Development of *Scolecolepis fuliginosa* (Claparède).

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With 16 Figures in Text.

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INTRODUCTION.

MUCH is already known of Spionid larvæ from descriptions of planktonic forms, but very few species have been reared from the egg through the larval stages to metamorphosis. The egg and early stages of Scolecolepis are figured by McIntosh (1915) and by Claparède and Micznikow (1868), but there is no complete account of the development to be found in the literature. By the courtesy of the Director of the Marine Laboratory at Plymouth I was able to undertake this work, and I am indebted both to Dr. Allen and Mr. D. P. Wilson for advice and help during the course of the research.

In the arrangement of the paper the aim has been to describe fully certain stages in the life history, and to give as concise an account as possible of the development from one stage to the next.

METHODS.

Scolecolepis fuliginosa (Claparède) lives in black mud containing a large percentage of decomposing organic matter, and though localised, the worms are plentiful. At Plymouth they were obtained near the high-tide mark at Rum Bay, where they are covered by the tide for only two to three hours out of the twelve. The oxygen content of this mud is probably low. The worms live in sandy tubes lined with mucus, and the specimens were obtained by lifting loose stones and examining the mud beneath.

The mature worms were carried to the laboratory with the mud in which they live, and there allowed to clean themselves in sea-water. As it is impossible to ascertain the sex without injury to the worm, the whole sample was placed in a finger-bowl, where eggs and sperm were slowly extruded. Half an hour later, the eggs were removed with a pipette, washed free from sperm and placed in a sterilised finger-bowl with filtered sea-water. As soon as the young larvæ had begun to swim, the unfertilised eggs were removed and a few drops of Nitzschia culture, kindly supplied by Dr. Allen, were added as food. When the larvæ were found to be healthy, most of them were transferred to a plunger-jar, the remaining few being retained for continuous observation in the finger-bowl. These latter did not grow as quickly as those in the plunger-jar. From time to time, larvæ were removed and trapped on a cavity slide for observation, care being taken that they were not distorted by pressure ; others were killed at various ages by squirting hot Bouin on to them when swimming in a watch-glass. Bouin between 60° and 70° C. was found most suitable. Before sectioning they were first orientated on a piece of stained Ulva, to which they were attached by a solution of collodion in clove oil, which is hardened in equal parts of xylol and chloroform. This is a modification of the process recommended by N. Yatsu (1903). In general, the methods employed were those of Mr. D. P. Wilson.

Larval Development.

The unfertilised egg (Fig. 1) is very similar to that figured by Cunningham and Ramage (1888), Pl. XXXVI for Nerine. It is ellipsoidal, averaging 160μ long and 100μ broad, but size and shape are both variable. The cytoplasm is brown both by transmitted and reflected light. The margin of the egg is lobulated and there is a pale germinal vesicle near the centre, the whole being enclosed by an egg-membrane which appears to be very thick on account of its curious folds, which give the surface the appearance of a honeycomb. This membrane is punctate both internally and externally, the depressions on the one side corresponding to the elevations on the other.

About two hours after fertilisation the germinal vesicle and the lobulated margin are lost, and the cytoplasm rounds off within an inner fertilisation membrane (Fig. 2). Between the rigid egg-membrane and the contracted mass of cytoplasm a space is left and in this cavity several transparent spherical vesicles are to be seen ; these originate on the inner surface of the egg-membrane. Their function is not apparent and they are soon lost in the succeeding cleavage stages. The first cleavage is horizontal, the two cells so formed being unequal in size. Later a four-cell, an eight-cell, and between nine and ten hours after fertilisation

a sixteen-cell stage is reached, with four large yolk-laden macromeres and smaller and paler micromeres (Fig. 3). Gastrulation follows by epiboly.

Thus far the egg-membrane remains unchanged, but as the developing mass of cells increases in volume, the membrane is pushed out before it.

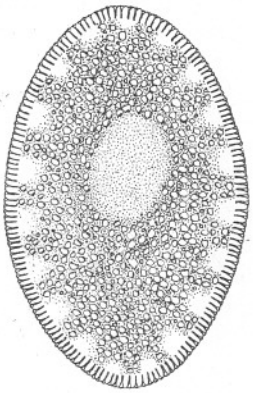

FIG. 1—Unfertilised egg. × 320. Actual length 160μ.

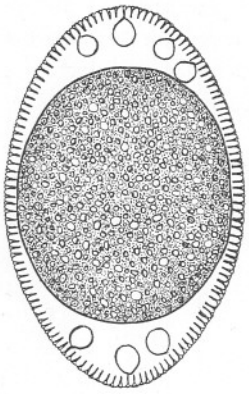

FIG. 2.—Fertilised egg. × 320. Actual length 160μ.

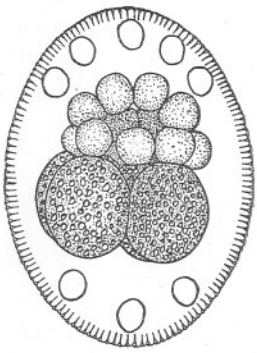

FIG. 3.—Sixteen-cell stage. × 320. Actual length 142μ.

This change in shape is not due to actual stretching of the egg-membrane, but rather to flattening and broadening of the papillæ on its surface. In cases of abnormal development, one part of the egg-membrane may be completely flattened so that a bubble appears on the surface of the larva.

The Trochophore.

The first trochophore (Fig. 4) becomes active and begins to swim less than twenty-four hours after fertilisation. It is about 200μ long, roughly coffin-shaped and dorsoventrally flattened. The colour is brown with a darker area where the gut is foreshadowed by the presence of yolk granules. There is a transparent space between the rigid egg-membrane and the developing mass of cells.

The prototroch is not a continuous line but as in Nerine, it is broken into groups of cilia. In this species there are fourteen groups well separated by longitudinal ridges of protoplasm and the containing egg-membrane. There are eight dorsal groups divided by a very broad median dorsal ridge into two groups of four. On the ventral surface there are six groups, three on either side of the mid-ventral line. The cilia of each group come through a single elongated slit in the egg-membrane.

A group of five very fine cilia form the apical tuft. It is probable that each of these cilia comes through a separate hole in the egg-membrane, for in later stages the apical cilia become separated. There is a single pair

of eyes set wide apart on the dorsal surface, at first red but later black. The mouth and anus are formed later.

