 8.

FIG. 10.—Larva about six weeks old. Dorsal view. Actual length approx. 310μ (see page 223).

FIG. 11.—Ventral view of the same larva as shown in Fig. 10.

PLATE I.

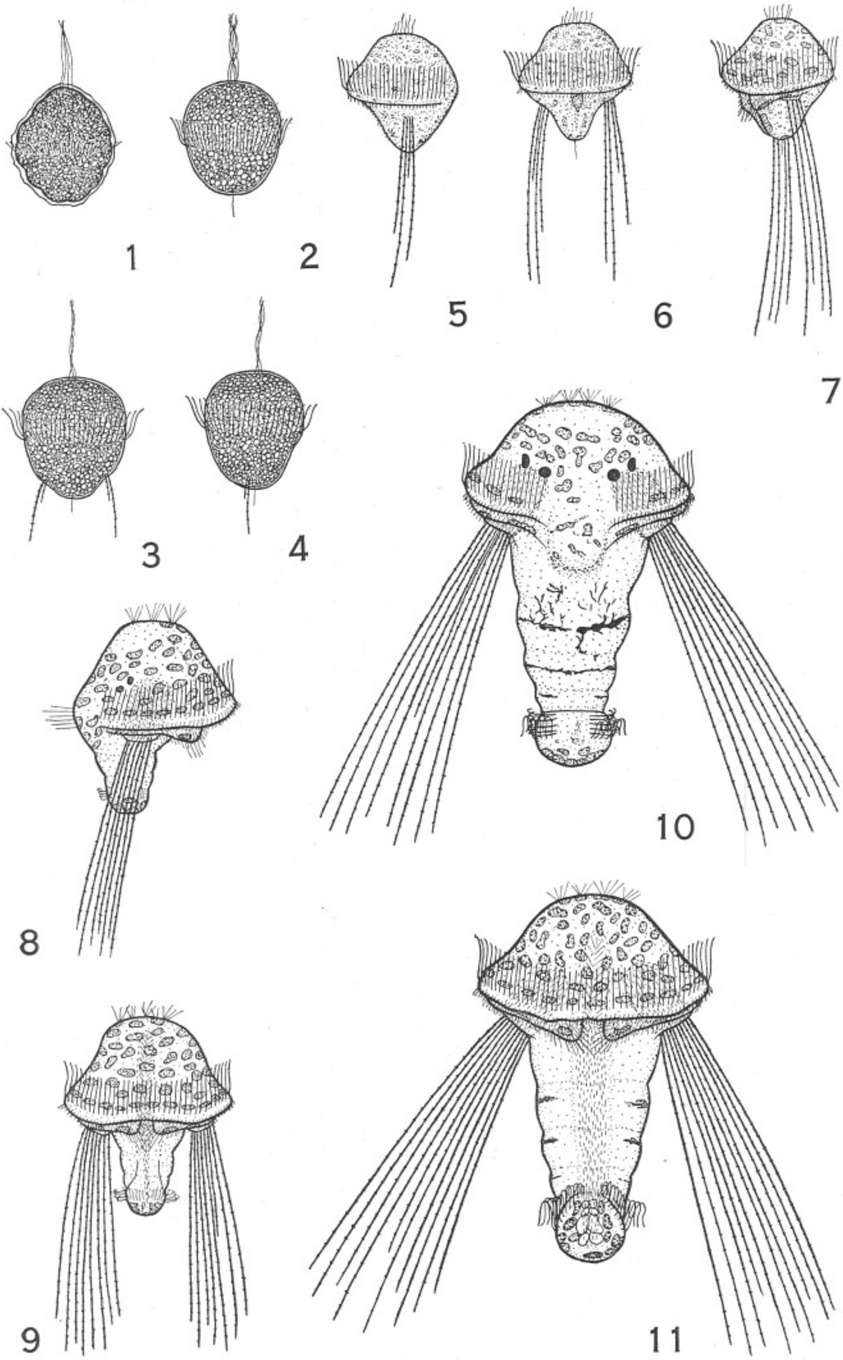


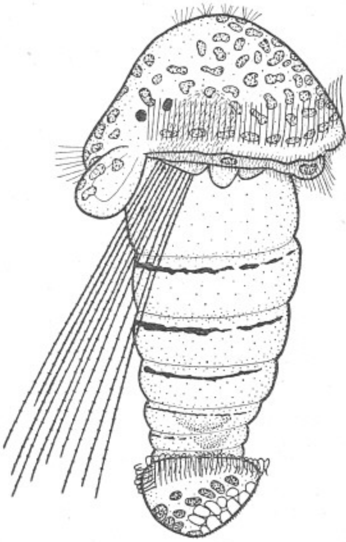
PLATE II.

