Studies on the Development of Annelida Polychaeta I[1]

By

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(With 17 Plates and 33 Textfigures)

Contents

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1) Contributions from the Akkeshi Marine Biological Laboratory, No.

I. Introduction

Although a relatively large number of papers dealing with the early stages from the first cleavage to the trochosphere of Polychaeta are found scattered in literature, the contributions to our knowledge concerning the metamorphosis are comparatively scanty, and, moreover, only a few attempts have previously been made to trace successively the development by rearing larvae from eggs to metamorphosis. The chief important pioneer studies on the later development of Polychaete were made by Agassix (1885), Claparéde et Mecznikow (1869), E. B. Wilson (1882), Fewkes (1885), Malaquin (1893), Häcker (1896), Gravely (1909), Herpin (1926) and others. Recently Aiyar (1831), Day (1934, 1936), Nolte (1936, 1938) and Segrove (1941) have rendered a great service to our knowledge of the development of Polychaetes, but the most valuable contributions must be due to D. P. Wilson (1929–1936), who published a lot of the important accounts on the development of about a dozen species belonging to the various families. As already pointed out by Wilson (1926), the development of seventeen among thirty-six families of Polychaetes has been studied more or less in detail, but information as to the development of the rest remains, if any, fragmentary. Such being the case, it would accordingly be futile to attempt to give detailed diagnoses of larvae of different families and genera of Polychaetes and to observe the metamorphosis from the standpoint of the phylogenetic relationships.

For the sake of affording a basis for more complete study on the Polychaete larvae, the present investigation has been carried out during the last two seasons at the Akkeshi Marine Biological Laboratory. The present study starts in general with the early trochosphere and finishes with the young worm a few days after metamorphosis; the cleavage and very early stages having been excluded.

The chief interest centres at the metamorphosis and a special attension has been paid to those characters which appear to have phylogenetic values respective to different larvae. The technical terms which are adopted in describing different stages and larval organs existing during the development, are based on those defined by Häcker (1897) and Gravely (1909).

Before going further it is with real pleasure that I have to offer my most grateful thanks to Prof. Dr. Tohru Uchida, through whose continued interest and encouragement the work has taken its present shape. The expense of the present investigation was partly defrayed out of a grant from the Foundation for the Promotion of Scientific and Industrial Research of Japan.

II. Material and Methods

The material forming the subject of the present investigation includes the following 12 species belonging to the 9 families.

Eunicidae

1) *Lumbriconereis latreilli* Audouin et M. Edwards

Nereidae

2) *Neanthes* sp.

Ariciidae

3) *Nainereis laevigata* (Grube)
4) *Haploscoloplos kerguelensis* (McIntosh)

Spionidae

5) *Spio filicornis* (O. F. Müller)

Cirratulidae

6) *Cirratulus cirratus* (O. F. Müller)

Terebellidae

7) *Lanassa nuda* (Moore)

Arenicolidae

8) *Arenicola claparedii* Levinsen

Sabellidae

9) *Chone teres* Bush
10) *Potamilla myriops* Marenzeller

Serpulidae

11) *Spirorbis spirillum* Linné
12) *Spirorbis nipponicus* Okuda

Though diverse in the spawning habits, all of these species, with a single exception of the species, *Potamilla myriops*, lay their eggs in the form of jelly-mass which affords with both food and protection for the development of the larvae. *Lumbriconereis latreilli, Neanthes* sp., *Haploscoloplos kerguelensis, Spio filicornis, Lanassa nuda, Cirratulus cirratus* and *Chone teres* collect their eggs in the mass of jelly, whatever the shape may be, attached to the ground or the sea-weeds. The eggs of *Nainereis laevigata* are discharged in gelatinous ribbon-like clusters knit loosely together. *Arenicola claparedii* forms a tube-like egg-mass deposited around the parent's body. In *Spirorbis spirillum* the eggs are laid inside the tubes of the parent, while in *Sp. nipponicus* the operculum serves as a brood-pouch. Only in *Potamilla myriops* the sexual products are discharged directly into the sea and the parent take no further care of them.

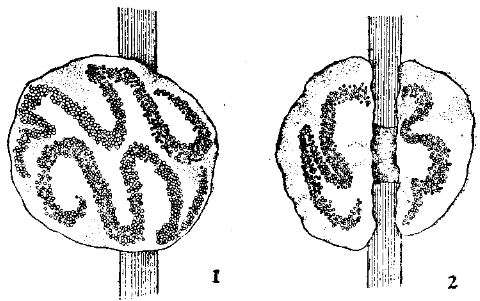
Except *Potamilla myriops*, the newly formed spawn-mass of all the species were brought to the laboratory and transferred to culture dishes. The larvae were reared in dishes and in a plunger-jars filled with sea-water which had been filtered through fine bolting silk. By the time the young worms were ready to feed the jar showed a good growth of diatoms. In warm weathers those plunger-jars were cooled and protected from rapid changes of temperature by running water. The water was remained as a rule unchanged throughout each experiment. After repetition of failures to observe an artificial fertilization of *Potamilla myriops* by using eggs and sperm from mature adults, it was decided to try to secure naturally spawned eggs. Several females and males were put into a jar. The sexes are easily distinguished at maturity by their body colours. By the next day they were found to spawn. The eggs thus deposited were transferred to the plunger-jar of sea-water and were reared by the similar method as doscribed above.

All the drawings were made from living active larvae, 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 eye-piece. The original larva of each drawing, as well as others, was fixed and mounted and the drawings, as far as was possible, were checked by them. No attempt has been made to illustrate fine cytoplasmic details, and the cytoplasm is for the most part conveniently dotted.

III. Development of *Lumbriconereis latreilli* Audouin et M. Edwards

(Plates XII–XIII, Textfigs. 1–5)

1. Breeding habit. The adult worms are found on the muddy bottom in the *Zostera*-region just below the low-water mark. The breeding season of the worm lasts from the middle to the end of June. During the breeding season we meet with a large number of spawn-masses, taking an appearance of the ground-cherry, attached to the leaves of *Zostera*, and bright orange eggs may be seen through the thick gelatinous mass. The spawn-masses are generally laid on the leaves of *Zostera*, but in some cases on other kinds of sea-weeds such as *Sargassum* and others. These masses have no special supporting stalks and they are immediately attached at their bases to the leaves



Lumbriconereis latreilli Audouin et M. Edwards
Fig. 1. Egg-mass laid on *Zostera marina*. Dorsal view.
Fig. 2. Ventral view of the same, showing a basement envelope by which jelly-mass is fixed.

or stems of the sea-weeds, enveloping them by a thin, slimy sheath. The eggs laid in the jelly-mass are arranged in a few wriggled rows as shown in Fig. 1, Pl. XII, and Textfigs. 1–2. The number of eggs in each spawn-mass varies to wide extent, but may be counted between 200 to 400 or more. The newly formed egg-mass is roughly spherical with wavy contour, flattened more or less dorso-ventrally and measures about 10–13 mm at its widest portion. The early development takes place within the spawn-mass. As development proceeds the jelly-mass becomes fragile and ultimately dissolved. Fewkes (1883) observed in other species of *Lumbriconereis* that the eggs are attached to the surface of the mud in the form of gelatinous clusters glued together in spherical masses. Though a number of the Eunicids have been known to collect their eggs in gelatinous masses, no representatives are known to lay their eggs on the sea-weed as shown in the present species. The various modes of incubation habits of the Eunicidae will be treated later.

2. *Development within spawn-mass.* The fertilized egg in newly formed egg-masses is more or less spherical and about 300μ in diameter. The egg is opaque and bright orange laden with a rich food yolk. Since I have not been able to ascertain the time of fertilization, it is impossible to give the accurate times for the early stages. The first cleavage furrow sinks in all round the eggs at the same time, and not first at the animal pole, as in many eggs containing rich amount of yolk like *Nereis* and *Lepidonotus*. The division of the first two blastomeres is subequal, simultaneous, and slightly oblique, so we have a four-cell stage in which the quadrants cannot be distinguished from one another. These four cells are divided simultaneously into eight cells by a right oblique cleavage, those of the anterior hemisphere being smaller than the other four. The next division is synchronous and sixteen cells thus formed are nearly equal in size.

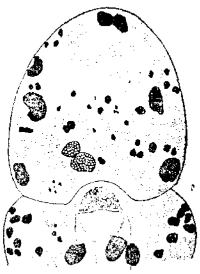
About twenty four hours later (Fig. 7, Pl. XII), the spherical embryo becomes elongated, a little narrower in front than behind. The body is dense, opaque and filled with the bright orange cells. There is a broad median thickening which indicates the future prototrochal region. A day later the so-called early metatrochophore is formed (Figs. 8–9, Pl. I). There is no true trochophore stage, that stage being omitted from the life history of the worm, probably on account of the development taking place in the jelly. The entire body is ovoid in shape, measuring about 350μ in length and 300μ in width. A very broad band of short cilia, the prototroch, surrounds the middle region of the body. At the anterior end is a small apical tuft of cilia, and just behind this is encircled by a narrow but distinct ring of cilia. On the midway between the apical end and the prototroch a narrow band of fine cilia, an akrotroch, appears. A paratroch consists of a complete ciliary band encircling the posterior body shortly behind the prototrochal broad band. A telotroch is also formed near the posterior end. A tuft of short sensory cilia are projected from the posterior extremity. The neurotroch is not formed throughout the development. Compared with the other Eunicid larvae the present species is provided with more complex cilia girdles.

Two globular dark orange pigment spots are found near the anterior dorsal end and three irregular similar spots behind the akrotroch on the ventral surface. At the anal end a few pigment patches are crowded. Very little of the internal structure can be made out, the whole body being dense with yolk. The embryo rotates slowly within the jelly-mass.

A day afterwards the body elongates slightly and the cephalic projection becomes distinct (Fig. 10). It is approximately 440μ in length and 320μ wide at the prototroch. The apical cilia markedly decrease in length, and the anal sensory cilia disappear entirely. The prototroch becomes also narrow. In other respects the ciliation is the same as in the previous stage. Just behind the prototroch there is a clear area on the mid-ventral surface which indicates the future mouth. The first chaeta-sac appears in the unciliated gap behind the paratroch. It consists of three simple bristles, of which one is limbate and being longer than others; one spatulate and the other needle-shaped with a pointed tip; the latter two being almost embedded in the body wall. The bristles are moved together, being protruded from or withdrawn into the body. The gut is roughly marked out from the rest of the body, which remains opaque. Three pigment spots appear near the apical end. The posterior end is packed with several pigment patches. The larva becomes contractile and creeps within the jelly by movements of the bristles.

3. *Metamorphosis.* Shortly after the appearance of the first bristles the larva is ready to metamorphose. Metamorphosis may be regarded as initiated by the loss of most of cilia. This is brought about by a shrinkage of the cilia and their basal cells. It could not be determined whether the cilia have been thrown off or absorbed. Fig. 11, Pl. XII shows the metamorphosing larva three days after the early metatrochophore. The body increases in length and girth, narrowing in the region of the prototroch. Excluding the cilia band of the prototroch all other locomotor cilia shown in the previous stages have fallen off. Only the prototroch still persists, though much narrowed. On the mid-ventral line of the prototroch exists a stomodaeal invagination as a round depression. In the region occupied by the paratroch in the preceding stage the dark orange pigment globules are arranged in a transverse row. A pair of bristles is protruded on parapodia-like prominences. The gut forms a large central mass packed with yolk granules.

A day or more later the second chaeta-sac appears. Indications of segmentation first come in view in the region in front of the first parapodium. New segments are formed between the first chaetigerous segment and the head. There are four segments between the head and the pygidium, of which the first two are achaetous. On each segment pigment globules of variable number are scattered in one or two rows. Especially at the pygidium these globules are found in clusters. On each lateral side of the posterior border of the prototroch a pair of large pigment patches is present. At the later stage of two setiger-bearing larva the prototroch is lost, and the metamorphosis is now completed. During the metamorphosis the larvae are enclosed inside the jelly, but when taken out they show rather active creeping movements. The larva lacks entirely the pelagic or swimming stage during the whole course of its development. The total time taken to metamorphose is about three days. The period at which the larvae creep out of the spawn-mass seems to be variable to some extent. In majority the larvae liberate from the jelly when they acquired four or more setigers. The most advanced larvae found in the jelly-mass had seven setigers. In the laboratory the larvae seem to escape the spawn-mass at earlier stage than in the natural condition. The fact may be due to temperature.

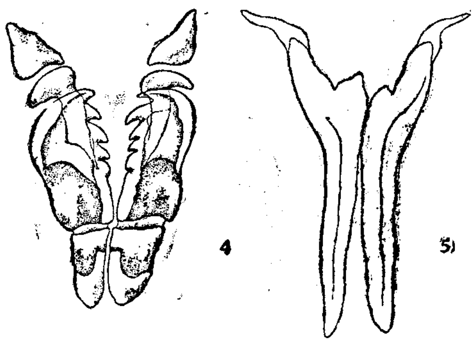


Lumbriconereis latreilli Audouin et M. Edwards
Fig. 3. Ventral view of head region of larva with four chaetigerous segments.

4. *Early bottom stages.* After metamorphosis the main changes are confined to the increase of segments, causing the elongation of the trunk and the new formation of the jaw-apparatus as well as the digestive tract. The new segments always arise back of those which have previously been formed. Figs. 14–15, Pl. XII represent the recently metamorphosed larvae about seven days old. The body is orange and rather opaque, measuring about 850μ in length. There are two achaetous segments behind the head, following to the successive three setigers. The loss of the broad prototroch results in direct joining of the prostomium with the peristomium. The head

is ovate, elongated and equal in length to the following two achaetous segments. At the anterior end a number of orange pigment globules are scattered, and a few number of yellow green globules are also found between them. A pair of large pigment spots occur on the posterior margin of the head at the dorsal and the ventral sides respectively, where the prototroch has previously been formed, taking an appearance of eye-spots. Each body segment is traversed by a row of pigment globules, the number of which being variable. In the pygidial region the similar spots are concentrated, especially on the ventral portion. The mouth and the anus are not as yet opened. The digestive tract is indicated as a sac-like structure narrowing to the posterior end. The larvae move sluggish within the jelly-mass.