Development of the Trochophore.

As the larva grows the wrinkled membrane is slowly flattened out, the papillæ becoming broader, the depressions shallower and the whole more closely approximated to the ectoderm.

The head becomes flattened anteriorly, the prototroch ridge forming

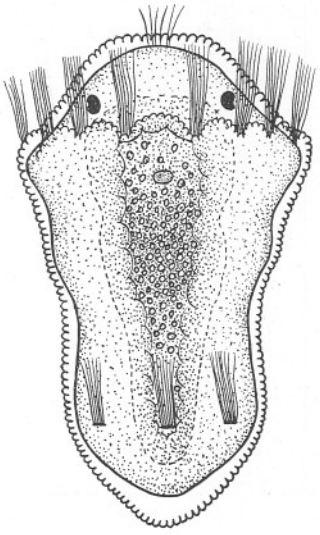

FIG. 4.—Ventral view of the trochophore, 36 hours old. × 320. Actual length 200μ.

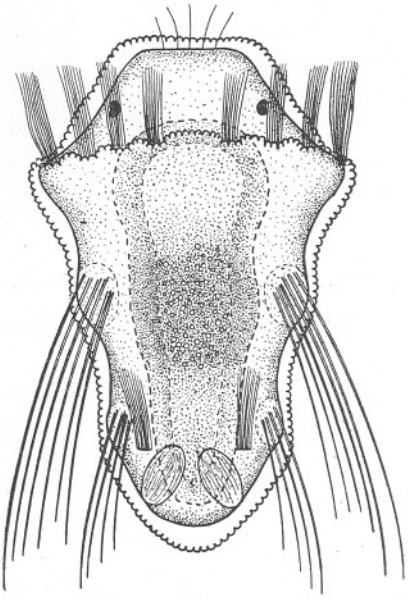

FIG. 5.—Dorsal view of the trochophore, 48 hours old. × 320. Actual length 206μ.

prominences on either side. A second pair of eyes and then a third are formed on the dorsal surface between the first two, which take up a lateral position anterior to the prototroch. Like the first pair, the second and third are at first red but soon change to black.

A rounded depression on the ventral surface foreshadows the position of the mouth. The egg-membrane dissolves at this point and the larva begins to feed. The circular mouth soon elongates and appears T-shaped with two anterior grooves. Meanwhile the outline of the gut becomes distinct and the dark yolk-granules are restricted to a rectangular area in the middle of the larva which lengthens and develops into the pigmented stomach-intestine or mid-gut. The anus is formed soon after the mouth.

Thirty-six hours after fertilisation the telotroch is formed, and like the prototroch is not continuous but appears as five separate groups. Two of these groups are dorsal and three are ventral. As the prototroch and telotroch develop, however, each cilia group broadens and the ridges between them disappear, so that the final result is a continuous line of cilia. The dorsal groups of the prototoch move round, and all except one on each side increase in size to form the swimming cilia of the prototroch. The ventral six groups remain small and are soon indistinguishable from the oral cilia which are formed on the sides of the mouth and extend to the ventral surface of the first setiger. The telotroch cilia increase equally in size, forming a continuous line ventrally and laterally, but leaving the broad dorsal gap that is characteristic of Spionid larvæ.

The provisional or larval bristles can first be seen as two minute structures within the prominences behind the prototroch ridges. At an age of two days the first bristle bundles are well developed, each with about four bristles, the largest is 150μ long, and reaches to the end of the larva (Fig. 5). All bristles are slightly curved and beset with spinules on the anterior margin (Fig. 14*a*). A second group and later a third are formed in the lateral elevations which become the parapodia of the second and third setigers. The larval bristles in these and succeding setigers are always slightly shorter than those of the first setiger.

At the time when the bristles of the third setiger become visible, a single pair and later numerous glandular cells are formed below the anus. They are large pale cells probably filled with mucus. Their openings to the exterior are on papillæ on the ventral and lateral surfaces of the anal segment. The function of these mucus cells is not apparent.

The Three-Setiger Larva.

When the larva is three days old the first three bristle bundles are fully formed. The larva is some 250μ long and having lost its coffin-like shape it has become more evenly cylindrical (Fig. 6). The egg-membrane is completely flattened and fused with the ectoderm, forming a persistent cuticle. The colour of the larva is pale brown with a darker area which extends from the beginning of the second setiger to the end of the third indicating the position of the mid-gut.

The head is square in front, a shoulder on each side bearing the swimming cilia of the prototroch. The three pairs of eyes are fully developed, two pairs being dorsal and a larger pair lateral. All three pairs lie on a transverse line across the head, anterior to the prototroch ridge.

There are five well-separated apical cilia. The swimming cilia of the prototroch are very large and like the telotroch cilia, are curled against the sides of the head when not in use. A single prototroch group on the dorso-lateral surface of the head remains small, while ventral groups form

the anterior margin of the oral cilia, which now cover the lips and most of the ventral surface of the head (Fig. 6). The oral cilia taper into a neurotroch which extends on to the second setiger. The cilia of the median ventral group of the prototroch have become longer and with the enlarged oral cilia of this region, form an efficient feeding organ. As shown by Wilson (1928) in the development of Polydora, large cilia appear which move independently of the others and probably have a sensory function. They are not as well developed in Scolecolepis as in Polydora, but even at

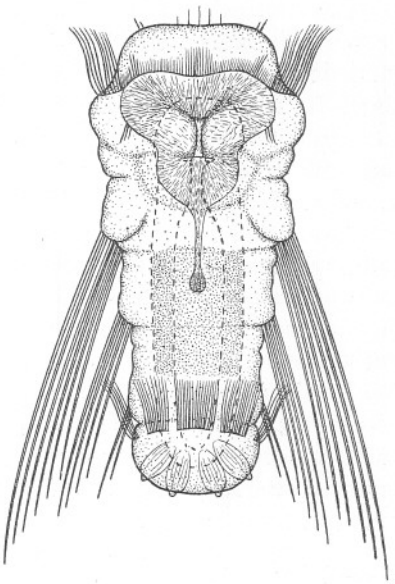

FIG. 6.—Ventral view of the three-setiger larva 4½ days old. × 250. Actual length 250μ.