Larvæ of *Sabellaria alveolata* Linnæus. All drawings from life $\times$ 156. All measurements exclude apical cilia and bristles.

FIG. 1.—Larva just over six weeks old. View of right side. Actual length approx. 435μ (see page 229).

FIG. 2.—Larva just over seven weeks old. View of right side. Actual length approx. 435μ (see page 229).

FIG. 3.—Larva about seven and a half weeks old. Dorsal view. Actual length approx. 500μ (see page 230).



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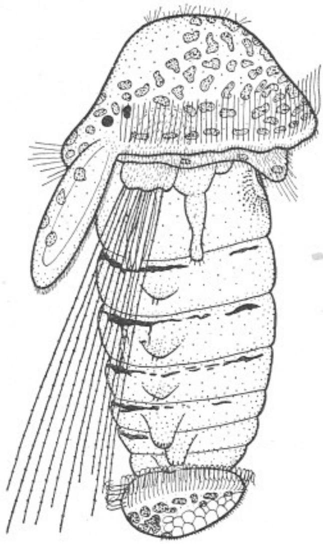

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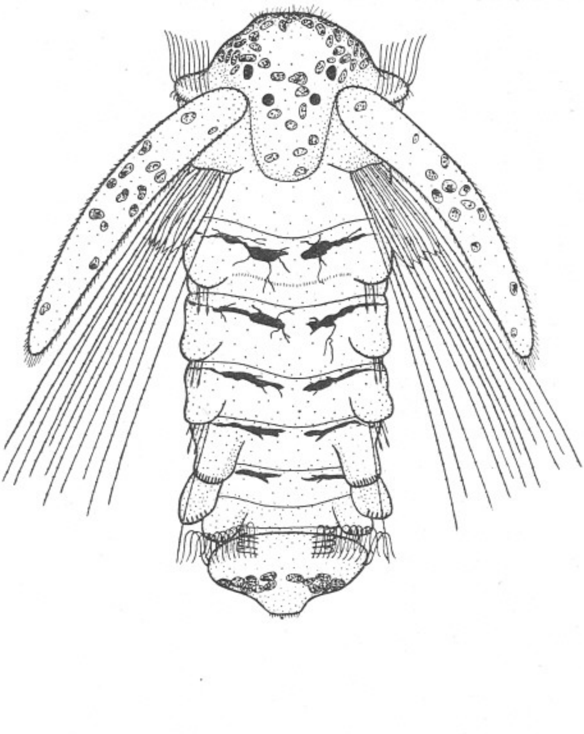