A day later the larva acquires one more setiger. The mouth and the anus are both formed at this stage. The mouth is a transverse slit just behind the head on the mid-ventral line and the anus is situated on the dorsal surface of the pygidium. The pigment spots found on each body segment are irregulary arranged in two transverse rows. The jelly-mass containing a number of the larvae becomes soft and disintegrates gradually, and in a short time the larvae begin to liberate from the mass of mucus and sink to the bottom. When five chaetigerous segments have been fully formed, a pair of the crescent-shaped mandibles makes its appearance in the pharyngeal region, but the other parts of the dental apparatus are not still distinguishable. Except *Marphysa gravelyi* observed by Aiyar (1931), in which the chitinous toothed plates, the second maxillae are formed prior to the appearance of the mandibles, the rudiment of the mandibles or "Unterkiefer" is the first to develop in other Eunicid larvae. The digestive tract may be, at present, divided into the anterior round fore-gut and the posterior short, narrow hind gut terminating to the anus. The larvae, however, does not begin to feed. The first two setigers have two pairs of the wing-like bristles. The crochet is not still formed at the stage. The rudiment of the maxillae or the upper jaw-plates first appears in the six-setiger larva. It locates above the mandible and develops rapidly. The eight-setiger larva, about twelve days old, is shown in Fig. 18, Pl. II. At this stage the body becomes distinctly worm-like and creeps about on the bottom showing active wriggling movements. Some of the young worms are able to swim with an undulating motion. The body is yellowish orange measuring about 1.3 mm in length. A number of orange pigment spots are scattered on segments, especially crowded near the intersegmental region. The shape of the head remains unchanged. At the terminal end of the head a pair of clear area destitute of pigment granules is marked at each lateral border. The paired large pigment patches are still present at the base of the head on both dorsal and ventral regions as shown in the previous stage. The pygidium is hemispherical with an anus in the dorsal portion. The mouth shows a cleft-appearance and leads into the pharynx. The intestine is less opaque and is marked segmentally by the annular constrictions. The pharynx occupies the region from the second achaetous segment to the posterior end of the first setiger. From the seventh chaetigerous segment onwards only crochets are borne on each parapodium instead of winglike bristles as shown in the anterior segments. About this time the



Lumbriconereis latreilli Audouin et M. Edwards
Fig. 4. Mandible from the young worm with ten-setigers.
Fig. 5. Maxilla from the same worm.

maxillae, light yellow brown in colour, are clearly defined. The whole dental apparatus is protrusible and becomes functional. The maxilla has short curved forcipitate processes. Supporting plates are shorter and broader than that of the adult. The dental plates are prominent, having five teeth on each side. The outer accessory plates above the dental plates are in two pairs, of which the upper one consists of triangular pieces and the lower one of curved sickle-shaped plates being devoid of the teeth. The mandible takes the form of an inverted V, diverging posteriorly and united anteriorly, bearing one big obtuse tooth near the junction of both pieces.

From now on growth proceeds gradually, and at the end of another week only a few individuals acquire the eleventh setiger, and there occur but little changes in the external feature. Ten-setiger larva is represented in Fig. 19, Pl. XIII. The pigment spots on the body segments become less distinct and decrease in number. The anterior extremity of the head, however, is densely pigmented with darker orange granules. Fig. 20 shows the young, which seems to be about thirty five days old, found in nature creeping about between tubes of *Potamilla myriops*. The body is about 3–5 mm in length. The entire external characters are well coincided with those of the adult worm. It has eighteen setigers. The pigment globules on the body surface become more obscure. The pygidium is now changed to form an anal cup. The supporting piece of the maxilla elongates. Otherwise the characteristics of the young are the same as those of the previous stage.

5. *Formation of bristles.* The bristle first formed is winged capillary. This bristle is accompanied by two more ones; one pointed, curved and the other limbate, spatulate, their major portions being embedded within the body wall. The two kinds of the latter bristles are provisional and are found only during the early developmental stages. During the subsequent stages a pair of winged bristles is added on the succeeding segments as far as the sixth parapodia.

Approximate stage of larvae	parapodia																
	1	2	3	4	5	6	7	8	9	10	11	12	13	…	16	17	18
2-setiger stage	1w	1w															
5-setiger stage	2w	2w	1w	1w	1w												
8-setiger stage	2w	2w	2w	2w	2w	2w	3c	1c									
10-setiger stage	2w 1c	2w 1c	2w 1c	2w	2w	2w	3c	3c	3c	2c							
12-setiger stage	2w 1c	2w 1c	2w 1c	2w 1c	2w 1c	2w 1c	3c	3c	3c	3c	3c	2c					
18-setiger stage	2w 1c	2w 1c	2w 1c	2w 1c	2w 1c	2w 1c	2w 1c	3c	3c	3c	3c	3c	3c	…	3c	2c	1c

c, crochet; w, winged capillary bristle. In this table no provisional bristles are included. They are always found until the stage in which about twelve setigers are formed.

After metamorphosis an additional pair of bristles is added to the first setiger. When the six chaetigerous segments were formed, two pairs of the winged bristles are found on each segment. In the next stage hooded crochet first appears on the seventh segment. When three pairs of the crochets have been formed in the seventh parapodium, the eighth setiger develops with a single pair of the crochets. Thus, only crochets are found in the seventh and in the succeeding segments for a considerably later stage. After the ninth setiger appeared, crochets are first added on the anterior bristle-bearing parapodia. In the ten-setiger larva each parapodium of the first four segments has a single crochet and two winged bristles and the succeeding two segments bear winged bristles only, while the remaining four setigers carry crochets exclusively. The appearance of the bristles is shown in the above table.

6. *Notes on the spawning habits of Eunicidae.* A number of Eunicid worms are known to lay eggs in a gelatinous mass, which affords both food and protection to the development of the larvae. The eggs of *Lumbriconereis* sp. described by Fewkes (1883) are attached to the surface of mud in the form of gelatinous clusters glued together in a spherical mass of slime. Borradaile (1901) observed that in an unknown species of *Marphysa* eggs are laid in pear-shaped mass of jelly, attached to substratum by the narrow end. A similar spawning habit is also observed in *Marphysa gravelyi* by Southern (1921) and Aiyar (1930). Wilson (1882) described the development of *Diopatra cuprea*, in which the larvae are found embedded in long strings of slimy jelly which may often be found attached to the tubes of the worm. Gravier (1923) also recorded in *Diopatra neapolitana* that the eggs are collected together and attached to the border of parent's tube. Monro (1924) described the post-larval stage of a species of *Diopatra* which was regarded as *D. cuprea* and he mentioned that the eggs of this species are laid inside the parent's tube and the larvae develop in that position. Recently Krishnan (1936) also observed that *Diopatra variabilis* collects the eggs inside the tubes in clusters held together in jelly, and the development takes place within jelly. According to Koch (1846) the embryos of *Marphysa sanguinea* undergo development in the body cavity of the mother and are born as young worms. In the present species, *Lumbriconereis latreilli*, the eggs are also laid in jelly-mass as shown in other species, but the spawn-mass is always attached to sea-weeds instead of bottom or tube. In these representatives of Eunicidae the special parental cares are taken for the development of the larvae and the larvae are protected from perils of environments. In all these forms there is no free-swimming phase and the early develop-

ment takes place within jelly-mass or inside the tube, and afterwards advanced larvae with several pairs of parapodia leave the shelter.

On the other hand, it has also been known among a number of Eunicid worms that the deposited eggs are always separate and free floating in water. *Eunice viridis* and *E. fucata* known as the Pacific and Atlantic "Palolo" respectively display swarming, discharging their sexual products freely at a definite phase of moon. In *Eunice harassii, Lysidice collaris, L. oele, L. ninitta, Staurocephalus atlanticus, S. rudolphii, Nematonereis unicornis* observed by various authors are all known to discharge the eggs and spermatozoa into the sea and to take no further care of them, and, accordingly, they have free-swimming stages during the larval developmental stages.

It is difficult to explain different sexual habits among the closely allied species, which markedly affect the early course of the development. Instances of such differences in oviposition are also known in other families of Polychaetes. For instance, *Platynereis dumerilli* and *P. pulchella* resemble each other in their atokous phases but their heteronereid forms are quite different. *Nicolea zostericola* lays eggs in cocoon, whereas *N. venustula* sheds eggs in water; *Dodecaceria concharum* and *D. caulleryi* also differ widely in their reproductive habits in spite of the close morphological resemblance in their asexual phases.

7. *General accounts.* Only two short papers describing *Lumbriconereis* larvae have so far been published, and in both the parent worms were not identified. Claparède and Mecznikow (1868) gave the short accounts on the development of so-called Müller's *Atrocha,* which was regarded as the larva of *Lumbriconereis* sp. In general the larvae observed by them develop very slowly. The locomotor cilia including the prototroch, which forms a broad band of cilia as usually shown in Eunicid larvae, were fallen off at the larvae with two setigers, eleven days old. In the larvae twenty-days old, the oldest stage that they have reared, only four setigers were found with a pair of anal cirri and eye-spots. By the time there was found no sign of appendages on the head. Because of the entire absence of any tentacular rudiments on the head in the considerably older larvae, Claparède and Mecznikow supposed that the parent worm of the unknown larvae may belong to "einer fühlerlosen Gattung" such as *Lumbriconereis* or *Notocirrus*. As they gave no accounts on the mode of life, it remains uncertain whether the larva had a free-swimming stage or

not during the development. As described later Lumbriconereid larvae are characterised by shortening of larval life and by the precocious appearance of several adult structures, and, moreover, eye-spots as shown in the larvae figured by Claparède and Mecznikow never appeared during the larval development. The larvae they described are not possibly belonged to *Lumbriconereis*, but seem to be very probably to belong to *Eunice* larvae, and seem to be closely allied to those of *Eunice harassii* observed by Herpin (1926) who traced the development of the species to a much later stage. In *E. harassii* there is a well marked pelagic stage lasting over ten days. At the close of the pelagic phase the fourth setiger first appeared, and by the forteenth day a median tentacle was formed for the first time. In the succeeding three months the larva was provided with only three tentacles and thirteen setigers. Such delayed appearance of the adult characters, e.g. the tentacles and parapodia, as shown in the larvae of *E. harassii* may also well be applied to the larvae observed by Claparède and Mecznikow, who failed to rear the young extending over the four-setiger stage.

Fifteen years later Fewkes (1883) studied the development of *Lumbriconereis* sp., giving no specific name. Apart from a few differences as one might be expected in two different species of the same genus, the general course of the development of Fewkes' larvae agrees well with that of *L. latreilli*. The cilia are less pronounced in Fewkes' larvae, in which only a broad prototroch was present. As to the occurrence of the other girths such as akrotroch, paratroch and telotroch he gave neither mentions nor figures. Fewkes also observed the prominent pigment globules scattered on the larval body, but these spots are much reduced in his species. The prototroch seems to disappear at the later stage of the two setiger larva. The time at which the larva liberates from the jelly-mass is uncertain. In the oldest larva with seven setigers no crochets are as yet figured. Fewkes' larva had also no free-swimming stage during the development.

The development of *Lumbriconereis* so far as observed is much abbreviated and rapid, as exhibited by the early appearance of some adult structures. The plentiful supply of food yolk in the eggs, that makes the feeding of the larvae in the early stages unnecessary and the parental care for the larvae may play also an important role on the omission of the free-living pelagic stage in the development of *Lumbriconereis*.

IV. Development of *Neanthes* sp.

(Plates XIV–XV; Textfigs. 6–8)

1. *Breeding habit.* The breeding season of the worm extends from the middle to the end of July at Akkeshi. The eggs are laid in clusters embedded together in jelly and protected by the tough, more or less elastic white silky envelope. During the breeding season such egg-masses are abundantly found attached firmly to the leaves of *Zostera*. The size and the shape of these masses are both variable to some extent; sometimes flattened, and broader but sometimes slender, cocoon-shaped as shown in Figs. 1–3, Pl. XIV. The average length of the egg-masses is about 15 mm. The early development up to hatching takes place inside these egg-masses. The larvae first liberate from the spawn-masses when they have been provided with three setigers, and enter immediately into the creeping life. Thus the free-swimming stage is completely lacking in this species.

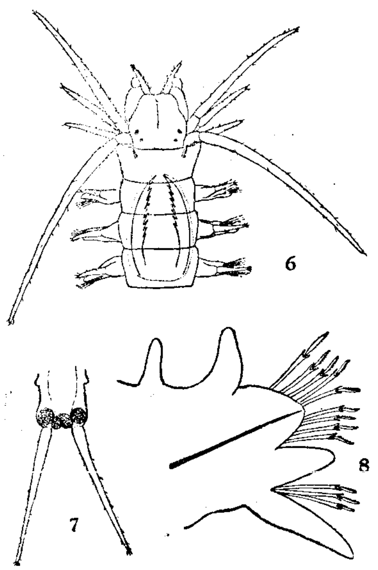
2. *Development within spawn-mass.* The eggs on the newly-formed spawn-masses are nearly spherical, about 280μ in diameter. Each egg is closely invested with a thin egg-membrane, and lies in a spherical cavity about 360μ in diameter, enclosed by a gelatinous and transparent envelope, by which the egg is fused with each other within the jelly. The egg is pale yellow in colour containing a large number of oily-looking globules and yolk cells. I was unable to ascertain the process of the fertilization, but think it be probable that the fertilization takes place before the eggs are laid, which is often the case in some other Polychaetes. The early cleavage proceeds very slowly, lasting for about three or four days before the early protrochophore has been formed. On account of the presence of a large amount of yolk and oil globules the early development seems to be retarded.

About five days later from the fertilization an atrochal larva is formed as shown in Figs. 5–8, Pl. XIV. The larva is more or less contractile and begins to rotate pressing the body against the inner wall of the gelatinous envelope. It is oval in shape with a fusiform anterior end, about 340μ long. The external larval cilia such as preoral, preanal and neurotrochal, found commonly in other Polychaete larvae, are never seen in the present species throughout the development. A pair of large yellow green masses containing rich yolk and oily globules is conspicuous and in contact with the dorsal ectoderm. Just ventral to these masses a pair of the similar but smaller round bodies is found. The provisional larval eyes appear as a pair of the transverse linear bands of golden refringent ectodermal granules on each ventro-lateral side of the anterior portion. These eyes, however, ultimately disappear when the larvae hatched out. A day or later three pairs of minute dorsal and ventral bristle bundles are protruded from the body sides. Both the dorsal and ventral bristles are short simple, finely pointed without any serrations and articulations. The posterior extremity is beset with a cone-shaped prominence which indicates the future anal cirri. During the one or two succeeding days the larvae develop rapidly and several important structures are formed. Fig. 11 shows the larva about two days after the atrochal stage. It is the latest larva that could be found in the egg-mass. The general colour of the body is yellow green. It measures about 460μ in length and 250μ in breadth at the widest portion. Three pairs of parapodia are present, each one having noto- and neuropodial chaeta-sacs which contain homogomph falcigers only. The first signs of the tentacles are seen at the anterior end of the prostomium as a pair of small round protuberances. At the same time the first pair of tentacular cirri are also distinguished as two small conical buds projecting laterally just in front of the first bristle bundles. A pair of the short anal cirri begins to appear at the posterior extremity. All of these appendages are provided with a tuft of short tactile cilia at the terminal portion. The prominent provisional eye-spots are still present. The jaws become visible within the buccal cavity.

Shortly after this stage the larvae begin to work their way out of the spawn-mass. When hatched out they sink immediately to the bottom, and commence their creeping mode of life. There is no pelagic larval stage. The larvae, unlike those of the majority of other Nereids, are altogether incapable of swimming and remain creeping at the bottom of the glass.