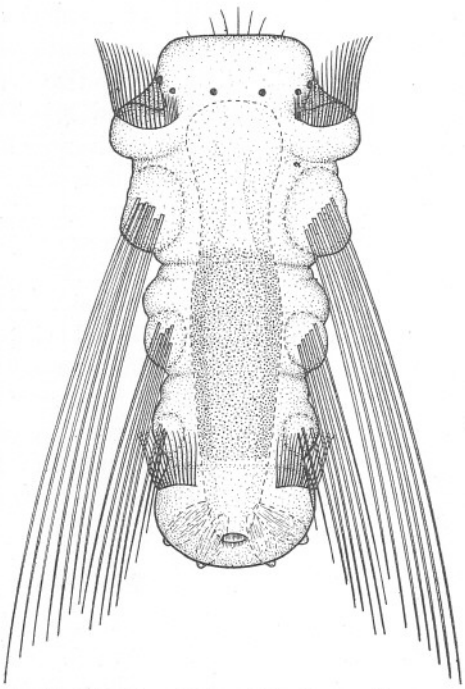

FIG. 7.—Dorsal view of the three-setiger larva, 7 days old. × 250. Actual length 280μ.

this stage three paired groups are visible, one on the anterior margin of what will become the prostomium, the second in line with the ventral part of the prototroch and the third on the lateral margin of the oral cilia. As has been shown, the oral cilia are continued posteriorly as a neurotroch ; this line of cilia ends on the ventral surface of the second setiger in a depression or " pit," on the margins of which are two or three large sensory cilia. The exact structure of this organ is described in the chapter on the fourteen-setiger larva (see Fig. 15). Paired groups of cilia later appear on the ventral surfaces of the first and second setigers.

The mouth opens into a ciliated vestibule, on either side of which are projecting lips. These lateral lips are separated from a third anterior lip by oblique grooves running from the anterior end of the slit-like mouth. When not feeding a fourth lip projects over the posterior portion of the mouth. But when actively swimming, the mouth is held open, and the shape of the lips is difficult to discern. The narrow gullet is followed by the stomach-intestine, which is characterised by the dark pigment cells that line it. This pigmented portion extends from the second to the end of the third setiger. The last portion of the intestine, the rectum, is pale, and the anus is ciliated.

The segments of the body are marked by projecting seta-sacs (Fig. 7). There are 8 or more larval setæ in the first bristle bundle, the longest of which is 200μ and extends considerably beyond the end of the body. In the second setiger there are 6 and in the third 4, but these numbers are soon augmented.

In the pygidium, the anal glands have increased to 4, each with a distinct papilla on the surface.

Development. With the attainment of the third setiger, growth is apparently less rapid. Though the larva continues to feed, it is not until the 9th day that the fourth setiger is formed. Meanwhile the structures already present increase in size, and the cilia groups develop greatly. The sides of the mouth become slightly pigmented, and the lips more prominent. The larval setæ increase in number as well as length. Finally with the advent of the bristles of the fourth setiger, paired groups of cilia appear on the third setiger which develop into a gastrotroch.

The Four-Setiger Larva.

The larva (Fig. 8) is about 400μ long, with a breadth of 160μ at the first seta-sac. The segments of the body are well marked off by constrictions, and a characteristic mark now forms on that part of the third setiger which becomes the ventral ramus of the parapodium. Pigment is also seen in the dark stomach-intestine, and pale variable marks sometimes appear on each side within the prototroch ridge, as well as a band of brown pigment on the anal segment.

The head is relatively smaller, being no broader than the other segments. The lateral pair of eyes are slightly larger than the others. The prominences of the lateral lips is accentuated, but their general shape remains the same.

The swimming cilia of the prototroch measure 60μ and the cilia of the telotroch 40μ. A single dorsal group of the prototroch remains small (Fig. 9), while the ventral groups have long since merged with the oral cilia. The cilia of the anterior lip and those in the oblique grooves as

well as those on the sides of the mouth have enlarged or fused to form broad, plate-like structures which sweep food-particles into the mouth. There are four paired groups of tactile cilia, the newly developed pair being on the posterior edge of the oral cilia. The neurotroch has become

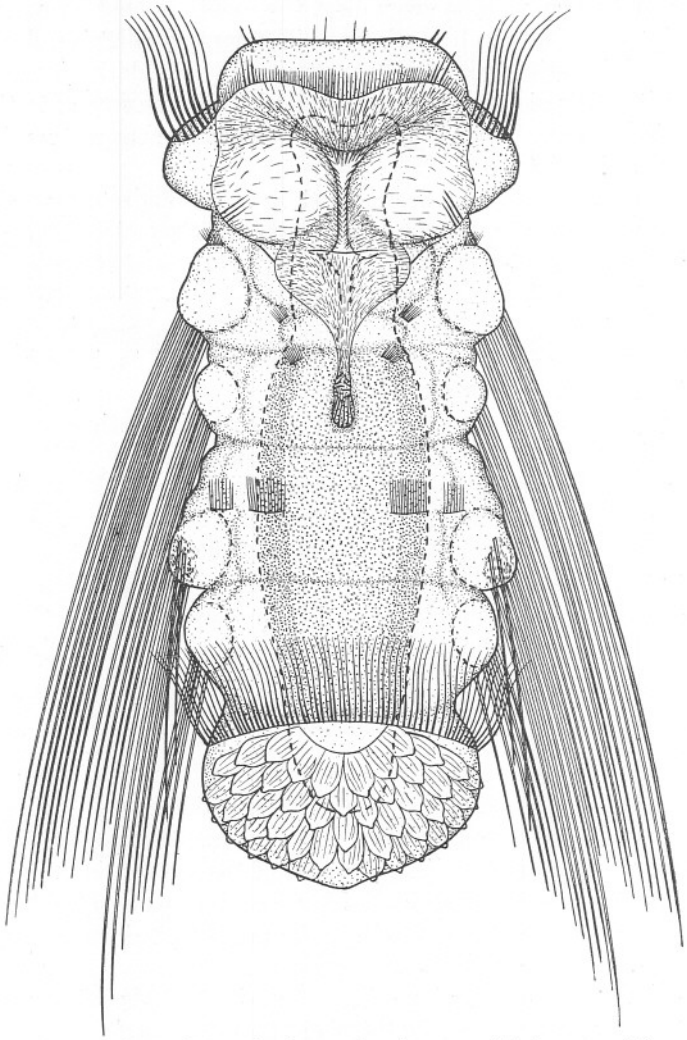

FIG. 8.—Ventral view of a four-setiger larva, aged 9 days. × 270. Actual length 412μ.

broader, the pit deeper, and the sensory cilia which surround it more numerous. There are paired gastrotroch groups on the first three setigers, two small groups on the first, one lateral and one ventral, a single pair on the second and two paired groups on the third.