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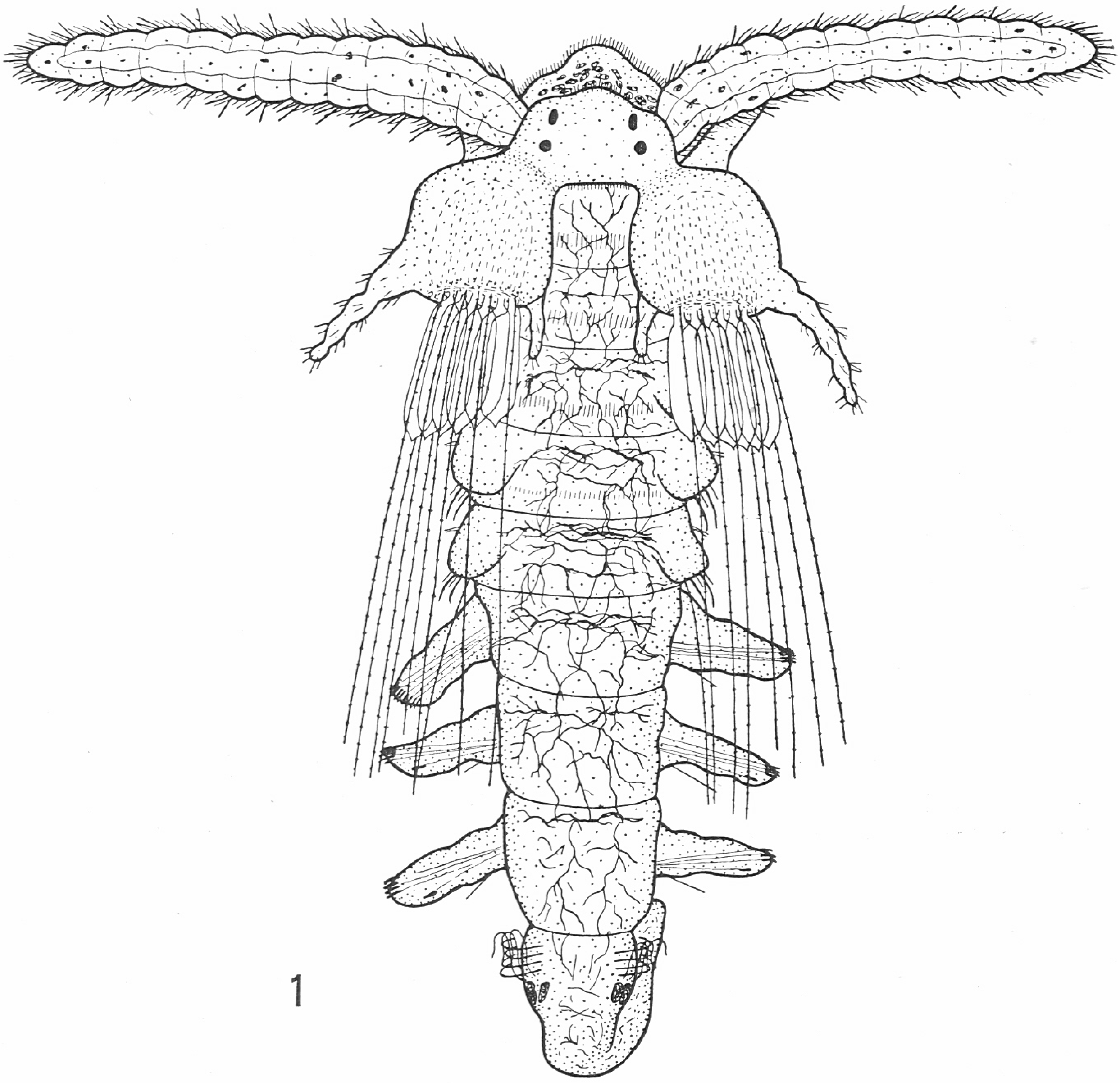
PLATE III.

Larvæ of *Sabellaria alveolata* Linnæus. All drawings from life $\times$ 156.

FIG. 1.—Dorsal view of metamorphosing larva about six and a half weeks old. Actual length, from anterior extremity of head to posterior bend, approx. 665μ (see page 234).

FIG. 2.—Ventral view of head region of larva just commencing to metamorphose. Stage earlier than that shown in Fig. 1 (see page 233).