3. *Early bottom stages.* The larva recently hatched out is represented in Fig. 12, Pl. XIV. The most important change takes place in the constitution of eyes. The large provisional eyes begin to disappear, and two pairs of the ordinary reddish eye-spots are newly formed on each dorso-lateral side of the first tentacular cirri. The anterior pair of eyes is large, bean-shaped, while the posterior

one is small and rounded. The first pair of parapodia which is destitute of the dorsal ligule as is shown in the succeeding parspodia, is gradually shifted forwards. On each paradium a knob-like ventral cirrus appears. The fourth pair of the bristle bundles is now forming. Development proceeds steadily but slowly. When the larva has been equipped with the fifth setiger the rudiments of the palps occur on the ventral surface of the head as a pair of the ectodermal outgrowth. At the same time the buds of the second pair of the tentacular cirri arise ventral to the first pair. The middle lobe of the first parapodial pair markedly elongates and the bristles of this



Neanthes sp.

Fig. 6. Anterior portion of young worm with sixteen setigers. Dorsal view.

Fig. 7. Anal cirri of the same worm. Dorsal view.

Fig. 8. Parapodia of the third setigerous segment of young worm about seven days after hatching.

pair begin to fall off. The provisional eyes become entirely vanished. About seven days after hatching the larva possesses six setigers, measuring about 800μ in length. The first pair of the parapodia found in the previous stages falls off the bristle bundles, and the middle ones of each pair form a pair of long tentacular cirri directed posteriorly just behind the first two pairs. Two or three short, fine bristles embedded at the base of the last tentacular cirri indicate the remainders of the bristles previously protruded from the first parapodia. The palps become fairly well developed and mobile, being each one composed of two parts, a large basal piece and a small terminal knob as is usually shown in the adult. The jaws may be now recognized as a pair of toothed chitinous projections within the pharynx. A pair of the anal cirri is elongated and cylindrical. The buccal and pharyngeal regions are characterized, but the middle portion of the gut is still occupied by a large mass of yolk globules, from which the intestinal region leads backwards to the anus. Each parapodium is provided with well developed dorsal, middle and ventral ligules, and the small ventral cirrus, but no dorsal cirrus is as yet formed.

After this stage the larval development proceeds more slowly. The larva bearing eight setigers measures about 1.5 mm long. Three pairs of tentacular cirri are well extended. The dorsal cirrus of the notopodium makes its appearance (Figs. 31–32). The yolk has been almost consumed up, only remaining as a paired small masse on the third setiger. The young continued to grow at very different rates by individuals. Textfig. 6 shows a young worm about sixty days old. It has sixteen pairs of parapodia. In general appearance it agrees closely with the adult. Paragnath did not yet appear at the stage. The jaw in the pharynx has eight teeth along the inner side of the piece. The tentacle and tentacular cirri are fully formed with a number of short cilia sparsely borne. The parapodium shows the typical adult structure. Some of the worms lived for some weeks longer without any great changes.

4. *Formation of bristles.* In the present species no provisional long bristles as shown in some other Nereids such as *N. pelagica* did not develop during the early stages. The three pairs of bristle bundles are formed simultaneously, not in succession. The first fully formed bristles are the ordinary jointed homogomph falcigers exclusively, and afterwards the heterogomph falcigers are added to the neuropodium. At the six-setiger larva there are two kinds of bristles: homogomph serrated and heterogomph falcigers. No heterogomph spiniger has as yet been appeared. The first and second setigers bear the homogomph falcigers only. From the third setiger onwards one or two heterogomph falcigers are found on the neuropodium. The notopodium carries but homogomph falcigers. With further development the heterogomph spinigers begin to appear on the neuropodium. The constitution of the bristles at the sixteen-setiger larva is as follows. In the notopodium there are the homogomph spinigers alone and in the neuropodium are three kinds of bristles; 1) the heterogomph falcigers on the lower division, 2) one or two heterogomph spinigers

on the upper division and 3) homogomph falcigers on the same portion. When about twelve parapodia are formed, the acicular bristle as shown in Fig. 31 occurs first on the notopodium from the eighth to the tenth or eleventh setigers. The occurrence of the acicular bristle confined to the certain segments in the larval stages is characteristic of the species.

5. *General accounts.* Although a great number of work have been made on the development of various species of the Nereids, and the general outline of the development of Nereid worms are well known, there are several species of which the development we are comparatively ignorant. A number of the Nereid worms, such as *Nereis japonica, N. limbata, Platynereis megalops, P. dumerilii, Perinereis cultrifera* and others, have been known to discharge their sexual elements during a particular phase of moon. And thus, the fertilized eggs floating separately undergo the further development in the water, and then the larvae sink to the sea-bottom after the swimming stage. On the other hand, some of the Nereids faster their spawned eggs by laying them in jelly or inside the tube. *Nereis caudata* (Herpin, 1926) lays the eggs in a soft gelatinous mass. *Micronereis variegata* (Racovitza, 1893) collects the large red eggs in mucus. The egg-mass formed by the present species is very particular in its shape as well as in its constitution. During the breeding season the majority of the Nereids undergo more or less extensive changes in the structure of the body. The body of the mature worms is then divided into the non-sexual and the sexual regions containing the generative products. Some species such as *Micronereis variegata, Nereis japonica, N. diversicolor, Platynereis dumerilii* and *Nereis caudata* show no marked difference between the immature and the mature stages (Nérédiens sans métamorphoses), in other words there is absent from so-called 'Heteronereid' phase. Except a few species all of the Nereid worms so far observed have the early ciliated larvae leading to the pelagic life, though the duration of the swimming stage is much variable. *Nereis caudata* observed by Herpin (1926) has no free-swimming stage as the present species. The larvae of *N. caudata* lose the larval cilia before they are liberated, and on hatching they can not swim but crawl at once. After liberation from the egg-mass the development of Herpin's larvae proceeds generally in the similar way as in the present species. *Neanthes* sp, however, is very divergent from

Herpin's species during the stage before hatching. The presence of the remarkable provisional eyes and the entire absence of the locomotor cilia from the early larvae are both quite characteristics of the present larvae. Such abnormal, but interesting development, in which many characters of the early larvae are suppressed, may due to the large eggs supplied with a large amount of yolk and protected in jelly-mass.

V. Development of *Nainereis laevigata* (Grube)

(Plate XVI; Textfigs. 9–12)

1. *Breeding habit.* The adult worms are abundantly found between the *Zostera*-region embedded in muddy bottom. They do not form any particular tube as shown in other tubicolous Polychaetes. The mature worms breed from the end of May to the middle of June at Akkeshi. The spawned eggs are not protected specially by jelly mass as is shown in the allied species, *Haploscoloplos kerguelensis.* The eggs are laid on the surface of the mud in the form of a thin irregular ribbon-shaped cluster invested with a delicate pellicle. These irregular pieces containing a number of the fertilized eggs are often found adhesive to the stems of *Zostera,* but there are no special apparatus to support the spawn-mass. The eggs in this position were all fertilized and in various stages of development.

2. *Early larval stages.* The fertilized egg is nearly spherical and about 250μ in diameter. It is enclosed in a thin egg-membrane and is quite opaque, cream yellow in colour. The first cleavage is horizontal and unequal. Following the four-cell and eight-cell stages a sixteen-cell stage is reached between nine and ten hours after fertilization.

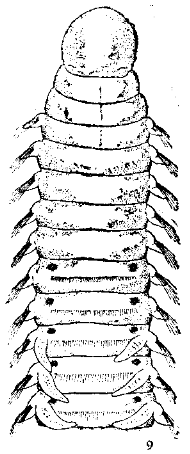
The first trochophore (Figs. 2–3), becomes active and begins to swim within thirty-two hours after fertilization. It is about 300μ long and 200μ wide at the prototroch, and is roughly coffin-shaped and dorso-ventrally more or less flattened. The colour is cream orange with a darker central area where the gut is foreshadowed by the presence of yolk granules. An akrotroch is a continuous band of fine, short cilia locating the midway between the apical end and the prototroch. The prototroch forms a continuous broad belt of cilia beating actively. Just behind the prototroch is a slight depression on each lateral body which seems to indicate the future segmentation. A pair of ocelli, each of reddish colour, is placed on the dorsal surface between the akrotroch and the prototroch. Posterior to the prototroch is a complete ring of short cilia, the paratroch. It is broader than akrotroch at this stage, but the size relation becomes soon reversible in the next stage. Near the posterior end a telotroch is formed of a circular band of cilia. Along the mid-ventral surface there is a longitudinal ciliary band, a neurotroch, running through the prototroch to the telotroch. No sensory cilia appears on both anterior and posterior ends. The mouth and anus are formed later. The movements of the larvae are rather inactive, but as the prototrochal cilia lengthen and become powerful the larvae begin to swim actively forwards, rotating along their longitudinal axes. About forty-six hours after fertilization the larva reaches the stage shown in Fig. 4–6, Pl. XVI. The body is elongate, measuring about 370μ in length. An akrotroch becomes broader than the paratroch, both being the complete bands of cilia. A number of the short sensory cilia project on the apical end. Otherwise there is little change from the trochophore stage. Shortly afterwards the larvae begin to creep on the bottom and are ready to metamorphose.

3. *Metamorphosis and early bottom stages.* Metamorphosis consists in loss of most of the cilia. In this species the disappearance of the cilia is gradual and apparently takes place step by step. Figs. 7–8, Pl. XII indicate the larvae about two days later than the foregoing stage. Several important changes occur in the larval body. The body becomes markedly elongate, measuring about 700μ long and 140μ wide. A pair of eyes is well developed bearing a lens directed outwards. The prototroch remains as a narrow band of rather long cilia leaving a broad gap in the median dorsal surface. It runs obliquely ventralwards forming a continuous ciliary band just above the mouth. An akrotroch remains unchanged. Immediately in front of the prototroch a minute crescent-shaped ciliated pit appears on each lateral side of the head. It is a nuchal organ. The paratroch and the telotroch are still present. The mouth opens as a narrow transverse slit ventrally just behind the prototroch. From the mouth a neurotroch runs backward to the posterior extremity. The body is now segmented. The segmentation is considerably distinct and there appear six segments between the head and pygidium. The first two segments succeeding to the head are achatetous. The para-

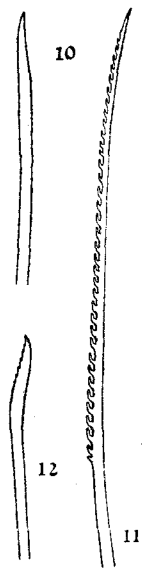
troch encircles the median portion of the second achaetous segment. Dorsal and ventral bristle bundles are projected from the third and the fourth segment. The digestive tract is fully formed, and then the larva begins to feed. The posterior extremity is now bifurcated, showing the future anal cirri. A day or more later the paratroch and telotroch disappear simultaneously. The eyes begin to degenerate in size and become more or less indistinct. A pair of bristles is added newly to the fifth segment. Fig. 10, Pl. XVI represents a later metamorphosing larva. It is about 1 mm in length. The akrotroch and prototroch are now entirely shedded off. The head is round and entire body becomes worm-like. The eyes are represented by the small pigment specks being destitute of the lens-like hyaline bodies shown in the previous stages. At a short distance posterior to the eyes a pair of the ciliated nuchal organs is well developed. The mouth is surrounded by the upper and lower lips. Of the larval ciliary bands only the neurotroch remains, extending from just anterior margin of the first achaetous segment to the last segment in front of the pygidium. Six setigers are present. The dorsal bristles are about twice as long as the ventral ones. Following to a buccal cavity a large spacious stomach occupies the anterior three setigers. The worms crawl actively when stimulated, but normally they glide slowly about the bottom of the bowl, probably dependent on their neurotrochs. When about seven chaetigerous segments have been formed the metamorphosis is completed. At this stage the neurotroch, which is the last to disappear, is thrown off eventually.

A worm recently metamorphosed, about ten days old, is shown in Fig. 12, Pl. XVII. The body is slightly flattened dorso-ventrally, and measures about 1.5 mm long, having nine setigers. The colour is light red. The prostomium is bluntly cone-shaped with a number of fine cilia along the outer margin. The eye becomes small, remaining only as a red pigment spot. The so-called dorsal sensory organ appears first on the sixth setiger as a pair of the round ciliated depressions. The homology of the dorsal sensory organ with the nuchal organ found in the head was thoroughly pointed out by Söderström (1922). The organs are added by and by to the succeeding posterior segments as the young develop. As shown in the early stage the first two segments are achaetous. The pygidium narrows and a pair of ovate anal cirri grows longer. The time taken to complete metamorphosis varies, but appears to be normally about four days, though often longer.

4. *Juvenile stages.* After metamorphosis the striking changes taken place during the juvenile stages are appearance of branchiae and the nototroch. Otherwise the main changes are confined to elongation of the trunk by the addition of the new segments in front of the pygidium and increase of the dorsal sensory organs. Fig. 13, Pl. XVI shows the more advanced young worm, about sixty old after



Nainereis laevigata (Grube)
Fig. 9. Anterior body of young worm with sixty-three setigers. Eyes become obscure.



Nainereis laevigata (Grube)
Figs. 10–12. Bristles from fourteen-setiger larva

fertilization. The body is slender, measuring 4.5 mm long. It has thirty two setigerous segments. The general shape of the body is similar to that of the adult. The young worm is reddish brown and more or less transparent. The digestive tract is well demarcated through the body wall. The prostomium is sharply defined, roughly ovate in shape. A pair of the small pigment specks near the posterior portion of the prostomium indicates the future eyes. The nuchal organs just posterior to the eyes shift to the lateral side. The dorsal sensory organs are found on the anterior margin of the chaetigerous segments from the fourth to the twenty-fifth. The branchiae occur from the fifth setiger at the base of the notopodium. They are leaf-like and densely ciliated along their entire border. With the growth of the worm the position of the first branchia seems to be shifted backwards. The nototroch is present on each segment from the sixth setiger onward as a transverse row of short cilia across the dorsal surface between the left- and right-hand branchia. The parapodia are of the adult type. Both the dorsal sensory organ and the nototroch first occur on the sixth setiger, and the branchiae on the eighth in the young worms with forty-three and sixth-three segments. The position of the first organs of them seems to be variable to some extent in the adult worm, in which the first branchiae occur generally on the setigers from the eighth to the twelfth. The pygidium is not changed. Two pairs of ovate anal cirri are first formed in the young bearing forty-three setigers. The eyes become sometimes quite obscure in the advanced young.

The comparison of this species with other Ariciid larvae has been given at the end of the next section.

VI. Development ot *Haploscoloplos kerguelensis* (McIntosh)

(Plate XVII)

1. *Breeding habit.* The breeding season of this species extends from the end of June nearly to the middle of July at Akkeshi. The adult worms are commonly found embedded in sandy mud bottom. During the breeding season, the female worms collect the fertilized eggs within pear-shaped masses of jelly attached to the bottom by their slender narrow stalks. The early stages of the development are passed inside the jelly. The newly-formed egg-mass is ellipsoid, 8–15 mm in length exclusive of the stalk and 7–12 mm in breadth. The supporting stalk, the major portion of which is embedded under the ground, is flexible, and 40 mm long or more. It is an empty tube densely clothed with the sandy particles. The spawn-mass consists of colourless transparent mucus, in which are envolved a number of small brown eggs in cluster. The mucus, which is not divided into parts corresponding to the eggs, appears structureless and contains numerous diatoms.