The mouth has not changed in shape but the granular pigment has increased on the inner surfaces of the lips ; the stomach-intestine is quite black, and anus is now dorsal in position.

The parapodial prominences show slight division into neuropodia and notopodia. The neuropodial part of the third setiger is slightly pigmented. The number of setæ in the four setigers is respectively 10, 8, 6, 4.

Glands in the anal segment are numerous.

Development. From now on the head remains unaltered, except that in late larval development palpi appear. There is also one more group

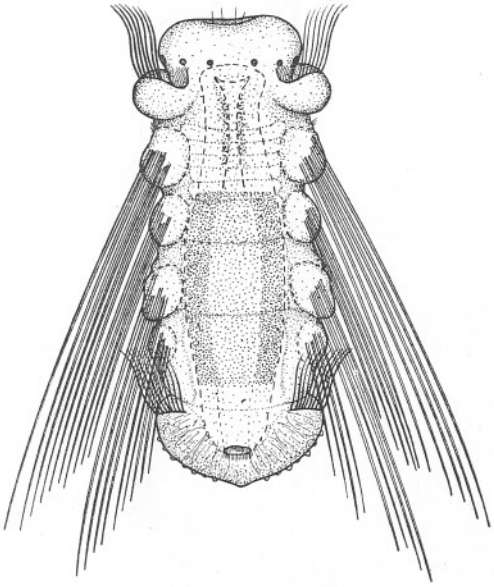

FIG. 9.—Dorsal view of a four-setiger larva, aged 9 days. × 150. Actual length 412μ.

of tactile cilia formed anterior to the pit on either side of the neurotroch. New segments are added in front of the pygidium, and gastrotroch groups appear on the fifth and later the seventh and ninth setigers, which, with those on the third become important swimming organs. Nototrochs are seen at the six-setiger stage, first on the third setiger and later on the succeeding setigers as well as on the second. In each case six groups unite to form a line across the dorsum. Finally there is the development of the ventral group of larval setæ and the elaboration of the parapodia. The pigment in the ventral ramus of the third setiger is repeated in succeeding setigers, but is not so striking.

From the four-setiger stage onward it is noticeable that the centre of growth seems to be the third setiger. It is as though growth had

previously centred in the head segment and at this stage had shifted back to the third setiger. Later important segmental structures arise first on the third setiger. For example, the differentiation of the parapodia is more advanced in this segment than in preceding or succeeding segments. The ventral groups of larval bristles, the nototrochs and the first group of adult bristles are first seen in this segment. As will be shown this pre-eminence of the third setiger is also evident during metamorphosis.

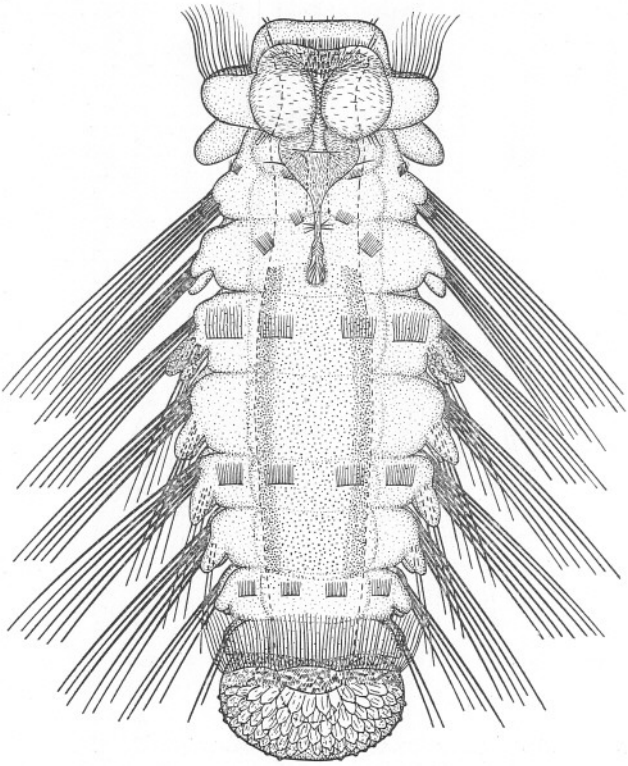

FIG. 10.—Ventral view of an eight-setiger larva, aged 20 days. × 125. Actual length 776μ.

The Eight-Setiger Larva.

The larva at an age of 18 days to three weeks is about 776μ long and has 7–9 setigers (Fig. 10). Larvæ collected from the plankton in Plymouth Sound at this time showed the same development. The body has grown considerably larger with the addition of the new segments. All the structures connected with the larval state are present, and further growth consists in the elaboration of these structures and the addition of new segments.

The body is fairly broad, the parapodia well developed and the head slightly narrower than the rest of the body, except at the prototroch ridge. The only important new pigment marks are pairs of dense black spots on the dorsal surface of the third, fourth, fifth and sixth setigers (Fig. 11). These appear white in reflected light. There is granular