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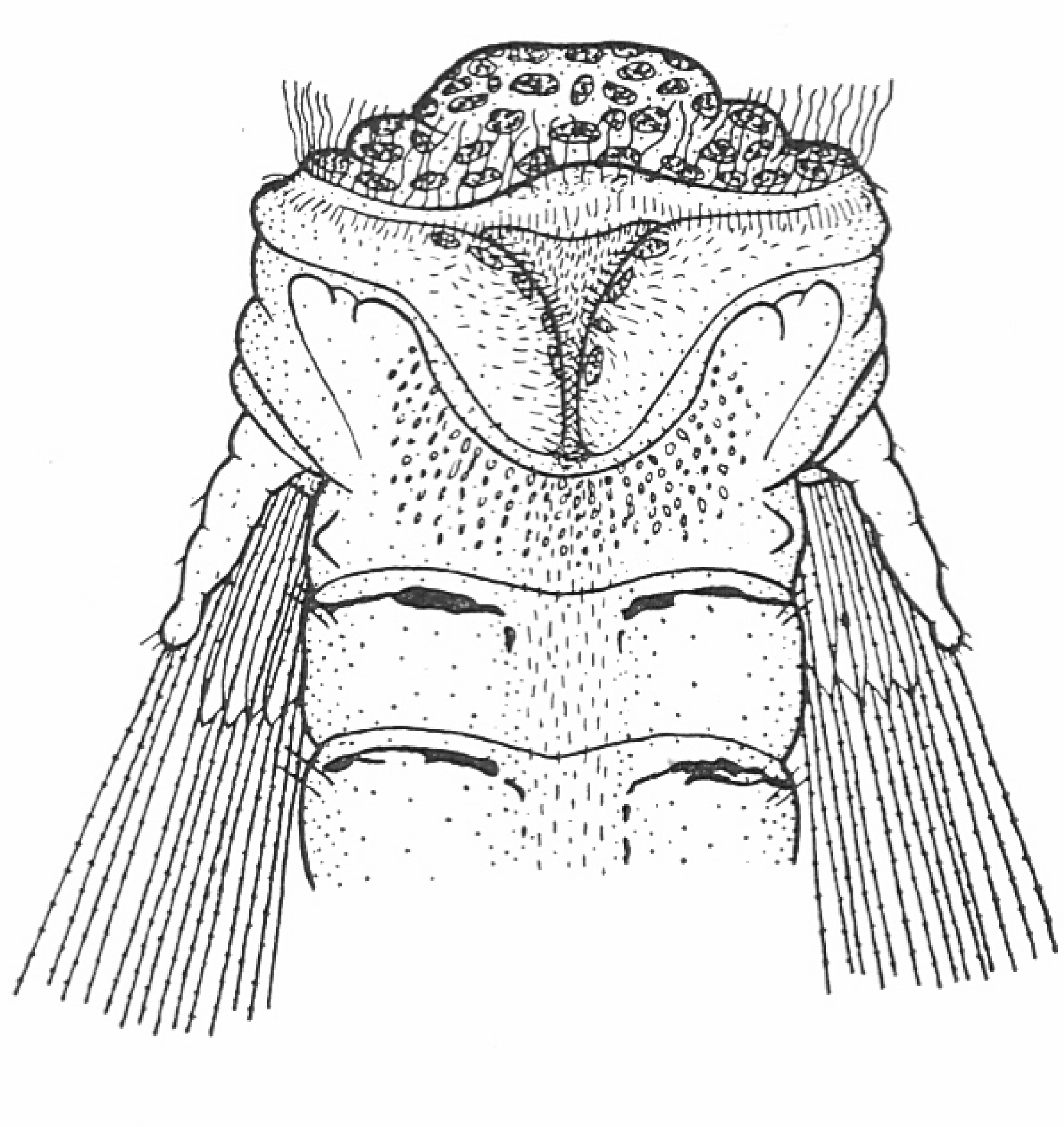

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PLATE IV.

Ventral view of early bottom stage of *Sabellaria alveolata* Linnæus. Drawn from life $\times 156$. Age just over seven weeks after fertilisation. Actual length, from tip of snout (seen between the peduncles) to posterior flexure, approx. 780μ (see page 234).

PLATE IV.