2. *Development within spawn-mass.* The fertilized egg is nearly

spherical, about 200μ in diameter, and perfectly opaque with brown tint, being invested with a thin egg-membrane. It is filled with a large amount of yolk. In a day after fertilization the embryo (Fig. 3, Pl. XVII) begins to rotate slowly inside the jelly. The body is ellipsoid, 220μ long. The prototroch consists of a broad band of short cilia encircling the anterior body. It is not continuous all round, but there remains a narrow dorsal gap. The ciliary band of the prototroch seems to be apparently consisted of three rows, but it is not as yet distinctly marked out as shown in the following stage. An unpaired eye-spot appears on the right side anterior to the prototroch. A telotroch forms a continuous band of short, fine cilia at the posterior body. As a whole the larva is very granulated and opaque, especially in the endodermal mass. Both the neurotroch and paratroch are not visible.

About thirty-two hours after fertilization the larva (Fig. 4, Pl. XVII) acquires the several locomotor ciliary bands. The larva elongates, measuring about 250μ in length and 140μ in breadth at the widest portion. It is oval, the whole body being dense with yolk. An akrotroch appears in the anterior half of the cephalic portion in front of the prototroch. A pair of eyes is present on each lateral side posterior to the akrotroch, each represented by a red conical spot with a lens-like cup. The prototroch, in which there remains a dorsal gap, has three bands of cilia, of which the anterior one being the longest and about 15μ in length. Round nearly the middle region of the entire body is a row of ciliated band, a paratroch. The ciliary band of the paratroch is also discontinuous leaving a broad ventral gap. Between the first paratroch just mentioned and the telotroch there are two paratrochs or gastrotrochs, each one composed of a pair of the short ciliated bands situated on both ventro-lateral sides of the neurotroch. These gastrotrochs can not be seen from the dorsal side. The neurotroch also appears along the mid-ventral surface. Fig. 6 and 7 show the larvae a day later than the foregoing stage. There is three more gastrotrochs of short cilia formed in addition to the first two. Indications of the segmentation appear in front of each gastrotroch. Several fine sensory cilia are found at the apical end. The larvae creep within the jelly. Further development takes place by the further addition of the gastrotrochs and the nuchal organs. The larvae are still enclosed inside the jelly but when taken out show active movement.

Thirty-two hours after the appearance of the first gastrotroch other eight pairs are formed (Fig. 11). At this stage a pair of crescent-shaped ciliated pits, i.e. nuchal organs, is first formed just behind the eyes. Akrotroch and prototroch remain unchanged, but both increase in length of the cilia. The neurotroch widens from the future mouth. Nine segments appear between the head and the pygidium. Only the first segment bears a paratroch forming a discontinuous band of rather long cilia interrupted by the neurotroch. On the second and the succeeding segments the gastrotroch occurs in pair on each lateral side of the neurotroch. The pygidium shows a slight depression at the terminal end, which indicates the future anal cirri. The entire body is still opaque, and the gut is marked as a sac-like structure. The larvae creep slowly in the jelly. Shortly afterwards the pear-shaped gelatinous mass gradually disintegrates and larvae now liberate from the mucus. They swim about in active manner in water by means of their cilia showing a positive phototropic reaction.

3. Pelagic stages. About three days after fertilization the larva hatches out from the jelly-mass and enters pelagic life. The larvae liberated from the egg-mass swim about actively near the surface of water. They swim always towards the brightest side of the vessel, where they so crowd together in large numbers as to form a cinnamon-coloured scum on water. The free-swimming life is very brief, lasting commonly no more than a day or two. During the pelagic stage the body becomes markedly elongated and acquires bristle bundles. Fig. 12 shows the larva immediately after hatching. It measures 700μ long with eleven segments except the head and pygidium. During this period the mouth and anus are opened and the larvae begin to feed. The gut is divided into several parts such as buccal cavity, oesophagus, stomach and intestine. A pair of the rudiments of the branchiae appears first on the last segment in front of the pygidium, i.e. on the eleventh segment. It is at first protruded as a round thickening of the ectoderm, and develops rapidly. The rudiments of the anal cirri also become distinct at the posterior end. They are beset with a number of short, fine cilia. One more pair of the gastrotroch is newly added in the tenth segment. In further development the gastrotroch does not increase in number. The gastrotroch is present on the space between ventral bristles and the neurotroch as shown in Figs. 9–10. The neurotroch extends from the mouth as far as the posterior margin of the tenth segment. A most remarkable change is the abrupt appearance of bristles on many segments. Both the dorsal and ventral bristles apparently occur simultaneously on the segments from the second to the ninth. When the larva acquired two pairs of branchial rudiments the akrotroch is completely thrown off. The larvae now sink to the bottom and commence their creeping life. With the commencement of the creeping habit the larvae are ready to metamorphose.

4. *Metamorphosis and early bottom stages.* Fig. 13, Pl. XVII represents the early metamorphosing larva. The general body colour is reddish brown and the larva is fairly transparent. Two pairs of branchial buds are formed in the two posterior segments. There are nine setigerous segments. No bristles are as yet found on the branchiate segments. An akrotroch is first to disappear. The prototroch shifted to the ventral surface leaving only a pair of dorsal patches. A pair of eyes now degenerate and lose the lens-like body as shown in the previous stage. About seven days after fertilization the larva completes the metamorphosis. When the cilia are entirely disappeared the larva acquires three pairs of branchiae. A larva recently metamorphosed is shown in Fig. 14. The larva has eleven setigers. It is 1.5 mm in length. The head is ovate, with a pair of small eye-spots and nuchal organs at the posterior portion. There are no dorsal sensory organ and the nototroch as shown in *Nainereis laevigata*. The branchiae are well developed, club-shaped, being arched over the dorsal surface. Along the internal border of branchia a row of fine cilia is present. The first branchia occurs on the tenth setiger. A pair of anal cirri elongates gradually. A short band of fine cilia is found on the dorsal surface of the pygidium. Whether this is the remainder of the telotroch or not I can not to determine. The largest individuals so far observed had twelve chaetigerous segments, and the fourth pair of branchia was growing (Fig. 16).

5. *General accounts.* The eggs of *Nainereis laevigata* are less safely protected than those of *Haploscoloplos kerguelensis*. In *Haploscoloplos* early developmental stages are passed in the spawn-jelly and a shorter free-swimming stage exists than in *Nainereis*; in the case of the latter the larva liberates from the egg-piece shortly after the trochophore stage. The larval ciliary bands such as akrotroch, prototroch, paratroch, telotroch and neurotroch are all found in the larvae of both genera. The prototroch of *Nainereis* forms a single broad

continuous ciliary band, while that of *Haploscoloplos* consists of three ciliated bands. In the latter the prototroch has a narrow dorsal gap. The occurrence of the paratroch on the second achaetous segment seems to be one of the characteristics of the Ariciid larvae. The paratroch found in the larva of *Haploscoloplos* does not form a complete ring of cilia around the body as shown in *Nainereis*. The gastrotroch is found only in the larva of *Haploscoloplos*. In the Spionid larvae the paired gastrotroch usually develops in the larval stage. In *Nainereis* bristles begin to appear when the larva acquired six segments, while in *Haploscoloplos* they first occur after ten segments have been completed. The branchiae, however, are budded out at earlier stage in *Haploscoloplos* than in *Nainereis*; in the former they develop some time before metamorphosis and in the latter the branchiae first appear after the larvae settled down. When the metamorphosis has completed the larva of *Haploscoloplos* has three pairs of well developed branchiae, and that of *Nainereis* has no indications of branchiae. The dorsal segmental sensory organ and the nototroch are the remarkable features in larvae of *Nainereis*. In spite of the presence of the organs in the adult of *Haploscoloplos* the larva so far observed has none of them. The dorsal sensory organ or 'segmentaler Wimperhügel' is generally found in the representatives of the family Ariciidae. It is a round depression densely ciliated and is located on each segment but absent in certain anterior segments. In the adult of *Nainereis* the dorsal sensory organ is present from the eleventh segment or more posterior segment. Söderström (1920) considers that these segmental sensory organs may be synonymous with the nuchal organ found in the prostomium. The nototroch of the adult or "dorsale Flimmerwülste" is only detected in the adult of *Nainereis* and *Theostoma* among the family. In the larvae it is usually found associated with the dorsal sensory organ. The larval eyes of the Ariciid worms are well developed and bear lens-like hyaline bodies at the terminal end. With the growth of the larvae the eyes gradually degenerate and become rather obscure in the young. As I could not consult with Salensky's paper (1883) on the development of *Aricia foetida*, an unique literature of the Ariciid larvae, it is unable to compare my observations with his results. So far as the present studies on the two genera of the Ariciidae go, the characteristics of the Ariciid larvae may be defined as fololws. Highly contractile trochophore with a short free-swimming existence, opaque due to large amount of yolk. Prototroch, telotroch and neurotroch all formed of continuous bands of cilia; an akrotroch is also present. Paratroch sometimes incomplete ventrally. The gastrotroch in the early stages, and nototroch and dorsal sensory organs in later stages may or may not be present. A pair of nuchal organs. Mouth and anus opened during metamorphosis. A pair of well-developed eyes bearing a lens in the early larvae. The eggs are not discharged freely, but are laid in clusters in jelly.

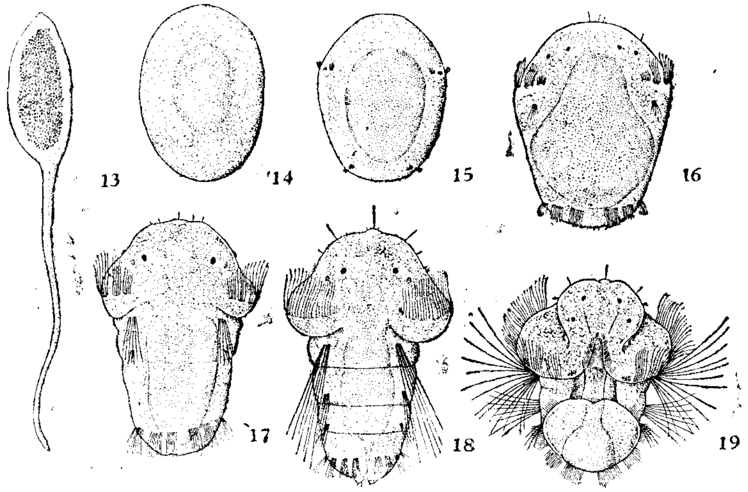
VII. Development of *Spio filicornis* (O. F. Müller)

(Textfigs. 13–21)

1. *Breeding habit.* The adult worms were found in mud between the *Zostera*-region living in soft sandy tubes lined with thin mucus. Specimens were often obtained by lifting loose stones and examining the mud beneath. At Akkeshi, during spring and summer season from April to July a number of the ellipsoidal spawn masses of jelly are found attached to the muddy bottom by their supporting tubular stalks and swinging to and fro with waves. These jelly masses contain a large number of yellow green eggs more or less evenly distributed. The newly formed egg-mass (Textfig. 13) measures about 10–13 mm in length and 5–6 mm in breadth at its widest portion. The jelly mass terminates at the base to form a slender stalk, by which it is fixed to the bottom. The stalk is about 22 mm in length and 1.5 mm in width. The mass with eggs and the stalk consists apparently of translucent mucus. In *Polydora* the eggs are generally laid in egg-sacs attached to the wall of the parents' burrow by filaments, and are fused with each other forming a long string. Differing from *Polydora* the eggs of the present species are always laid in a solitary jelly-mass as is shown in *Arenicola cristata*. Development takes place inside this jelly and in a jelly mass one may find eggs and larvae at various stages of development.

2. *Development within spawn-mass.* The fertilized egg is opaque and densely granulated with yolk. It is ellipsoidal, nearly 300μ long and 200μ wide, but size and shape are both variable. The cytoplasm is greenish brown both by transmitted and reflected lights with a darker vesicle near the centre. About forty hours after the fertilization the larva begins to rotate slowly (Textfig. 15). The

colour is pale green with a darker central area indicating the future gut. The larva is more or less rounded dorsally, but comparatively flat ventrally. The prototroch does not form a continuous band of cilia and is broken into groups of cilia leaving a broad dorsal gap. Owing to shortness the cilia are very difficult for detection; the number of the cilia groups is indistinct at the present stage. The telotroch also consists of a few cilia groups. The first sign of the mouth is indicated as a clear area just behind the prototrochal region. No sensory cilia at the extremities of the body are formed.



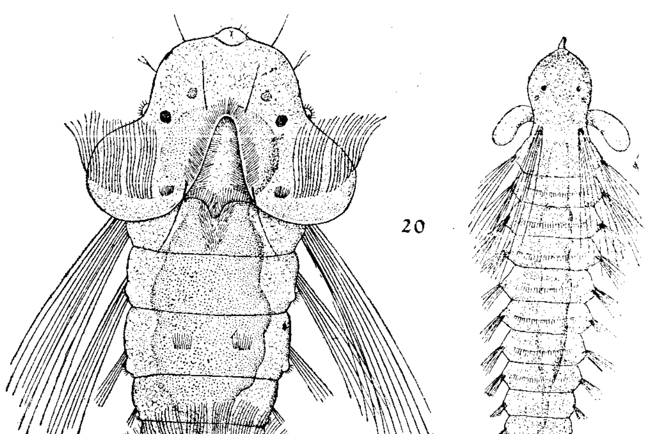
Spio filicornis (O. F. Müller)

Fig. 13. Spawn-mass of jelly.
Fig. 14. Fertilized egg. Actual length approx. 300 μ.
Fig. 15. Early larva forty hours after fertilization. Dorsal view.
Fig. 16. Larva about fifty hours after fertilization. Dorsal view. Actual length approx. 330 μ.
Fig. 17. Larva about three days old. Dorsal view.
Fig. 18. Larva about four days old. Dorsal view.
Fig. 19. Ventral view of the same larva as shown in Fig. 18 in contracted state.

About twelve hours later the first trochophore is formed. It is about 330μ long and 250μ broad at the prototroch. A few sensory cilia are found at the anterior end of the body. There are two pairs of eyes, a median pair set wide apart on the dorsal surface and a lateral pair situated more ventrally. On the dorsal surface the prototroch consists of six groups of cilia which is divided by a broad mid-dorsal space into two groups of three. On the ventral surface there are also six groups, three on either side of the mid-ventral line. Like the prototroch the telotroch is not continuous, but appears as twelve separate groups, of which six on the dorsal and the others on the ventral sides. The first pair of provisional bristles appears, each group formed of six bristles and the longest one is 25μ long. The gut is still very granulated, pyriform in shape. About thirty hours later the prototrochal and telotrochal cilia lengthen; each cilia group enlarges and is finally united, so finally forming a continuous line of cilia. The head is oval in front with a small round elevation at the extremity. The prototroch ridge becomes distinct forming a pair of the lateral outgrowth. The first bristle bundles are well developed and the second bundles are newly formed. The first indication of the segment is shown between these bristle bundles. The larva is active and wriggles about among other larvae.