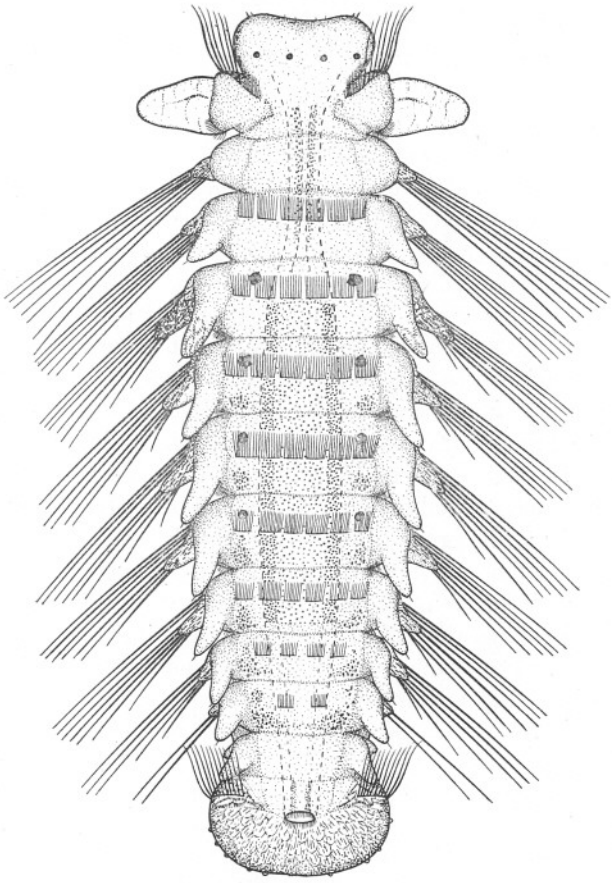

FIG. 11.—Dorsal view of a ten-setiger larva, aged 24 days. × 125. Actual length 0·874 mm.

pigment on the dorsal surfaces of the succeeding segments, but as these marks are variable they are unimportant for diagnosis. The pigment in the ventral ramus of the third parapodium is now a prominent distinguishing character.

The head shows little advance, except for the palpi, which appear on the prototroch ridges posterior to the swimming cilia (Fig. 10) and quickly develop into broad stumpy organs, ciliated on both the anterior

and posterior margins (Fig. 11). Though called palpi by Fauvel and Ehlers, they are identical with the tentacles described by McIntosh and others. In Wilson's paper on the development of Polydora (Wilson, 1928) they are called tentacles.

The prototroch and telotroch show no advance. The cilia associated with the head have grown longer but no new structures have been formed. In later stages a well-defined row of cilia becomes evident at the base of each palp (Fig. 11) where it arises from the prototroch ridge; scattered cilia cover the surfaces of these organs. The neurotroch with the associated pit cilia and the gastrotrochs on the first and second setigers show no advance. There is an extra group of tactile cilia on either side of the neurotroch near the pit. The gastrotrochs on the third, fifth and seventh setigers grow very large and extend transversely across the ventral surfaces of these segments. Nototrochs have been developed on the dorsal surfaces of all segments from the second to the sixth setiger. These structures never grow large, and though possibly of use in swimming, this is not their main function. They are not lost at metamorphosis and are probably precociously developed adult structures, in which stage they have an important function as will be shown later.

The shape of the mouth has not altered, but the gullet is more strongly pigmented. In each segment the parapodia are prominent, the notopodia and neuropodia well marked, and each notopodium is divided into a branchial and a setigerous region. The larval setæ have reached their maximum development. These number 12 to 14 in the first setiger and have a maximum length of 285μ. In the succeeding segments there are fewer setæ of a smaller size. Thus the third setiger has 8 with a maximum length of 250μ. The adult setæ now appear, but are extremely difficult to distinguish. They are first formed in the dorsal bundle of the third setiger, where a few, short, smooth and more definitely tapered structures indicate their presence.

Development proceeds steadily till metamorphosis, by the addition of new segments in front of the pygidium. About the time that the palpi appear, small groups of cilia arise on the dorsal surface between the parapodia (Fig. 11). These have been called " intersegmental cilia," and are probably homologous with similarly placed, though larger cilia in Polydora, which Wilson (1928) has named " grasping cilia," from their function of holding the larval bristles in place during swimming. These groups, like the nototrochs are precociously developed adult structures which remain small in the larval state. A little later hooded acicular bristles are developed in the neuropodial bundle of the eighth and succeeding setigers. Another pair of gastrotroch groups is formed on the ninth setiger. On the dorsal surface of the pygidium two pairs of small anal cirri are developed.

A résumé of the larva with fourteen setigers and ready to metamorphose is given at this stage.

The Fourteen-Setiger Larva.

At an age of 34–36 days most of the larvæ are about 1·0 mm. long and have fourteen setigers. The body (Fig. 12) is slightly flattened dorso-ventrally, and somewhat broader at the third setiger than elsewhere. The colour is a general pale brown, with scattered chromatophores on

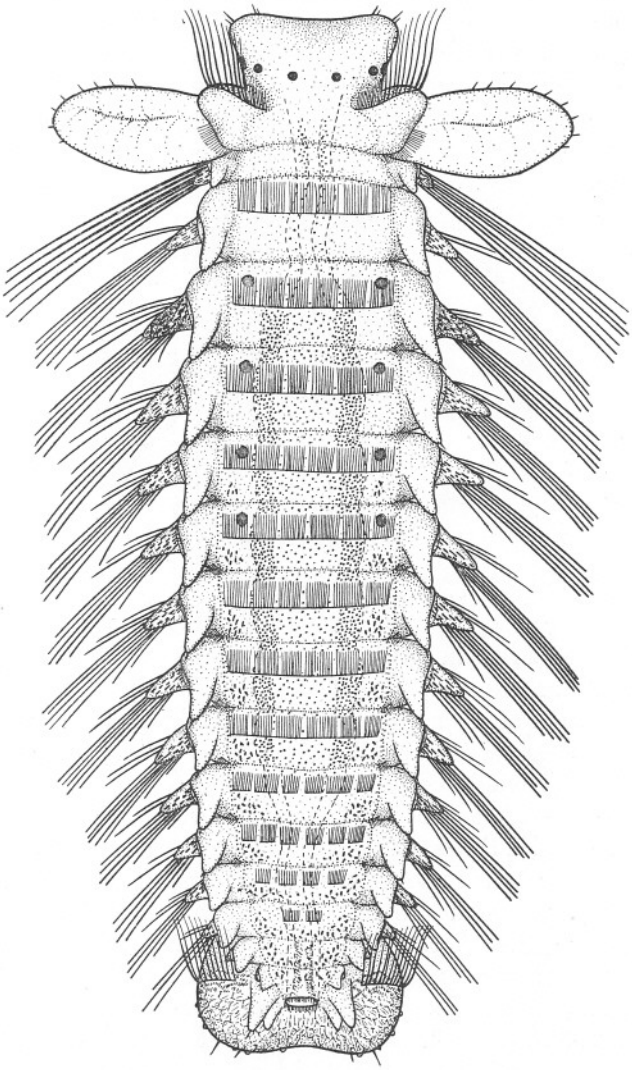

Fig. 12.—Dorsal view of a fourteen-setiger larva, aged 34 days. × 152. Actual length 1·062 mm.

the posterior segments. The neuropodium of the third setiger is dark brown and the third, fourth, fifth and sixth setigers have dense pigment spots. There is granular pigment in the œsophagus and the stomach-intestine is black. That part of the pygidium which bears the telotroch is brown and the posterior, glandular part is bluish.