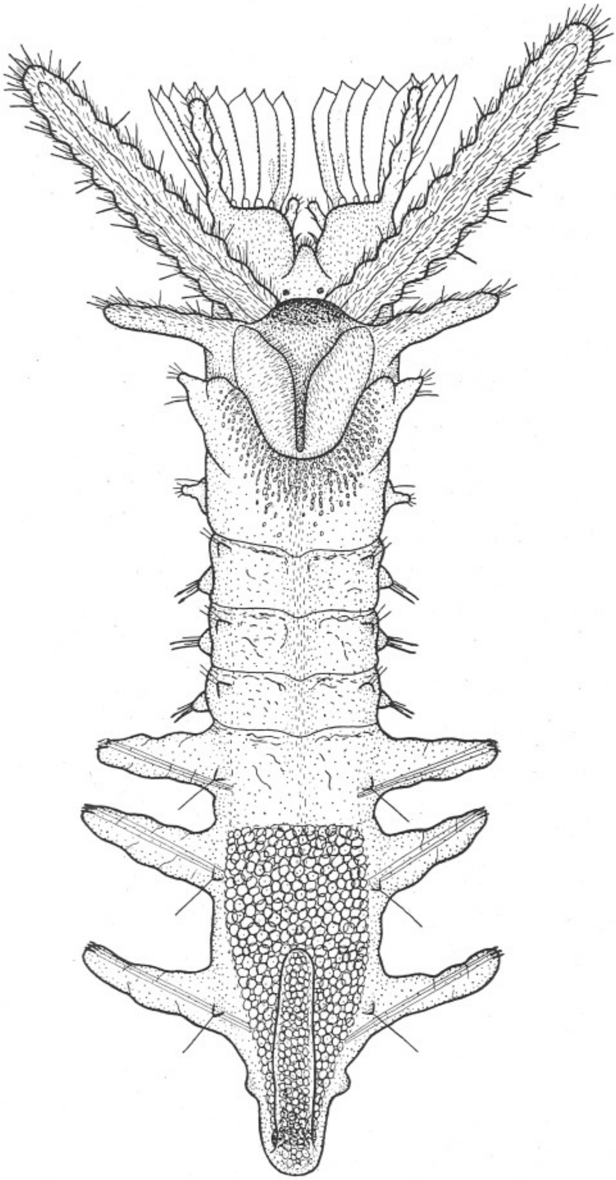

PLATE V.

Larvæ of *Sabellaria spinulosa* Leuckart. All drawings from life $\times 156$. All measurements exclude apical cilia and bristles.

FIG. 1.—Free-swimming embryo 31 hours after fertilisation. Dorsal view. Actual length approx. 90μ (see page 239).

FIG. 2.—View of left side of the same embryo as shown in Fig. 1.

FIG. 3.—Embryo 55 hours after fertilisation. View of right side. Actual length approx. 90μ (see page 239).

FIG. 4.—Ventral view of the same embryo as shown in Fig. 3.

FIG. 5.—Larva just over four days old. Ventral view. Actual length approx. 90μ (see page 239).

FIG. 6.—Larva about three weeks old. Ventral view. Actual length approx. 180μ (see page 239).

FIG. 7.—Larva about two months old. View of right side. Actual length approx. 370μ (see page 239).

FIG. 8.—Ventral view of the same larva as shown in Fig. 7.