About twenty-four hours later the emergence of the larva occurs as is indicated in Textfigs. 18–19. The general colour of the larva is pale brown with a darker area showing the position of the gut which extends from the first setiger to the posterior end. Two pairs of eyes are fully developed, one pair being dorsal and the other ventral. There are three rather long apical cilia. On both lateral sides of the head a patch of the fine cilia is present. On the midway between the apical end and the prototroch a pair of finely ciliated cubic swellings appears on the lateral walls. During the further development the similar structures are also found just behind bristle bundles. The function of these ciliated bodies remains unknown. The prototroch increases in length, forming a continuous line ventrally and laterally. The cilia groups situated just outerside the continuous ciliary band on both dorsal and ventral positions remain small. On the ventral surface a pair of lateral lips forms a funnel-shaped space in front of the true mouth. This space, or 'vestibule' termed by Gravely, opens widely to the exterior. The vestibule is lined throughout with fine cilia, which extend over the ventral surface of the lips as far as the prototroch. A pair of the long stiff sensory cilia is present on the inner side of the lips and on the anterior end of the vestibule between the ventral eyes. The three primary pairs of provisional bristles are well extended. The first bristle bundles are longest, the largest being 180μ long, and reach backwards as far as the end of the body. The larval bristles in the second and in the succeeding setigers are always slightly shorter than those of the first setiger. The telotroch still forms separate groups of cilia as shown in the previous stage. A pair of small hyaline anal vesicles (?) is indicated at the posterior extremity of the body. The presence of anal vesicles during the larval life is not an unusual case in the Sabellidae and the Serpulidae, but in the Spionidae no mentions as to the occurrence of such vesicles have hitherto been made. In the larva of *Scolecolepis* observed by Day (1934) numerous glandular cells are found below the anus which is probably filled with mucus. The anal vesicle found in the present species is not glandular but clear and transparent, filled apparently with a fluid. The function of this vesicle is not ascertained. The anal end is bifurcated to form a pair of small knobs with a few sensory cilia on the dorsal surface. This is the first indication of the dorsal notch of the future anal cup. In one or two days the larvae are liberated into the sea and begin to swim freely.

2. *Development in plankton.* The larvae liberated from the spawn-mass swim very actively towards the lighted side. They are strongly positively phototropic. Shortly after liberation at the stage



Spio filicornis (O. F. Müller)

Fig. 20. Larva recently liberated from egg-mass. Ventral view.

Fig. 21. Recently metamorphosed larva caught in plankton. Dorsal view.

figured in Fig. 8 four bristle bundles are formed. Between the mouth and the posterior end of the first setiger a short row of fine cilia is present along the mid-ventral line. The prominences of lateral prototrochal ridges are accentuated, but their general shape remains unchanged. Both the prototroch and telotroch consists of a continuous band of long, fine cilia. The cilia on the anterior lip of the vestibule and those on the oblique groove increased. Two pairs of stiff sensory or tactile cilia at the upper and lower lips of the vestibule become long. The cubic-shaped ciliated swellings shown in the previous stage in front of the prototrochal ridge are now newly added to each setiger just behind the bristle bundles. A pair of the similar bodies is also found near the terminal end posterior to the telotroch. There is a pair of gastrotroch on the third setiger. As development proceeds these paired gastrotrochs are subsequently formed on other setigers. The body segments are well marked by the constrictions. The number of provisional bristles in the four setigers is 20, 10, 6, 3 respectively. A pair of the anal vesicles is highly developed and vacuolated. The entire body is pale brown in colour.

The larva drawn in Fig. 9 is one of the members caught in plankton. It is supposed to be the larva recently metamorphosed. All of locomotor cilia shown in the early stages are fallen off. The body is slightly flattened dorso-ventrally with twelve setigers. Nototrochs are developed on the dorsal surface of all segments from the second to the eighth setigers. A pair of tentacles appepars at the base of the head, where the prototrochal ridges were present formerly. It is a club-shaped organ. The head is fusiform, bearing an unpaired short median tentacle at the anterior end. Two pairs of eyes are still present. The first provisional bristle bundles are borne on the dorsal surface at the level of the developing lateral tentacles. From the tenth setiger onward, crochets are present in bristle bundles. The pygidium is short, broad and flattened posteriorly. No anal vesicles could be detected. The larva can swim rapidly by use of the nototroch, the gastrotroch and the provisional bristles.

4. *General accounts*. Though a number of literature on Spionid larvae caught in plankton, especially on *Polydora* larvae, are published, very few species have been reared from the egg to metamorphosis. Leschke (1903) appears to be the first to rear the larvae of *Polydora ciliata*. Recently Wilson (1928) described the development of *Polydora ciliata* and *P. hoplura*, and Day (1934) also observed

the larvae of *Scolecolepis fuliginosa* tracing the stages from the egg to the young worm. In *Scolecolepis* the eggs are pelagic as shown in *Nerine*, and in both species of *Polydora* the eggs are laid in egg-sacs attached to the wall of the parents' burrow. As is already mentioned the present species does not form a long string of egg-sac as shown in *Polydora* or *Pygospio* (Söderström, 1920), and, furthermore, the eggs are not spawned freely as shown in *Scolecolepis*, but are always laid in the solitary jelly-mass. The larvae of *Polydora ciliata* are released at the stage with three chaetigerous segments and spend a long pelagic life. On the other hand, *P. hoplura* are released at a very late stage, and have only a short planktonic life. As to the period of liberation and the duration of pelagic life the early larvae of the present species agree well with those of *P. ciliata*. The larva of *Scolecolepis* has three pairs of eyes, the third pair disappeared in the young worm. As is mentioned by Day, it is apparent in all Spionid larvae that the centre of differentiation is located firstly in the third setiger and then the fourth setiger onwards, so that the segmental structures, such as the gastrotroch and parapodia, differentiate first in this segment. The occurrence of anal vesicle is a remarkable characteristic of the present species. Though the similar vesicular structures are found in the head of a number of the Polychaete larvae, the anal vesicles are limited in distribution and conspicuously developed in the Sabellidae and the Serpulidae as described elsewhere.

The larvae of the Spionid worms may be in general characterised by the presence of long provisional capillary bristles, of which those of the first segment are considerably longer than others. The Spionid larvae are one of the predominate forms among the Polychaete larvae found in plankton organisms.

VIII. Development of *Cirratulus cirratus* (O. F. Müller)

(Plates XVIII–XIX)

1. *Breeding habit.* *Cirratulus cirratus* is found in large numbers inhabiting the sandy somewhat foul mud between the tide marks and also in rock pools lying with its body beneath stones or pieces of rock embedded in the mud. The presence of the worm in its natural habitat is indicated by a group of delicate, elongate, rosy or yellow coloured filaments of tentacular appearance which is protruded from

the sand into pools left by receding tides. The animals are not easy to be collected owing to the marked propensity to lie the body beneath stones or pieces of rock embedded in the mud.

From the beginning of May to the prime of July we can find a large number of pale blue fusiform egg-masses of jelly spawned by the worm between the tide marks. These jelly-mass (Fig. 1, Pl. XVIII) has a central elongated oval portion provided with narrow cylindrical stalks extending to both opposite ends which fix the egg-mass to the bottom. The species does not form the pear-shaped jelly-mass supported by a single long stalk floating on the surface of water as is shown in *Arenicola* and others. The central portion of the jelly-mass contains two egg-sacs involving a large number of fertilized eggs. The length of the whole egg-mass together with the stalks measures about 40 mm or more and that of central sac about 20 mm by 10 mm at the broadest portion. The entire mass pretends rather loose appearance. The egg-mass is laid nearly parallel to the substratum being attached to rocky particles or muddy bottom by a pair of stalks. Jelly-masses of recent formation are nearly transparent, and pale bluish eggs may be seen shining through a thin gelationous mass. But most of the masses in nature are of dirty colour, being invested by a covering consisting mainly of soft ooze and organic debris adhering to the outside of the jelly.

2. *Early larval development.* The eggs in newly formed egg-masses are spherical with a transparent membrane. It is about 100μ in diameter and is closely invested in a thin membrane. The general colour is pale green by reflected light. The cytoplasm is finely granulated. About twenty four hours after fertilization the larvae, about 110μ long and 100μ broad, begin to rotate by means of the cilia of broad prototroch. The cilia can be seen inside the egg-membrane, which is separated from the egg surface before the first cleavage. Afterwards forms this membrane a cuticle around the larva. The telotroch and apical tuft do not yet make their appearances. The prototroch consists of a broad band of short cilia extending about one-third the entire body from the anterior end. The endoderm forms a large oval central mass of big cells, the outline of which is clearly visible. About fifteen hours later the trochosphere stage shown in Fig. 4, Pl. XVIII is formed. It is about 130μ in length and 110μ in breadth. The larva is widest in the region of the prototroch, which forms a broad band of rapidly beating cilia measuring about 9μ in

length. The prototroch encircles the body completely. The telotroch is also a complete band of cilia, shorter and narrower than those of the prototroch. An apical tuft of several long fairly strong cilia springs from the anterior end, directed forwards along the line of locomotion. The locomotion is relatively rapid. An akrotroch is formed across the dorsal surface of the head situated a short distance behind the apical tufts. Several yellow green large pigment patches are scattered on the body surface. They are specially concentrated at the pygidial region. The stomodaeal invagination is visible as a transverse slit just posterior to the prototroch in the mid-ventral line. The larvae swim actively when they were liberated from the jelly-mass. A few hours later an additional band of cilia, neurotroch, appears. The neurotroch passes through the ventral gap in the telotroch in its course from mouth to anus. There are two or three very fine short sensory cilia near the anus. The larva becomes contractile. A number of refringent yellow green pigment patches scattered over the entire body become more distinct. The central endodermal mass is also elongated, showing as yet no sign of division. A faint segmentation appears as an indication of a slight lateral constriction between the prototroch and the telotroch. Meanwhile, the larva reaches the four days' old stage shown in Fig. 7–9, Pl. XVIII. The trunk is indistinctly segmented, and is rather difficult to determine how many segments are there. The prototroch becomes narrow remaining as a linear band encircling the head portion. The apical tuft decreases in their length and the akrotroch has entirely fallen off. The endodermal central mass is now segmented and divided into several portions such as oesophageal, stomach and intestinal regions. The anus is situated on the dorsal side. The neurotroch still remains as shown in the foregoing stage. The mouth is a transverse slit immediately behind slightly overhanging rim of the prototroch; anterior to it a longitudinal tuft of cilia is found. The larvae are now ready to metamorphose.

3. *Metamorphosis and early bottom stages.* The individuals in a culture do not metamorphose simultaneously, some are more advanced than others. The first larva metamorphosed about ten days old and the last about five days later. Metamorphosis is undergone in loss of most of the cilia. It is interesting that the cells comprising the prototroch and telotroch are definitely got rid of by internal absorption. In both regions the cilia are shedded off by the destruction

of the cells and their contents are rounded up into large oily looking brown and yellow spheres of varying size. These spheres eventually disappear. There can be little doubt that they are internally absorbed. Fig. 10, Pl. XVIII shows the dorsal view of a metamorphosing larva. It is about 440μ in length. Most of the cilia of the prototroch have fallen off but a small dorsal patch remains. The dorsal akrotroch disappeared. The ventral semicircular patch of cilia situated just anterior to the mouth, however, remains and it is usual for the species to be present for a while after metamorphosis. The telotroch also disappeared. The neurotroch is scarcely affected by metamorphosis. A pair of crescent nuchal groove first appears on each dorso-lateral side of the head region just above the dorsal patch of the prototroch. They are finely ciliated. The buccal region is fully formed and the creature begins to feed. The anus is situated on the dorsal surface of the pygidium. A pair of bristles is protruded for the first time. There is one dorsal and one ventral bristle on each side. These bristles are minute, almost straight in shape. The first bristles appear in the third segment behind the head. The yellow green patches which are abundantly found in the foregoing stage decrease in size and in number. The larvae glide slowly about the bottom of their bowl.

Four or five days later three pairs of bristle bundles are protruded. The first pair contains two dorsal and one ventral bristles and the next two pairs have each one dorsal and one ventral bristle. When four chaetigerous segments have been formed, the first two ones each bear two dorsal and two ventral bristles and the third one two dorsal and one ventral bristles. Besides the structure of the bristles the body characters are almost identical with the preceding stage. The neurotroch still remains unaltered as is previously shown in the early stages. The worm increases in length. When the fifth setigers are added, the branchial filament appears for the first time. It arises from the posterior margin of the last achaetous segment immediately in front of the first setiger, and is situated indifferently on either right and left side. Figs. 13 and 14 show a somewhat older young with a pair of well-grown branchial filaments and a tentacular bud on the right side. The bristles are more numerous than before. They are mainly consisted of crochets, some plain and some toothed. The neurotroch no longer reaches the extremity of the pygidium, but extends in this stage from just behind the mouth to the posterior margin of the first chaetigerous segment. The eye-spots can not yet be detected. The young worms crawl actively when stimulated, but normally creep slowly about on the bottom. The body increases in length and girth by the addition of new segments and by growth of old ones. Additional branchial filaments are budded out from posterior dorsal borders of the achaetous region and from the first, second etc. setigers. Their relative lengths are extremely irregular; they are never alike on the both sides and in two individuals. Sometimes the branchial filaments of one side are very long, while those of the other sides are indicated by small buds; more often there are long and short ones on the same setiger. Fig. 21, Pl. XIX shows a larva about forty days old. It has sixteen setigers, measuring about 2.6 mm by 0.2 mm. There are a pair of the branchial filaments, a longer one attaining backwards as far as the eighth setiger, and an unpaired right tentacular filament. No other branchial buds can be found in the succeeding segments. The larva about sixty old is illustrated in Fig. 20, Pl. XIX. The body is slender and cylindrical, bearing twenty-one setigers. On the posterior margin of the last achaetous segment are found a pair of the branchial filaments and a pair of tentacular filaments. The latter arise a little nearer to the mid-dorsal line than the former. They are rather thicker filaments than the ordinary branchial filaments and are finely ciliated along the mid-ventral line. The second pair of the branchial filaments springs from the third setiger, of which the left one is much longer than the right. The second setiger is destitute of any indication of the branchia. The fourth setiger has an unpaired brachial bud behind the right notopodium, while the arrangement of them is reversed on the sixth setiger. The asymmetry and size of the branchial buds is expressed to different extents by individuals. The dorsal and ventral bristle bundles are present on each chaetigerous segment. In the anterior six or seven segments long capillary bristles with fine minute serrations are predominent on both dorsal and ventral podia, but they become scarce and short on the posterior segments, and the last few segments bear only crochets. The crochets carry fine teeth along one lateral border. The neurotroch is fallen off at the present stage. The bristles on the anterior five or six segments is four in number on both noto- and neuropodium and then it decreases in the succeeding setigers to three, two and one successively. The anus is dorsal. The digestive tract, yellow brown in colour, is distinctly divided into the buccal, oesophageal, gastric and intestinal regions.

The oesophageal region occupies first four chaetigerous segments and the gastric portion is located between the fifth and the eleventh setigers. On the head portion is found a few pigment spots of varying size, scattered near the nuchal groove. Whether these pigment spots are homologous with the eye-spots or not is at present uncertain. The worm is transparent and very contractile. The whole animal is enclosed in a soft mucus membrane deposited with debris. In a larva of the same age shown in Fig. 20 the first pair of long branchiae springs from the posterior border of the achaetous region, and a pair of thicker tentacular process arises nearer to the dorsal side. The first setiger bears no branchia on both lateral sides and the third setiger has a long branchia on right side, just behind the bristle bundles and a short branchial bud on left side. The fourth setiger carries no branchia and the fifth setiger has a branchia of moderate size on the left.