The prostomium is square in front with a slight median depression. The three pairs of eyes form an inverted crescent across the dorsal surface, the outer pair being almost hidden by the prototroch ridge, which forms the base of the palpi. From now on this part of the head will be called the palpophore. The palpi themselves are broad and flattened.

The swimming cilia of the prototroch are now 68μ long and the telotroch cilia 55μ. The other cilia structures associated with the head and the neurotroch are unchanged. The gastrotroch groups on the

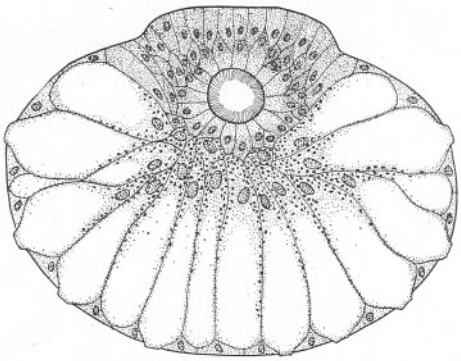

FIG. 13.—Transverse section through the anal segment of a fourteen-setiger larva. × 400.

anterior segments remain small, but those on the third, fifth, seventh and ninth setigers are large swimming organs. Although Wilson has found that the position of the gastrotrochs is variable in Polydora, in Scolecolepis they seem constant. All setigers from the second onwards bear nototrochs and intersegmental cilia.

The structure of the pit is shown in Figure 15, which represents a longitudinal section through a slightly contracted larva. As the histology of the larva otherwise conforms with the general Spionid type, only the remarkable pit is described here. It is an invagination of the ectoderm lying just behind the fold of the contracted lip. The edges are ciliated, but the cavity itself is unusual in that the contents are apparently non-cellular and do not stain. In cross section the pit is reminiscent of a vertebrate notochord. The suggestion that the pit has a sensory function is upheld by its location between the circumœsophageal nerve cords. The first commissures of the double ventral nerve cord (in the second

setiger) are shown just behind the pit. Thus the latter is almost entirely surrounded by nervous tissue. The neurotroch in front of the pit is composed of short cilia and commences at the infolding of the posterior lip. There are two groups of strong cilia behind the pit, and it is these that have been referred to as the pit cilia. The third posterior group shown is part of the gastrotroch of the third setiger. It is possible that the function of this organ is similar to that of a statocyst, though no sense organ similar to this is figured in the literature consulted.

Though the shape of the mouth and vestibule remains the same, the œsophagus and rectum are now sinuous in outline, and the stomach-intestine itself is swollen between the septa. The proctodæum is ciliated for a considerable distance internally.

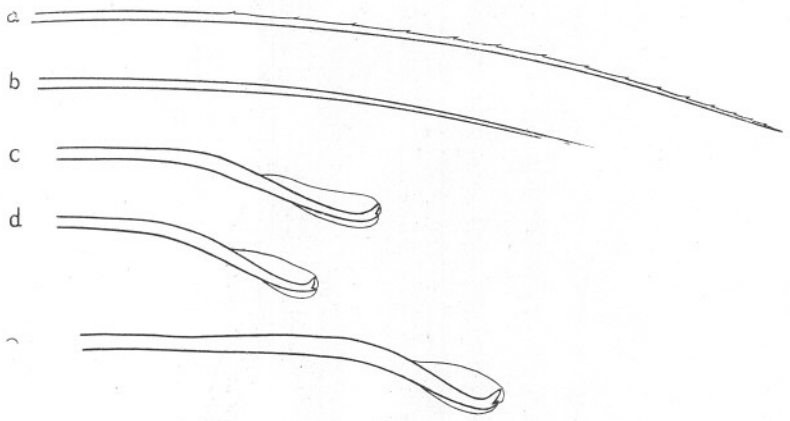

FIG. 14.—(*a*) Larval bristle from a fourteen-setiger larva.
(*b*) Adult type of bristle from the same larva.
(*c*) Crotchet from the 8th parapodium of the same larva.
(*d*) Crotchet from the 10th parapodium of the same larva.
(*e*) Crotchet from the 22nd parapodium of the adult worm.

The parapodia are slightly flattened and there are elongated branchiæ dorsally. In all setigers, with the possible exception of the first, adult setæ (Fig. 14*b*) are present in both the dorsal and ventral bundles. From the eighth setiger onward, crotchets are present in the ventral bundle as well. It is noteworthy that the first crotchets to appear, those in the 8th setiger (Fig. 14*c*) are slightly different from those in the succeeding setigers (Fig. 14*d*), while both are different from the adult type (Fig. 14*e*). The larval bristles (Fig. 14*a*) fall out readily when the animal is trapped on a slide.

The pygidium is short, broad and flattened posteriorly. There are two pairs of anal cirri, which, like the glandular part of the segment and the parapodia, possess tactile cilia. Figure 13 shows a cross section through the

anal segment anterior to the anus itself. The large vacuolated cells contain mucus, the limited cytoplasmic contents having large brown chromatophores. These mucus cells, which are themselves ectodermal in origin, open on papillæ which project through the thin ectoderm covering the surface.