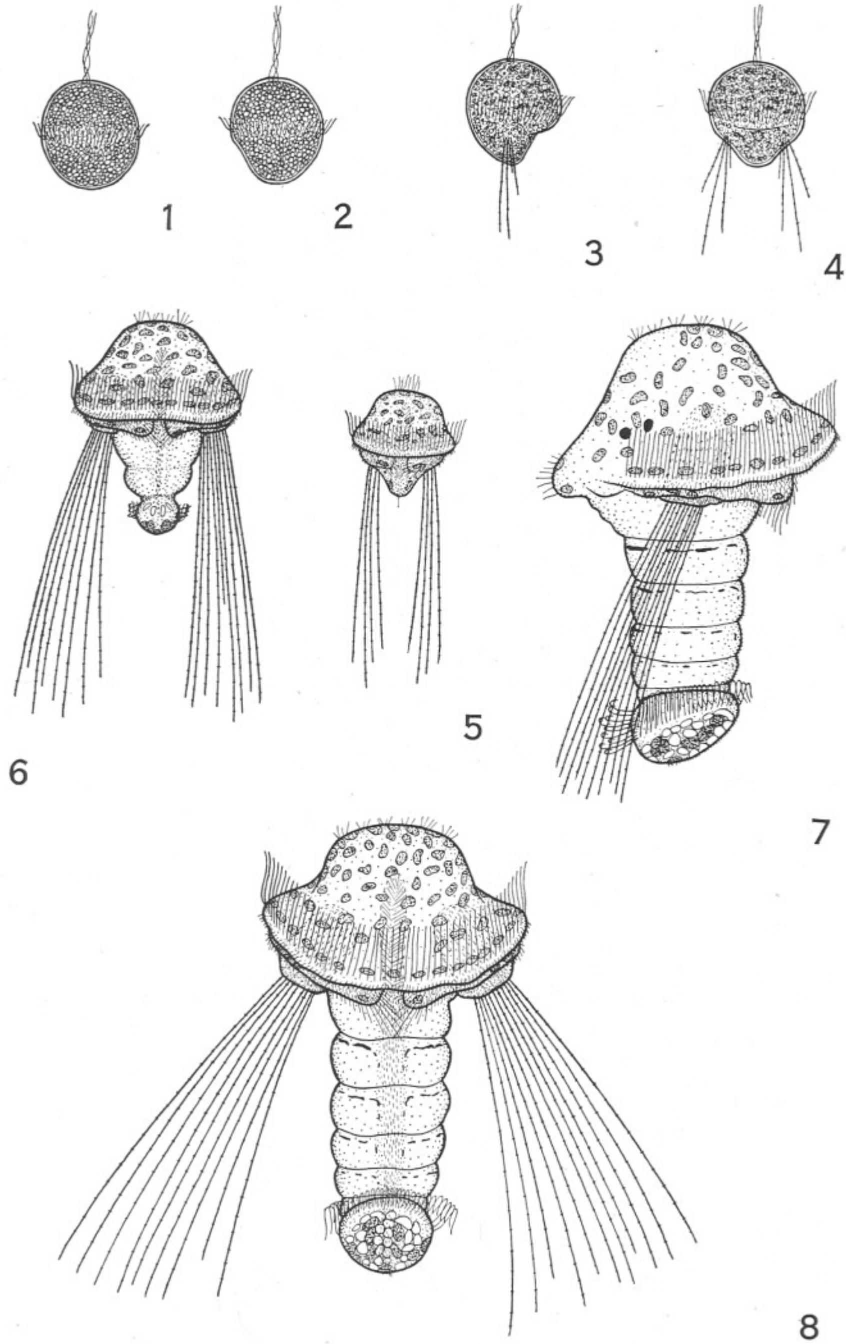
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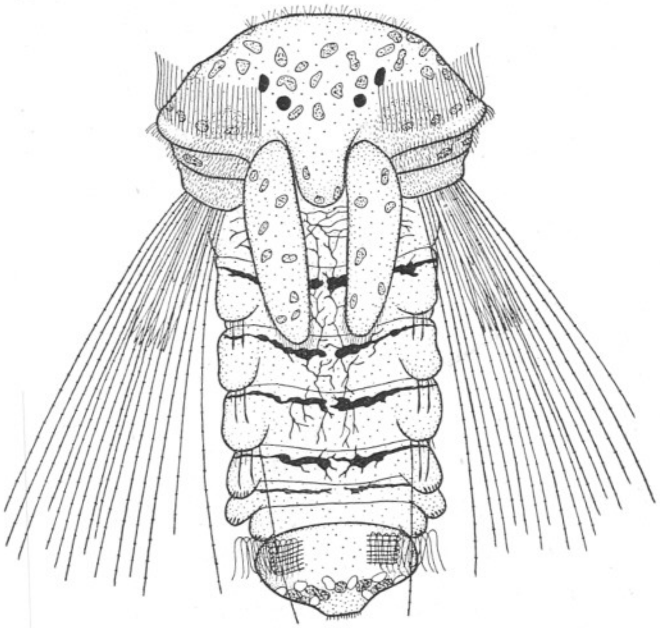
PLATE VI.

Larvæ of *Sabellaria spinulosa* Leuckart. Drawings from life $\times 156$.

Fig. 1.—Larva about two months old. Dorsal view. Actual length approx. 500μ (see page 239).

Fig. 2.—Ventral view of head region of a metamorphosed early bottom stage (see page 240).

PLATE VI.



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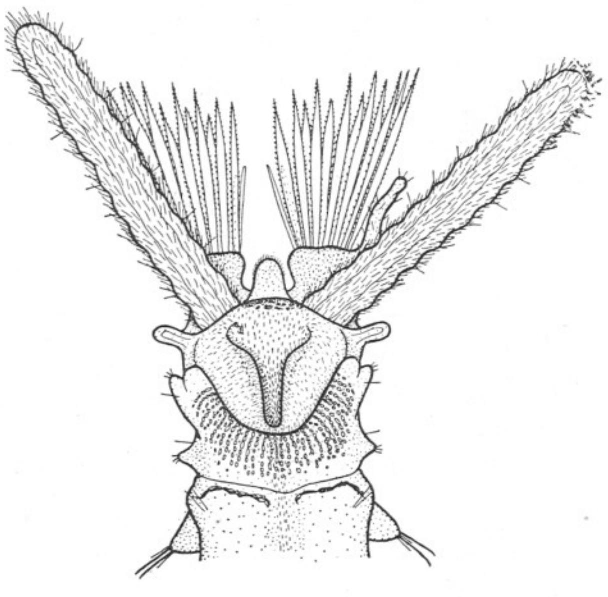

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PLATE VII.