4. *General accounts.* The earliest account about the development of the Cirratulidae was given by Claparéde and Mecznikow who in 1868 described and figured two young Cirratulid worms. One of these larvae belongs to *Audouinia filigera.* It has nine setigers and two pairs of branchiae. The other species treated by the same authors belong to a viviparous species which had segments bearing five to six bristles and two pairs of long branchiae. Cunningham and Ramage observed the spawning of *Cirratulus cirratus* in 1887. They reported that the eggs are enveloped in clusters of mucus secreted by the parents. Caulley and Mesnil (1898) gave an account of the larval stages of *Dodecaceria concharum.* The species is viviparous and spends the early stage of the worm in the mother's body cavity, and the larva first liberates when about three segments are acquired. In 1911 Sokolow gave also a detailed account of the viviparous species *Ctenodrilus branchiatus.* In this case the larvae pass their entire developmental stages within the body cavity of the mother untill they reached the size as large as the parents. In 1930 Hofker described the larvae of other Cirratulid worm which was ascribed to *Streblospio dekhuyzeni.* More recently Wilson (1936) reared the adults of *Audouinia tentaculata* and induced to spawn in the laboratory. He first succeeded to rear the fertilized eggs to metamorphosis and early bottom stages. The species does not form egg-mass, but the discharged eggs are always separated.

The larvae of *Audouinia tentaculata* observed by Wilson, though agreeing in the general trend of development, behaved different from *Cirratulus cirratus* in detail. In the former the eggs are less safely protected, i.e. discharged eggs are always separate and development takes place freely in sea-water. The ciliation of the larva of *A. tentaculata* is more complex than those of *Cirratulus*. In the former there appear two ciliary bands in the anterior part of the trunk, which may be regarded as the gastrotrochs, while in the latter no such ciliary bands are present. An akrotroch first appears in the larva of *Audouinia* three days old, whereas it is already formed in the early trochophore of *Cirratulus*. Yellow green patches which are scattered abundantly on the body surface in the larva of *Cirratulus*, were not found in those of *Audouinia*. The larva of *Audouinia* has eye-spots composed of brown oily globules. After metamorphosis a few irregularly shaped pigment spots were found in the head region of *Cirratulus*, but it is difficult to assume them as the eye-spots. The eye-spots shown in the adult worm seem to be appeared in considerably later stage of the young. Wilson observed that the teneacular buds first appeared in the larva about three-months old and the branchiae in the five-setiger larva about sixty days old. In these points the larvae of *Audouinia tentaculata* seem to be more slowly developed than those of the present species. The disappearance of the neurotroch is also considerably late in *Audouinia*. The larva of *Audouinia* three months old has only fourteen chaetigerous segments, while that of *Cirratulus* has more than twenty setigers in about two months. The crochets of young *Audouinia* bear a secondary tooth above a main fang, whereas in *Cirratulus* all the crochets are unidentate with fine serrations.

IX. Development of *Lanassa nuda* (Moore)

(Plate XX)

1. Breeding habit. The adult worms inhabit soft muddy bottom among sea-weeds near the low tide-mark, and are occasionally found among roots of *Laminaria* and other algae. From the beginning of May to the end of June the spawn of this species may be found as a light pinkish gelatinous cluster with a long stalk, by virtue of which the mass is fixed to the muddy bottom. The mass (Fig. 1, Pl. XX) consists of mucus, which is quite hyaline and colourless, with the outer wall much wrinkled, and contains the eggs or larvae to a considerable number. These eggs are pinkish, minute and scattered. The outer part of the gelatinous mass is stiffer than the central part, to which the eggs are confined. The mass is continued at the base to a narrow tube or stalk invested with minute sand grains. The stalk extends straight down into the muddy ground inhabited by the parent worms. The newly formed spawn-mass is broader than long, measuring 5–8 mm in length and 6–10 mm in breadth. The stalk is 10–13 mm long, and 2–3 mm wide. As in the case of other Terebellid worms the early larval stage of the present species is passed through within the spawn-jelly, from which the young creep out having a few pairs of parapodia. And thus, free-swimming stage is omitted during the development.

2. *Development within spawn-mass.* The newly-shed fertilized egg is nearly spherical measuring about 170μ in diameter. It is filled densely with pinkish granules and beset with a thin egg-membrane. Each egg is laid in a sac of very transparent thin membrane, and each sac is fused with its neighbours at either end forming a cluster. This thin egg-sac may be homologous with the egg-shell as usually found in the Turbellarian spawn. An egg is generally present in one sac, but it is also not uncommon to find two eggs within one sac. About twenty-four hours after fertilization the larvae begin to rotate by means of the prototroch prior to the appearance of the telotroch and neurotroch. The cilia can be seen through the egg-membrane, which forms a cuticle round the larva. The prototroch is a broad band of short cilia. The internal structure is not clear, the region of the gut being granulated, and darker. A day later neurotroch and telotroch are newly added. The larva (Fig. 4, Pl. XX) is widest at the region of the prototroch, which occupies half the length of the entire body and consists of a continuous ciliary band. The telotroch is a narrow ring of cilia, shorter than those of the prototroch, and forms a complete band. The neurotroch is a band of fine cilia running from the prototroch to the telotroch along the mid-ventral line. A few short cilia, possibly sensory ones, appears at the anterior extremity. In this stage a bud-like outgrowth at the anterior end appears as a rudiment of the median tentacle. Very little of the internal structure can be made out, the whole body being dense with yolk. In *Nicolea zostericola* observed by Herpin the rudiments of bristles are already projected from the part behind the prototroch

at the corresponding stage of *Lanassa nuda* described above. Such precocious development of the bristles was not found in the present species. A day later the larva shown in Figs. 5 and 6, Pl. XX was formed. The body markedly elongates measuring about 280μ in length and 100μ in breadth. It is opaque and pinkish in colour. The prototroch remains as an extremely broad band of short cilia. The rudiment of the median tentacle with a few rather stiff cilia becomes more prominent. It is now protruded as a small round knob at the anterior cephalic portion, bending a little to the ventral side. The telotroch and the neurotroch are unchanged. A faint indication of segmentation is detected at the region posterior to the prototroch. The larva is quite contractile and its creeping movement is very slack. When the larvae are about four days old the first bristle bundles begin to appear. The first segment is achaetous and the following two have notopodial bristles; the first setiger with a pair of longer winged capillary and provisional spatulate bristles, and the second with the spatulate ones only. These chaetigerous segments seem to be formed simultaneously. The prototroch becomes narrow. The rudiment of the median tentacle is retractile, showing no further development. After this stage, the most striking feature of the larvae lies in their extreme contractility. The larvae continues to elongate and segmentation becomes more distinct. In a few days the larvae begin to metamorphose and liberate from the spawn-mass. Fig. 8, Pl. XX shows the larva seven days old just before the completion of metamorphosis. About three days later the larvae begin to build a mucus tube. The body becomes transparent, measuring about 450μ in length. The prototroch is reduced losing its major portion of cilia to a linear ring of fine cilia at the anterior end of the peristomium. The neurotroch is also fallen off at the posterior body, leaving two separate cilia groups on the first and second setigers. Each of these cilia groups is found confined to the posterior half portion of the segment. From the anterior end to the posterior border of the prostomium there is a rather broad band of cilia extending over the mouth and prototroch. Whether this band is a remnant of the neurotroch or not is uncertain, but whatever it may be, it remains to exist to the considerably later stages. The telotroch is replaced by several patches of cilia round the pygidial region. A number of rather stiff cilia are found at the anterior extremity and the dorsal surface of the trunk. The median tentacle elongates, showing highly contractile activity. There are four setigers, of which the first three bears each two notopodial bristles, one winged and one spatulate, and the last carries spautulate bristles only. Just ventral to the notopodial bristles an uncinus appears on each setiger except the first one. No ventral neuropodial muscular projection is as yet formed. The gut is now well observable through the body-wall. The mouth opens just behind the prototroch. The upper lip does not grow. Following to the mouth is present a sac-like process at the floor of the buccal cavity, which is also found in the other Terbellid larvae such as *Lanice* and *Loimia* and is called as 'buccal organ'. According to Wilson (1928), who described the post-larval development of *Loimia medusa*, this organ may probably be used in fashioning the tube. The oesophagus passes as far back as the anterior end of the first setiger to open into the stomach which is followed by a thin-walled intestine looped into folds. The stomach is thick-walled, spacious sac extending over three setigers.

3. *Early bottom stages.* When the larvae are about ten days old, with about six setigers, the external cilia shown in the early stages are lost, and the larvae begin to settle down. They secrete around themselves a thin-walled tube of mucus. In Fig. 9, Pl. XX is shown a larva recently metamorphosed about two weeks old taken from a mucus tube. The body excluding a median tentacle measures about 500μ in length. New segments are added posteriorly and there are now eight setigers. Below each of the notopodial bristle bundles, except the first, there is a small muscular process bearing distally a single uncinus of a larval type. Along the ventral surface of the anterior achaetous region is a broad band of cilia. There is no nototroch as shown in *Loimia*, but a number of stiff cilia are scattered on the dorsal and ventral surface of the body. The median tentacles strech for a considerable length in front of the prostomium above the upper lip which is now protruded forwards. When well extended, the tentacle measures about 100μ in length. It is tongue-shaped, being densely beset with short fine cilia along the lower margin and with several patches of stiff cilia on the upper dorsal surface. The gut is longer than the body and is thrown into folds. As development proceeds the larva grows, with the median tentacle markedly longer. Fig. 20, Pl. XX shows a larva about a week later than the previous stage. The median tentacle is longer than the body at extreme extension, but much shorter at contraction. The ventral surface of the

tentacle is densely ciliated, bearing a number of longer stiff cilia which are sparsely distributed. They are also found on the dorsal surface. Additional tentacles are not yet appeared. A ring of ciliary patches at the pygidium has been disappeared. Ten setigers are formed, of which first two being destitute of uncinus. The posteriormost three setigers bear well developed neuropodial muscular projections. The anus is situated on the ventral side. The other details are similar to those already described for the previous stage.

Development then proceeds steadily, new segments are added to the posterior portion, new tentacles appear and the older ones become elongate. The succession of the appearance of new tentacles agrees closely with that of *Loimia*. When the larvae acquire twelve setigers, new tentacles arise alternately on one side and then on the other. Thus repeating it results in the disparity of tentacles on both the sides; on one side one more tentacle always existing and the tentacle being longer than the corresponding tentacle on the other side. The enamsimorphism is variable in individuals. The upper lip of the prostomium grows anteriorly and gradually into a prolonged tongue-shaped flap on the floor of the tentacles. The uncinus previously found in the third setiger becomes to be lost, so the first three setigers bear notopodial bristle bundles alone. The provisional spatulate bristles occur but are confined to the first five setigers. There are only ordinary winged bristles on the sixth setiger backwards. The prolonged muscular projection bearing uncinus is developed on the eighth and the succeeding setigers. The entire body is light pinkish in colour. The mucus tube is covered with irregular clusters of diatoms and other debris, among which some of the larval provisional bristles are visible.

The oldest larvae I have reared are shown in Figs. 21 and 22, Pl. XX. They are about thirty days or more old, bearing fifteen setigers. Except fewer number of tentacles the general appearance is almost similar to that of the adult. The median tentacle is greatly elongated, about four or five times the body length when well expanded. A pair of tentacles, unequal in length, is also found on both lateral sides of a median tentacle. The prostomium bears four or five dark red pigment spots, i.e. eye-spots, on each dorsal side. The number and arrangement of eye-spots varies slightly. Below these eye-spots a number of minute pigment specks are distributed in transverse row to form a ring round the dorsal surface of the collar. As the adult

Lanassa has no eye-spots, these pigment spots appeared at the stage are provisional and must disappear during the succeeding stages. Bristle-bundles are formed until ten pairs are present, and then the parapodia undergo transformation and take the shape of the abdominal type. The first three setigers are devoid of uncinus. The uncini found in the bristle-bearing segments are of larval type and ultimately fallen off. The uncini of the abdominal region bear about four rows of teeth above a main fang. The central stomach region is deeply pigmented with bright red granules. A pair of the anterior larval nephridia and the developing glands of the ventral shields are visible through the body wall. The provisional spatulate bristles are fallen off and are entirely replaced by the ordinary winged type.

4. *General accounts.* In spite of a number of literature concerning the larvae of the Terebellids no works have ever been devoted to the development of *Lanassa* belonging to the Polycirrinae including several genera mainly characterized by the entire absence of the branchiae. There is no instance with the exception of Herpin (1926), which studied the early Terebellid larva to metamorphosis. Wilson (1936) gave a detailed survey on the larvae of *Loimia medusa* for the post-larval development from the stage in which the first tentacle was just appearing in a juvenile stage. As to the segmentation, gastrulation, origin and nature of mesenchyme etc. of a Terebellid worm, *Amphitrite ornata* the complete account was given by Mead in 1897. Other workers have mostly only described on larvae caught in the plankton or those reared for a short period without tracing serially. The earliest record of the Terbellid larva is that of Miline-Edwards who in 1845 described and figured the telotrochal larva of *Polymnia nebulosa* with four or five chaetigerous segments. Agassiz (1866) described briefly the larva of *Terebella fulgida*, which is possibly identical with *Loimia turgida*; Claparède and Mecznikow (1869), *Polymnia nebulosa*; Salensky (1883) and Willemoes-Suhm (1871), *Nicolea zostericola* and *Terebellides stroemi*; Giard (1878), Cunningham and Ramage (1888), Nordenskiold (1901) and Elrington (1909), *Lanice conchilega*; Auparavant (1894) and Saint-Joseph (1906), *Nicolea venustula;* Saint-Joseph (1894), *Polymnia nesidensis*; Fauvel (1916), *Amphitrite cirrata*. Earlier works on the Family Terebellidae have indicated that there are two possible types of development: in one case the larvae develop into the

pelagic existence, growing and developing at the expance of micro-plankton before metamorphosing into the adult worm, whereas in the other the larvae have no free-swimming stage during the life-history, and the eggs are sheltered and developed within gelatinous mass of jelly. In the former case *Terebellides stroemi*, *Loimia turgida* and *Loimia medusa* are counted, and to the latter *Polymnia nebulosa*, *Nicolea zostericola* and the present species of *Lanassa* may be classified. The species having no free-swimming stages during their larval developments lay the eggs in jelly clusters. The early stages of development of them pass through in the jelly and then the larvae librate from the jelly at the considerable later stage with several parapodia. The spawn-mass of *Nicolea zostericola* is attached to marine algae such as *Hydrallmannia* by several filaments. In general the larva of *Nicolea* develops more rapidly than that of *Lanassa*. In the former the first sign of bristles appears in much earlier stage than the latter. In both *Loimia medusa* and *Nicolea zostericola* the first bristle bundles, one or two pairs, are temporary and are lost during the further development. The fact could not be seen in *Lanassa*, though there occur provisional bristles accompanied with the ordinary winged capillary ones.