From now on growth proceeds slowly and at the end of another week,

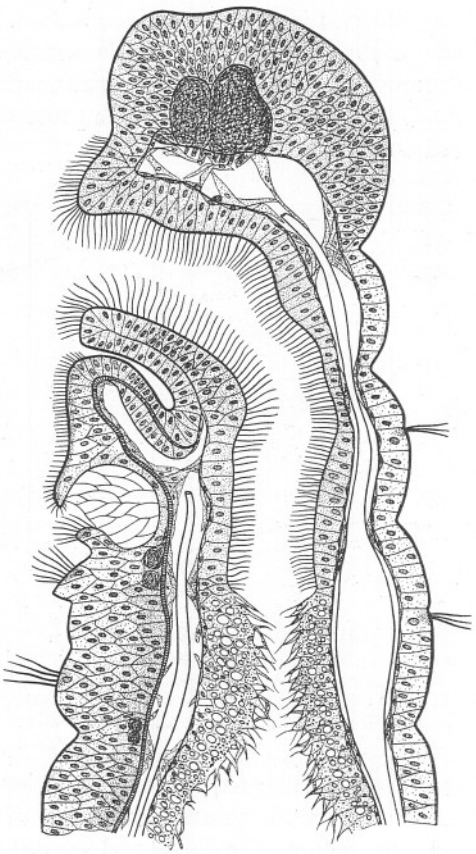

FIG. 15.—Anterior part of a longitudinal section through a fourteen-setiger larva, showing the ciliated pit. × 400.

only a few individuals develop a fifteenth setiger. As will be shown in another paper (Day and Wilson, 1934), experiments were started at this time which show that when kept in conditions unfavourable to metamorphosis larvæ do grow, but so slowly that in another month only four new setigers are added.

In the meantime, some of the largest larvæ were put into a vessel

containing purified silver sand and filtered sea-water, to which Nitzschia culture had been added. The larvæ were at this time thirty-four days old. Though they at first explored the bottom, they soon started swimming again, showing a preference for the lighted side of the vessel. After twenty-four hours, however, two of the largest attempted without success to burrow below the surface. It was evident that the sand was too coarse.

A finer sandy mud was obtained, purified by boiling, and placed in a finger-bowl, to which the filtered sea-water and larvæ had been transferred. After crawling on the sand for an hour, the larvæ began to burrow below the surface and to metamorphose.

Metamorphosis of the Young Worm.

The actual process of metamorphosis is not easy to follow, since the larvæ first secrete mucus to which sand grains adhere, making observation difficult. These notes are compiled from the examination of larvæ at different stages of metamorphosis. Fortunately the changes cannot be described as "cataclysmic" so that it is possible to obtain a fairly complete picture by removing larvæ from their tubes and trapping them under a cover-slip on a ringed slide.

When a suitable place has been found, the head is bent down, and with its palpi held forward, the larva jerks from side to side, burrowing below the surface. While crawling the larva secretes mucus, by means of which sand grains adhere to the body, but as the larva burrows further sand grains and larval setæ are left behind in a trail of mucus. Not all the larval setæ are lost at once, for those of the first setiger persist till much later.

Possibly under the influence of burrowing, the palpi soon change both in shape and position. The sides of the palpophores grow unequally, so that the palpi are directed forwards, increasing in length and slenderness. Sooner or later the metamorphosing larva constructs a tube of sand grains and debris loosely stuck together with mucus. Here it remains fairly quiet, with its head at the mouth of the tube and the palpi waving freely in the water.

While in this position many changes occur, some gradual, some rapid. A sudden change such as the loss of the gastrotrochs is easily noted, but others such as the gradual development of the antennæ proceed slowly and continuously, so that it is impossible to say definitely whether the antennæ are developed before or after the loss of the gastrotrochs. This point should be held in mind in the perusal of this chapter. Cataclysmic changes—if the loss of the different larval organs can be called such—are recorded in their true succession, but a more correct picture of the metamorphosis is obtained if these superficially striking changes are regarded merely as milestones in the gradual evolution of the adult organs.

Most of the cilia that are functional only during larval existence are now lost. In this category are included the gastrotrochs, the neurotroch and pit, the telotroch and the prototroch. These disappear in the above order, though the telotroch and prototroch persist long after the others have gone. The other groups of cilia, the nototrochs, intersegmental cilia, oral, anal and tactile cilia may change in character but are never lost for they are functional in the adult as well as in the larval stage. The gastrotrochs go first. The actual loss of the cilia is difficult to follow, for when a larva is isolated on a slide for long periods, metamorphosis either stops or proceeds more slowly, and in the meantime plasmolysis takes place. It was ascertained in many cases, however, that when a group of cilia is about to disappear, most of the protoplasm of the cilia is withdrawn into the body of the larva so that a mere wasted shell remains. Whether this falls off or is also absorbed could not be determined with certainty, but it seemed as though a part appreciably shorter than the original was thrown off. The former position of a cilia group can be detected for a few hours by the presence of a paler mark on the surface of the body.

Just before the pit closes, a lump arises on either side, then lengthens out and the depression fills in. The neurotroch is then lost, and within six hours no trace of the pit can be found externally. The prototroch and telotroch, which up to this time are functional when the larva is forced to swim, now disappear. Changes in the shape of the head and the body generally, become visible. The notch in the middle of the prostomium is accentuated and the prominences on either side foreshadow the future antennæ. The lateral lips grow forward, bringing the reduced posterior lip with them, thus covering part of the mouth so that the opening is V-shaped and anterior. The oral cilia are restricted to the sides of the mouth and the surface of the posterior lip. The two dorsal pairs of eyes form a rectangle, the third pair remaining unchanged laterally. The body meanwhile increases in length, becoming more slender and rounded. The pygidium narrows and the anal cirri grow longer.

Twelve hours after the commencement of burrowing the only larval features which remain are the third pair of eyes, the temporary ventral hooks, and the dark pigment of the mid-gut, of the neuropodium of the third setiger, and of the posterior part of the anal segment. These features persist long after metamorphosis is otherwise complete, and disappear gradually in the life of the young worm.

Development proceeds with the further modification of larval structures. The mouth, lips, antennæ, palpi and eyes change in the manner already indicated and soon conform to the adult type. The rami of the parapodia are further flattened, while the branchial portion of the notopodium becomes more distinct. With the lengthening of the setigerous segments,

a corresponding change occurs in the pygidium. The two superior pairs of anal cirri grow considerably, but whereas they were colourless from the start, the third pair arising from the division and prolongation of the glandular region of the segment, contain the bluish pigment which characterised it. In the adult worm, however, they can be distinguished only by their larger size. Twenty-four hours after metamorphosis the young worm has reached a stage shown in Figure 16. As there are still differences between this and the adult a brief résumé of its characters is given.