Larvæ of *Sabellaria spinulosa* Leuckart. Drawings from life $\times 156$.

Fig. 1.—Ventral view of anterior end of a larva just commencing to metamorphose (see page 240).

Fig. 2.—Dorsal view of anterior end of metamorphosing larva about four months old (see page 240).

Fig. 3.—Ventral view of metamorphosing early bottom stage. The drawing is from a specimen picked out from the plankton before it was ready to metamorphose. A single specimen has been reared from the artificially fertilised egg as far as this stage with which it corresponded in every important particular. It was then nearly three and a half months old. Actual length (excluding tentacles) approx. 670μ (see page 240).

PLATE VII.

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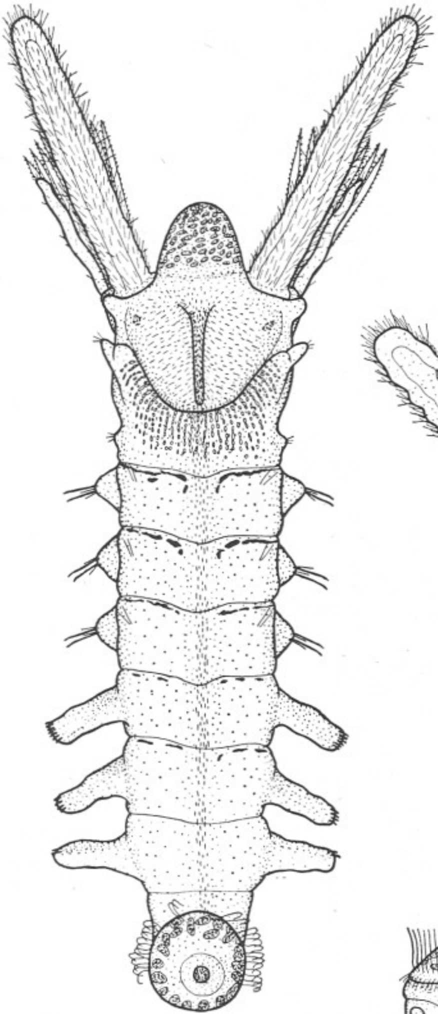

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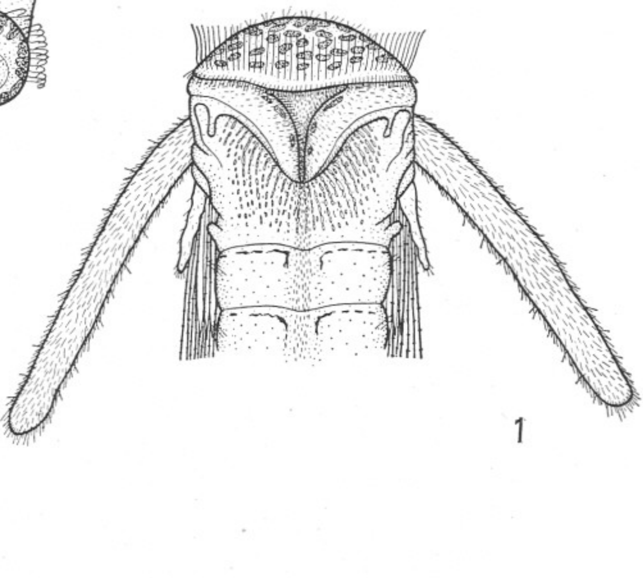