X. Development of *Arenicola claparedii* Levinsen

(Plate XXI)

1. *Breeding habit.* The worms occur in great abundance on the sand or sandy mud bottom containing rich organic matter in the littoral zone. Often the flats in which the worms burrow are exposed for several hours during the ebb-tides. On account of the existence of coiled castings above the opening of the burrow we can easily indicate the presence of the worm dwelling beneath them. The difference in the time of spawning in different localities appears mainly to be dependent on the favourable temperature for worms in bringing about their spawning acts. In Japan the worms breeds from July to August at Toshi Island (Takahashi, 1933), and from the later part of April to the first of June at Akkeshi (Okuda, 1934). At Naples the breeding takes place from November to May (Lobianco, 1893). During the breeding season the body cavity of the worm in the both sexes is filled with ripe sexual elements which are discharged outwards through the nephridium. The ripe spermatozoa consists of the head, the middle piece and the tail. The head is roughly spherical

in shape, 1.7μ in diameter, with a triangular acrosome 1.5μ in length and subdivided in its proximal part. The middle piece is oval, flattened, 1.4μ in length, and is deeply stained by Toluidin-blue. The tail, attached to the median portion of the middle piece, is a slender thread-like body which is from seven to eight times as long as the head. During the breeding season these spermatozoa are crowded together into several bundles, floating in the body fluid. The mature, yet unfertilized egg, is discoidal in shape with large nuclei and well defined nucleoli. The yolk granules are scattered abundantly in the cytoplasm, especially around the nucleus and less in the peripheral part.

As regards the mode of oviposition, so far as I am aware, the species has not been recorded, though there are several observations on other species of the same genus. The present species shows an unique, interesting spawning. Guberlet (1933) had made in vain causal attempts over a period of several years to obtain some information in regard to the spawning of the same species, and he could not find any egg-mass which could be attributed to the worm throughout the summer. And then he supposed that the eggs may, immediately after fertilization, become adhesive and adhere to sand. The oviposition of this species is quite unlike anything which I have ever seen among annelids. The female worm never lays the eggs in jelly so as to form the cylindrical baloon-shaped mass as usually the case in other *Arenicola*, but she discharges the eggs directly around the entire body embedded in the burrow forming an 'egg-tube', and thus the eggs are exposed to a certain extent to perils of the environment. Accordingly it is always in vain to search any kind of egg-masses near the surface of burrow unless digging out the famale worm who dwells within the 'egg-tube' formed by herself.

The following accounts dealing with the spawning habit were made upon specimens in an aquarium kept in a large glass vat containing filtered sea-water and sterlized mud to a depth of 5 or 6 inches. The whole process of the oviposition was observed on May 25th early in the morning at about 1 a.m. First the male discharged the spermatophore through his nephridiopores by a peristaltic movement of the body. The discharged spermatophore was an oval pellet, 0.5–2 mm in diameter, and enveloped with a thin gelatinous membrane. In sections the spermatophore showed a large number of ripe spermatozoa with their heads nearly perpendicular to the membrane. The spermatophores were shot out one by one, ten to twenty per minute, into water from the burrow of the male worm. The process remined one of an intermittent eruption of a minute volcano. The ejection of the spermatophores continued for about two hours; the number ejected decreased gradually as time went on. The discharged pellets were deposited around the entrance of the burrow, and some of them were observed to flow accidently into an adjacent hole in which a female lives. I saw several times the discharged pellets enter directly the hole of the female worm instead of falling on the bottom. When a spermatophore sank into the burrow of the female worm which lay adjacent to the male, it was caught by the bristles. The membrane of spermatophore was so thin as to easily burst and the spermatozoa thus liberated swam about actively in water. At this time the oviposition began. The unfertilized eggs, slightly yellow in colour, were discharged first from the last nephridiopore, then from the fourth, third, second and finally from the first. This process was repeated several times in accordance with a peristaltic movement of the body. The eggs which were fertilized outside the body, gradually settled down into a gap of the burrow occupied by the female worm. By the time when the spawning which had lasted two to three hours was over, the eggs had accumulated outside the body into a cylindrical tube as shown in Fig. 1. At the first glance the tube composed of a number of eggs appears like a real tube constructed by other tubicolous annelids. But in reality the tube consists of from three to five layers of eggs. Immediately after spawning these eggs of a fresh cream-yellow colour are connected firmly to one another with a thin chorion. But with development the connection becomes loose and the colour fades. The larval development takes place in this egg-tube, and the larvae hatch out when they acquire the first chaetigerous segment.

In the natural condition the spawning takes place after sunset and before sunrise, on calm days at low tides while the sea-water still flows over the burrow. The spawning operation takes place in the similar manner as described above. During the breeding season the average temperature was 11°C.

2. *Development within 'egg-tube'*. The fertilized eggs are large, cream-yellow, and ovoid in shape, slightly flattened against the sides of the burrow. They vary from 200μ to 220μ in diameter. The eggs are dense and yolky. About twenty-four hours after fertilization the

anterior cilated band is recognisable and the larvae were found to be rotating slowly within the vitelline membrane. A day later the early metatrochophore (Fig. 3, Pl. X) is formed. It is ovoid in shape, opaque and cream yellow, and the yolky endoderm cells are seen darker than the ectoderm layer by the transmitted light. These yolk cells are contained in most of the body. The prototroch and telotroch are well marked; the former is a broad band of cilia just anterior to the mouth and the latter is a narrow one near the posterior end of the body. Both are the continuous bands. In this stage the rotatory motion becomes much rapid. No apical cilia can be made out. A day or so later the larva reaches the later metatrochophore stage. The body now increases in length, measuring about 320μ long and 70μ broad. As the yolk in the gut is absorbed the lumen of that organ becomes evident. The eyes of orange-red colour appear just in front of the prototroch. A number of fine cilia at the anterior end may be called as the apical sensory cilia. Similar tube of cilia is also present at the posterior end. Refringent ectodermal globules of yellow green colour are scattered at both extremities of the body. The prototroch and telotroch show little advance. The neurotroch first appears passing along the mid-ventral line from the prototroch to the telotroch. The segmentation is rather indistinct, but there is apparently three segments between the head and pygidium. The central gut shows a spacious, sac-like structure, being destitute of the mouth and anus, both of which develop later. A pair of the provisional short spatulate bristles appears first on the second segment on each lateral side. The larvae are contractile and wriggle about within the egg-case. They continue to elongate and the segmentations become more distinct. The long tube-like string, which is composed of a number of the egg-sacs closely knit together in the early stages, becomes loose in consistency and ultimately disintegrates. Thus the larvae liberate from the egg-case and enter into the free-swimming life.

3. *Pelagic stages.* The larvae just released the egg-sac swim about actively on the surface of the water, showing a positive reaction towards a source of light. Fig. 6 represents a larva shortly after liberation. The general body is light yellow orange in colour and is rather opaque owing to the plentiful supply of yolky granules. It measures about 400μ in length and 100μ in breadth. Yellow green refringent globules are densely crowded at the anterior and the posterior extremities, and there is a transverse row of the same

globules along the telotroch. A pair of the red eyes are well marked out. Two pairs of the bristle bundles are present, each one with a winged capillary and a provisional spatulate bristle. The ciliation of the body is the same as shown previously, otherwise a patch of the fine cilia on the mid-ventral line in front of the prototroch. A simple cylindrical gut is packed with numerous yolk granules and the larva does not feed before metamorphosis. The segmentation of the body is indicated by the constriction of the lateral body wall.

When the larva possesses the three setigers (Fig. 7) the neuropodial crochet is first formed; a single pair to each setiger. It is hook-shaped with about four teeth above a main fang. The stomodaeal invagination becomes more or less distinct just behind the prototroch. The neurotroch begins to disappear at the posterior portion. Development proceeds steadily by the addition of new segments in front of the pygidium. At the four-setiger stage a pair of the nuchal ciliated grooves appears on the head between the eyes and the prototroch. It is formed by an invagination of the ectoderm. The cilia associated with the head become less evident, and the prototroch and the telotroch are narrower than in the previous stage. The majority of the larvae swim about the bottom, unless stirred up away from it, and a day or so later they may even rest thereon. They can crawl well under a cover-glass. The larvae are now ready to metamorphose.

4. *Metamorphosis and early bottom stages.* Metamorphosis is induced by the disappearance of the telotroch, prototroch and neurotroch in the definite order. The apical cilia disappear earlier. About three days after hatching the larvae begin to metamorphose and bear five setigers. When the cilia begin to disappear the larvae sink to the bottom and secrete a thin gelatinous substance into which they creep actively. Thus conditioned, the larvae live more than three weeks in the aquarium. Fig. 14, Pl. XXI shows the larva recently metamorphosed. The body is vermiform with yellow orange colour. All the external cilia have fallen off. There are six pairs of bristle bundles, the first being on the second segment. Each one of the first five setigers bears a pair of winged capillary and provisional spatulate bristles, and the last sixth one with a single provisional bristle only. The crochets are also found in two pairs on each setiger. The loss of the prototroch makes the prostomium directly joining to the peristomium. A pair of eyes and the nuchal grooves remains unaltered. The refringent ectodermal globules on the anterior end of

the head decrease in number and become inconspicuous gradually. The gut is divided into several portions; the anterior protrusible buccal mass, the looped oesophageal region, the spacious stomach and the narrow intestine. The larvae begin to feed. The buccal mass can be everted from the mouth which is situated on the mid-ventral line. The oesophagus extends backwards as far as the anterior portion of the second chaetigerous segment. The stomach can be easily distinguished from the intestine by the presence of densely packed yellow brown granules, and the latter terminates to the anus situated on the dorsal side. The large corpuscles floating in the coelomic fluid are noticeable.

After this development proceeds very slowly. Though the larva continues to feed, it is about ten days later that the tenth setiger is formed. During further development the body elongates and the new segments are added subsequently. The provisional bristles begin to fall off from the first setiger and are replaced in succession by the ordinary wing-like capillary bristles.

The larva with fourteen setigers is shown in Fig. 16, Pl. XXI. It measures about 1.7 mm in length. The first ten setigers have winged bristles only, while each one of the following two setigers is provided with a pair of the winged, capillary and provisional spatulate bristles. The last two segments still retain provisional bristles only. In the oldest larva that I have reared the segments increased to the number of the adult, and the entire body could be already distinguishable with an anterior chaetigerous and a posterior achaetous regions. The gills alone have not yet make their appearances. In that young worm a most remarkable change lies in the new addition of eyes just posterior to the older ones, accordingly, there are two pairs of red eyes on the head. Okada (1941) also observed the occurrence of two pairs of eyes in *A. cristata*, in which the smaller pair of eye-spots is added to the former pair in the early stage with about three setigers. The prostomium shows no change and is bluntly rounded. There are nineteen setigers and the body segments are well defined, but no annulations on each segment yet appear. The provisional bristles are entirely lost. The dorsal blood vessel is seen quite distinctly through the body wall. The narrow oesophagus leads from the buccal mass to a wide stomach occupying the seven segments from the fourth to the tenth setigers. The oesophageal glands which are characteristic of the adult are not yet formed. The young worm is surrounded by a structureless gelatinous-like envelope or tube which is obviously secreted by itself.

5. *General accounts.* The earliest record of the young stages was made by Max Schultze who in 1885 described briefly the larva of *Arenicola marina.* The larva has a narrow ciliated ring posterior to and another anterior to the broad prototroch. The eyes lie in the broad band of cilia instead of anteior to it. This larva probably does not belong to the genus *Arenicola.* No further work on this subject was published until Wilson (1882) described his researches on the early development of *A. cristata.* He had reared the larva to the six-setiger stage. As far as his observaticn goes, the young larva of *A. cristata* resembles well that of the present species, but duration of the pelagic life is very short in the former, lasting only no more than a day or two. The larva leaves egg-mass in the early meta-trochophore bearing a pair of bristle bundles. According to Okada (1941), who also studied the development of *A. cristata* from early cleavage to the larvae before metamorphosis, the larvae of this species hatch out of jelly-mass when they have been provided with 3–5 pairs of bristles. He found no apical cilia on the anterior head region. Two pairs of eyes are formed in the early larva shortly after liberation from the spawn-mass. Nothing is known concerning the duration of the pelagic life. In *A. claparedii* the larva leaves the egg-string at the same stage with that of *A. cristata* observed by Wilson, i.e. at the one-setiger stage. On the other hand, the pelagic life of *A. claparedii* is more prolonged than in *A. cristata,* lasting four days at least. Child (1900) studied in detail the early stages of segmentation of *A. cristata.* In 1904 Ashworth gave a brief description on the early larvae of *A. claparedii* as also the post-larval stages of *A. marina.* He reared the larvae of the former species to the stage shortly after hatching, showing only three or four chaetigerous segments. The early development of *A. claparedii* described by him appears to be very similar to that of *A. cristata.* In the larva of *A. claparedii* observed by Ashworth the small spade-shaped bristle appears for the first time after hatching. The term 'hatching' employed by him seems to mean that the larva works its way out of the vitelline membrane instead out of the egg-tube naturally spawned. The larvae liberate from the egg-case after the first setiger was formed. Benham (1893) described the juvenile stages of *A. marina* with a full adult number of segments and a few gills on some posterior segments.

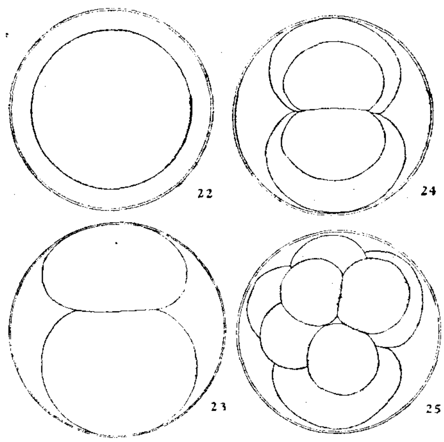
The eggs of *Arenicola* are abundantly supplied with yolk, and accordingly the larvae do not take the food during the pelagic stages as well as during metamorphosis, though the mouth has been formed in the earlier stages. The *Arenicola* larvae developing from the egg with a large amount of yolk are independent of external food-supply, and hence the pelagic life is of less importance. The absence of the true trochophore stage, the poor development of the locomotor cilia and a short free-swimming existence may all be due to the facts just described.

XI. Development of *Potamilla myriops* Marenzeller

(Textfigs. 22–30)

1. *Breeding habit.* The adult worms living in a tough leather-like tube are abundantly found in colonies between rocky crevices from just below the low-water mark to a considerable depth. The breeding habit of this species is very different from the allied species, *Chone teres.* While the latter is known to lay the eggs at the definite period in early summer, the present species breeds at any time during the summer from the end of June to the beginning of Sptember. The discharged eggs seem to be always separate, free and are not enveloped in mucus to form a cluster as shown in *Chone* and *Dasychone. Branchiomma* observed by Wilson also laid the eggs freely in the water. I removed many hundreds of *Potamilla* from their tubes, but have never observed anything resembling a cluster of eggs enclosed in mucus. Under the most favourable circumstances I have also sought in vain for the eggs deposited under natural condition. They seem to discharge the eggs freely into the water, usually at night, and the eggs are probably scattered by the tides. The females may carry fully ripe eggs for a long time before spawning, for nearly all females captured, even early in the breeding season, could be induced to deposit their eggs on the very day they were collected. There is no difficulty in separating the males and females, for the former are whitish while the latter are yellow brown in the abdominal region.