Characters of the Recently Metamorphosed Worm.

The general shape of the body is similar to that of the adult. When forced to swim it does so with a serpentine motion, using its fan-like setæ and flattened parapodia as oars. The young worm is considerably paler and more transparent than the larva, and except for the scattered pigment granules on the head and dorsum, the few dark patches are the remains of the larval pigment. The mid-gut is brown, as is also the neuropodium of the third setiger. The posterior part of the pygidium and the ventral urites are bluish. The bands of yellowish pigment, seen on the palpi of the adult, are not yet developed.

The prostomium is sharply defined. It is roughly oval, slightly notched in front and rounded posteriorly. The antennæ are conical, but soon grow longer and more regularly cylindrical. The palpophores are short, and the palpi which are long, tapered and slightly grooved dorsally, project beyond the antennæ. There are three pairs of eyes, two dorsal, and a lateral pair hidden by the palpophores.

The large lateral lips are protuberant, and curve posteriorly to enclose the V-shaped mouth. There is an indefinite posterior lip and a larger anterior lip that is separated from the laterals by oblique grooves. The opening of the mouth is anterior and ventral, the pharynx is contractile and the œsophagus is thrown into folds by the contraction of the body. The dark stomach-intestine begins about the third setiger and continues till the fourth from the anus; this pigmented part of the gut is characterised by segmental swellings between the septa. Posteriorly the rectum is again folded, and the proctodæum is ciliated for a considerable distance internally.

The lips are beset with short cilia and the antennæ and palpi are sparsely covered with short tactile cilia. In addition there are rows of cilia at the base of the palpi. All setigers except the first, and those that are undeveloped posteriorly have nototrochs and intersegmental groups of cilia. The gills and the anal cirri possess only a few tactile cilia.

The parapodia are of the adult type, but the branchial part of the notopodium is short and does not as yet arch over the dorsum. Both

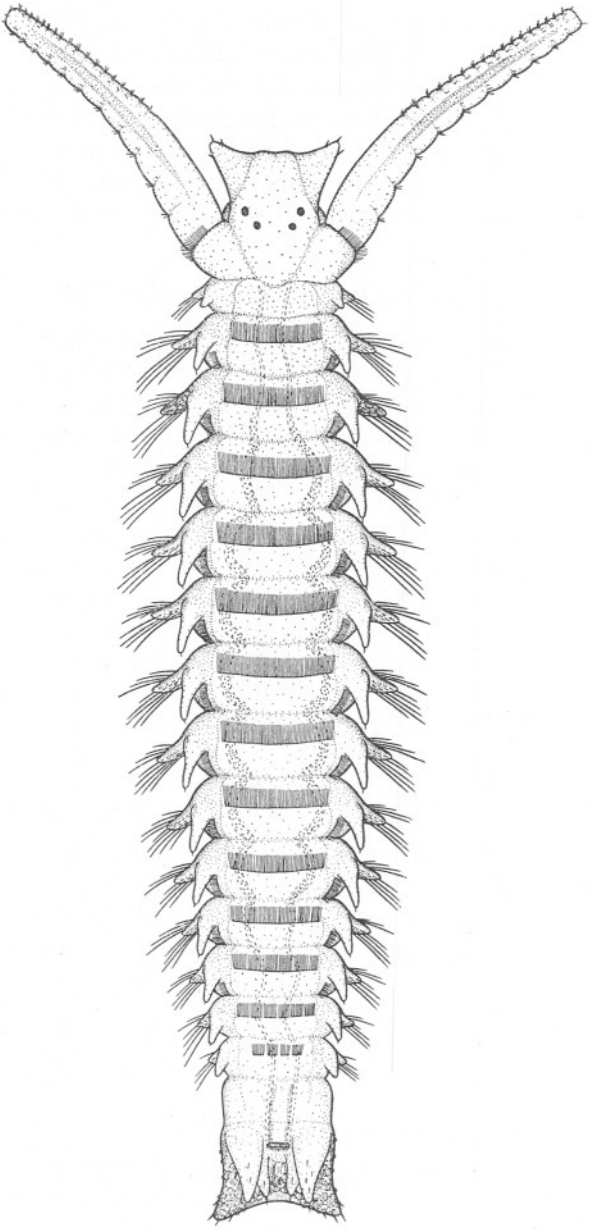

FIG. 16.—Dorsal view of a recently metamorphosed worm. × 104. Actual length 1·367 mm.

the dorsal and the ventral bristle bundles arise on the anterior side of the flattened parapodia and project outwards like a fan. From the eighth setiger onwards, hooded crotchets as well as capillaries are present in the neuropodial group, but these are only temporary, and in the adult crotchets are found only in the twentieth and succeeding setigers.

The pygidium is long and transparent and pigment is restricted to the ventral pair of anal cirri.

From now on the worm grows rapidly. The third pair of eyes are first hidden and then lost. Pigment disappears from the mid-gut, the third parapodia and anal segment. The anal cirri, antennæ and palpi increase greatly in length. As the gills grow longer, they become richly ciliated and arch over the dorsum, and the function of the cilia groups now becomes obvious. Normally the worm rests with its head at the entrance of its mucus-lined tube, the antennæ and long palpi waving freely in the water. In this position there is a free passage between the dorsum and the arched gills, and the motion of the nototrochs, intersegmental cilia and the rows of cilia on the branchiæ draws a current of water down along the dorsum. Part of this current is diverted ventrally at each segment by the action of the intersegmental cilia, thus ensuring a complete circulation of fresh water along the whole length of the body.

SUMMARY.

1. The development of *Scolecolepis fuliginosa* (Claparède) is described from the egg to the young worm for the first time.

2. Comparison of reared larvæ with larvæ from the plankton did not reveal any important difference.

3. The eggs are pelagic, and are similar to those of Nerine.

4. A description is given of the histological structure of a ciliated pit which arises in early larval existence and disappears at metamorphosis. The structure of the glandular region of the pygidium is also described.

5. It is apparent that from the attainment of the fourth setiger onwards, the centre of differentiation is located in the third setiger, so that segmental structures arise first in this segment and then appear in the first and second setigers as well as in the succeeding ones.

6. The larva of Scolecolepis has three pairs of eyes, the third pair disappearing in the young worm long after metamorphosis is otherwise complete.

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