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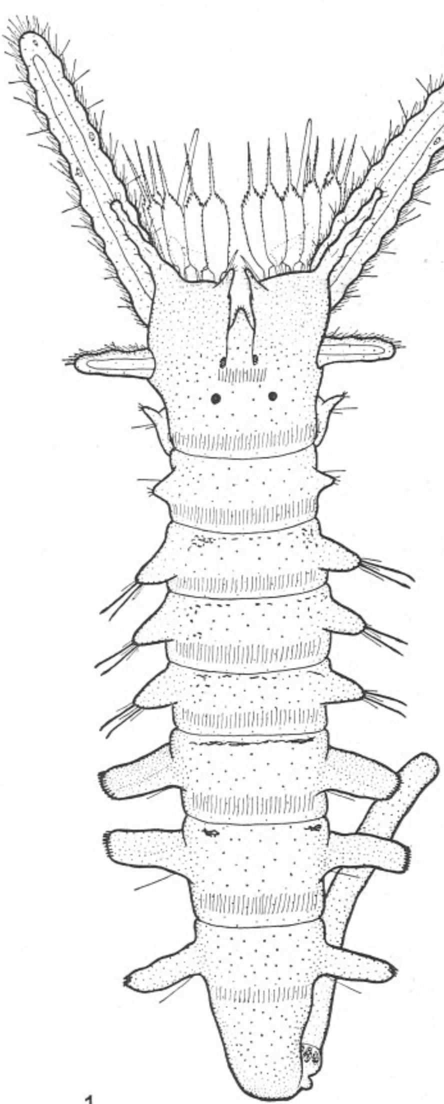
PLATE VIII.

Fig. 1.—Early bottom stage of *Sabellaria spinulosa* Leuckart. Dorsal view from life $\times 156$. Actual length, from tip of snout (seen between the peduncles) to posterior flexure, approx. 665μ (see page 240).

Fig. 2.—Mucus and first sandy tube of early bottom stage of *Sabellaria alveolata* Linnæus $\times 39$. Actual length of sandy portion about 1·9 mm. (see page 238).



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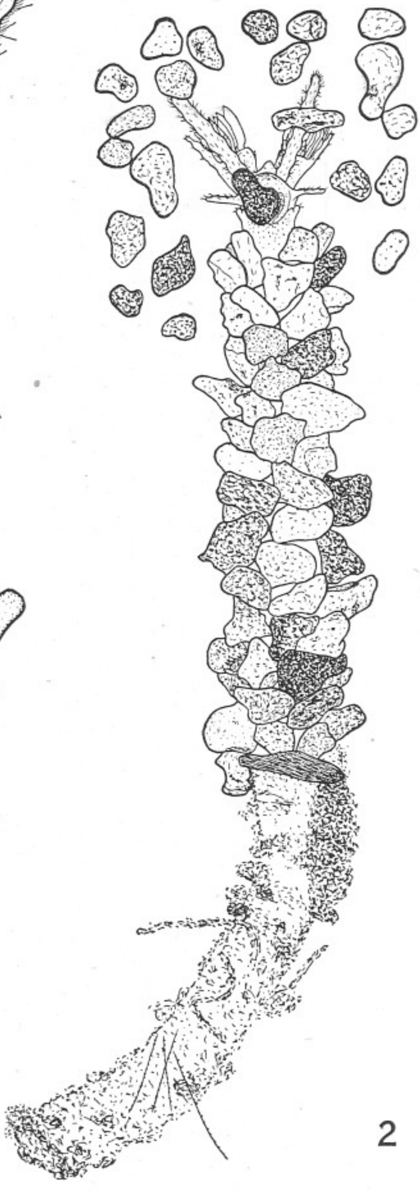

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PLATE IX.

All drawings, except Fig. 19, $\times 620$.

A. Chætæ from larvæ and early bottom stages of *Sabellaria spinulosa* Leuckart.

FIG. 1.—One of the primary crown paleæ.

FIG. 2.—One of the secondary crown paleæ.

FIGS. 3, 4 and 5.—Paleæ from one crown of the individual drawn in Fig. 1, Plate VIII.

FIG. 6.—Bristle from crown.

FIG. 7.—Bristle from crown.

FIG. 8.—Spear-shaped bristle from a parathoracic segment.

FIG. 9.—Slender bristle from a parathoracic segment.

FIG. 10.—Uncinus.

B. Chætæ from larvæ and early bottom stages of *Sabellaria alveolata* Linnæus.

FIG. 11.—Portion of ringed provisional bristle.

FIG. 12.—One of the primary crown paleæ.

FIG. 13.—Bristle from crown.

FIG. 14.—Bristle from crown.

FIG. 15.—Bristle from inner side of peduncle.

FIG. 16.—Spear-shaped bristle from a parathoracic segment.

FIG. 17.—Slender bristle from a parathoracic segment.

FIG. 18.—Uncinus.

C. Hood and lip-fold of *Sabellaria alveolata* Linnæus.

FIG. 19.—Diagrammatic section through prototroch of an early larva to show roughly the extent of folding at the sides of the body.

PLATE IX.