The worms lived well under circulation in the laboratory and could be used for a considerable time after collection. Many attempts to fertilize the eggs were unsuccessful. When a number of male and female worms were cultured in a large glass vessel containing relatively little sea-water, the natural spawning took place. The eggs thus fertilized were distributed between a flat-bottomed glass vat so that they are laid on the bottom universally. By the next morning a few larvae could be found swimming near the surface. In captivity the worm would rarely spawn in the daytime. At night, frequently from 8 to 10 o'clock, they can usually discharge their eggs. The eggs and the swimming larvae were pipetted off into clean filtered sea-water in other finger bowls, where they developed without further care. The following accounts are restricted only to the early larval development before setting in the sedentary life.

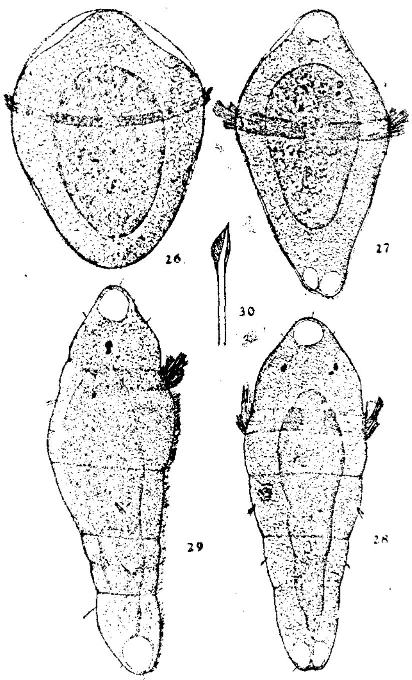


Potamilla myriops Marenzeller
Fig. 22. Fertilized egg. Actual length approx. 140 μ.
Fig. 23. Two-cell stage.
Fig. 24. Four-cell stage seen from above.
Fig. 25. Eight-cell stage.

2. *Pelagic stages.* The eggs laid are quite opaque, yellow brown by reflected light and more or less irregular in form. They soon become approximately spherical, about 140μ in diameter and are enclosed in a thin membrane. This membrane consists of at least two layers. The rate of cleavage is apparently influenced by temperature. The first furrow is meridional, parallel with the vertical axis and appears all round the eggs at about the same time. It divides the egg into two blastomers of unequal size, and in a few minute the blasto-

meres are divided nearly simultaneously, though the larger (C–D) is sometimes a little advance. The cell D of the four-cell stage is considerably larger than the other cells. All four cells undergo an almost synchronous right oblique cleavage, and the eight-cell stage is reached.

Textfig. 26 shows a larva which begins to swim. The cephalic portion anterior to the prototroch is nearly pyramid in shape. The entire body is 200μ long and is 150μ at the maximum breadth of the



Potamilla myriops Marenzeller

Fig. 26. Early trochophore. Dorsal view. Actual length 150μ.

Fig. 27. Dorsal view of the late trochophore a day later than the last.

Fig. 28. Larva three days old. Dorsal view. Actual length approx. 260μ.

Fig. 29. Lateral view of the same with two pairs of bristles.

Fig. 30. Winged bristle from the same larva as shown in Fig. 27.

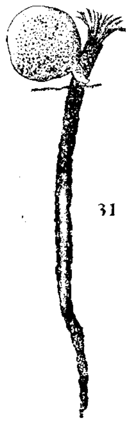
prototrochal region. It is opaque, yellowish brown, and by transmitted light the yolk endoderm cells are darker than the ectoderm layer. The prototroch is composed of three narrorw bands of fine cilia that arise through the egg membrane. The cilia of the anteriormost band are shortest and those of the median one are longer than those of others. These bands are not continuous all round, there being a slight gap in one place, which subsequently develops dorsally. A day later the larva attains 230μ in length. The body is widest at the prototroch. At the extreme end of the head a round head vesicle is present and a pair of the similar vesicles also appears at the posterior end of the body. They are likewise apparently filled with fluid. Only right eyes are developed at this stage. Such a curious asymmetry in the development of eyes is often the case in other Serpulid and Sabellid worms. The trochosphere of *Pomatoceros* has also at first only right eye and afterwards the left eye-spot develops in the corresponding position. In our species the right eye consists of two reddish pigment spots. The prototroch becomes broad, remaining a slight dorsal gap. From just behind the prototroch to the posterior end of the body runs a neurotroch along the mid-ventral line. The neurotroch consists of the narrow band of the short cilia. The larva is contractile and swims actively. When they are three days old, the larvae become segmented (Figs. 28–29). The body measures 260μ in length. The head and anal vesicles are the same in the previous stage. The left eye-spot now appears and the symmetry is restored. The two eye-spots appear to be similar in structure and develop simultaneously. There are a few sensory cilia at both ends of the body, and one or two long, exceedingly fine cilia can occasionally be glimpsed on the back immediately behind the prototroch and in front of the pygidium. Two of the segments carry notopodial bristles. There are no uncini. The first segment bears two pairs of bristles, each consisted of the winged and the capillary ones. The second segment bears a pair of winged bristles only. The third setiger is not still marked out. The larva is granulated in tissue with yolk granules and yellow orange by transmitted light. The larva can swim more actively than the previous stage. There have not as yet been observed any signs of the rudiments of the branchiae or collar. The further development through metamorphosis could not be observed.

Comparison with *Chone teres* and other Sabellid worms has been given in the following section.

XII. Development of *Chone teres* Bush

(Plates XXII–XXIV; Textfigs. 31–33)

1. Breeding habit. The adult worms inhabit the muddy bottom between the *Zostera* bed, bearing a soft membranous tube with minute sand particles and other debris. The tube, of which a major portion lies vertically embedded in the mud, gets narrowed as it passes deeper into the soil with a slight portion of the upper extremity exposed from the surface. At low tide when the receding sea-water leaves the large areas of *Zostera*-bed exposed, a little experience enable one to spot out the presence of the tubes. The worms are extremely shy and retract to a deeper part of the tube when disturbed. The mature male and female worms are easily distinguished by the colour of sexual products seen through the body wall. The male is whitish and the female bright blue in the abdominal region. In Akkeshi Bay the mature worms breed from the end of April or early of May to the middle of June. During the breeding season the worms discharge the sexual products in three or four occasions in definite periods. The reproductive activity appears to take place during the



31

Chone teres Bush
Fig. 31 Spawn-mass attached to parent's tube,

first and third quarter of moon and lasts but one day. The discharged eggs are collected in jelly to form a round mass like a miniature baloon which is supported by a short gelatinous stalk adhering to the outerside of the parents' tube near the opening as shown in Texfig. 31. In the calm day these spawn-masses float to and fro after the manner of baloons, held in position by their stalks. The fully formed spawn-masses vary in size measuring from 7 mm to 20 mm in diameter. The egg-mass newly spawned is transparent, and bright blue eggs can be seen through a gelatinous envelope. A number of these spawn-masses were brought to the laboratory and the larvae were reared in a vessel of sterlized sea-water until they settle down and build the tubes. Development takes place inside this jelly-mass, and in the same spawn-mass may be obtained eggs and larvae at various stages of development.

2. *Development within egg-mass.* The eggs newly shed are bluish in colour by reflected light, very opaque owing to the highly granular cytoplasm and possess germinal vesicles. They are more or less spherical about 200μ in diameter. The egg is enclosed in a thin membrane which closely invests it at fertilization. The polar bodies seem to be extruded after fertilization, and in early cleavage stages can be seen attached to one of the blastomeres inside the egg membrane. The egg membrane is retained and subsequently becomes the cuticle of the larva. The cleavage and early larval stages have not been studied in detail. The so-called trochosphere larva is fully formed in two days. From Fig. 1, Pl. XXII it will be seen that it is not markedly larger than the egg from which it arises. It marks a definite stage in the development of the larva which persists for some days without noticeable change beyond a considerable growth in size. It is 200μ long and the maximum width across the prototroch is about 100μ. Its shape approximates closely to that of a hen's egg. The persistent egg-membrane forms a conspicuous cuticle covering the whole surface of the animal, through which various cilia are growing. The locomotor cilia of the prototroch form three complete bands all round, instead of four as shown in the later stage. The prototroch forms a continuous band, being not interrupted by a dorsal gap as generally the case in *Branchiomma* and *Potamilla*. The cilia of the anteriormost ring are longest, about 50μ long and are stouter than others. The second ring has short cilia, about 6μ in length. A few sensory hairs are sparsely borne at both anterior and posterior ends of the body. The meagre development of the feeding or swimming apparatus such as apical tuft and other locomotor cilia seems to be dependent on the facts that the larvae of the Sabellid worms so far observed previously have developed from the egg supplied with rich yolk and they do not capture any other organisms for food before the metamorphosis taking place. The telotroch is composed of fine short cilia arranged in a single row encircling the body completely. As the Sabellid and Serpulid larvae have hitherto been known to be devoid of the telotroch during the development, the occurrence of the telotroch in the larva of the present species is an unique feature

markedly different from other allied species. The neurotroch consists of a narrow band of short cilia running along the mid-ventral surface from the prototroch to the posterior end of the body. As a whole the larva is very granulated and opaque, bluish brown in colour. A large central endodermal mass is darker than the other parts. The larva is contractile and rotates slowly inside the jelly. Fig. 2, Pl. XXII shows a larva a day older than the former. Excepting the size of the body the other characters remain unchanged.

About a day later the larva becomes the form shown in Fig. 3, Pl. XXII. It is approximately 270μ long. In this stage the eyes as well as the head and anal vesicles appear for the first time. The prototroch consists still of three bands of cilia. An eye-spot appears on the right side, and sometimes a supernuerary smaller one is added. At the posterior end a pair of anal vesicles is present, which seems apparently to be filled with a homogenous fluid. A single vesicle is also present and lies in the ectoderm of the anterior end of the head. Though the similar structures are found in other Serpulids and Sabellids the function of these vesicles is still open to speculation. According to Segrove (1941) it may possibly play some part in the fixation of the larva prior to metamorphosis.

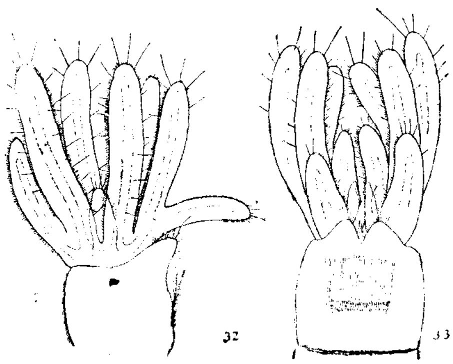
In the subsequent development of the trochophore the gradual increase in size is due entirely to the elongation of the post-trochal region. There is no increase in the diameter of the prototroch, a slight decrease in width being frequently observed. When two days old, it is about 400μ long and 140μ broad at the prototroch. A pair of statocysts is newly added, otherwise it is very much the same with the previous stage. The rudiment of the statocyst is a pearl-like refringent body situated dorsally on each lateral sides just posterior to the prototroch. A left eye-spot develops in a corresponding position to the right one and thus the symmetry of the eye is now recovered.

During further growth the body elongates a little and the tissues becomes less granular and more transparent as the yolk in them is absorbed. A day later the larva reaches the stage represented by Figs. 6–7, Pl. XXII. The body is now segmented. It is about 500μ long and 140μ broad at the prototroch. The prototroch consists of four continuous bands of cilia instead of three as shown in the earlier stage. The first band is broadest and has the longest cilia, 60μ long. The cilia of the third band are shortest, 6μ in length. The five segments behind the prototroch are now indicated. A pair of the notopodial bristles is protruded from the lateral sides of the second segment. The rudimentary bristles are seen developing just beneath the hypoderm on the third segment. The three setigerous segments are not simultaneously formed as usually the case in the Serpulid worms. A pair of the otocysts is located on the first achaetous segment. The neurotroch becomes discontinuous just anterior to the telotroch. The head and anal vesicles show no change. The larvae can actively swim when the jelly has been broken off. About twelve hours later the larva acquires two more setigers having protruded bristles. The apical portion in front of the prototroch increases in length and width. The neurotroch leaves a short gap between the posterior border of the third setigerous segment and the telotroch. The larva is very active, and wriggles about among larvae in the same egg-mass.

3. *Pelagic stages.* A day or later the larvae escape from the jelly-mass and swim about in sea-water. Their general appearance in this stage is indicated in Fig. 10, Pl. XXII. The body measures 520μ in length. At this stage the branchial buds are first protruded as an outgrowth of the ectoderm of the head region. At the same time the larvae are provided with four chaetigerous segments. The future branchial crown is first represented by two bud-like protuberances on each side of the head between the prototroch and the eyes. Quite soon after their appearance a number of short cilia develop on these branchial rudiments. They are arranged in similar manner on both sides of the head, each lobe being slightly notched at the anterior border. The head decreases gradually in size. A pair of the otocysts situated on both lateral sides of the first setigerous segment is well marked out, and a small round opal-like otolith is seen through the body wall. The cilia of the neurotroch are absent from the region between the last setigerous segment and the telotroch, otherside they form a continuous band extending from the prototroch to the posterior end of the body. A few patch of the sensory cilia occur on both anterior and posterior extremities. The larvae swim actively showing the positive phototropic reaction. They are in the last pelagic stage before metamorphosis. Both the mouth and anus are not still opened.

4. *Metamorphosis.* About one or two days later the larvae begin to crawl below the surface and to metamorphose. Metamor-

phosis may be regarded as initiated by the retrogression of the neurotroch and prototroch. During the metamorphosis many changes occur, some gradual and some rapid. A sudden change such as the loss of the neurotroch is easily noted. The larva loses the power of swimming owing to the degeneration of the prototroch and neurotroch, but does not secrete a tube to be sessile. It may remain quite stationary for considerable length of time, occasionally bending the trunk from side to side and sometimes rotating slowly. In general course of the metamorphosis, especially in the change of the head, the species resembles well that of *Branchiomma* observed by Wilson (1936), but the development takes place more slowly in the former. The body measures 540μ in length and 100μ in breadth at the prototroch (Figs. 13–14). The head begins to decrease in volume taking a form of so-called "snout" or "proboscis". It appears attached to



Chone teres Bush

Fig. 32. Anterior end of the recently metamorphosed larva. Lateral view.

Fig. 33. The same. Ventral view.

the trunk by a narrowed neck between the branchial rudiments and the mouth. The head vesicle shrinks gradually. As the head continues to decrease in size, the rudiments of the branchial crown are growing and branching. There are now two lobes to each, and are ciliated ventrally carrying a number of sensory cilia. Most of the dorsal cilia of the prototroch have disappeared, but ventral band remains. The neurotroch is fallen off entirely with the exception of a tuft of cilia locating on the ventral portion of the first achaetous segment. It is a narrow band consisting of two rows of cilia, the one longer and beating slowly and the other, just behind the former one, much shorter. The eyes gradually shift backwards and ultimately occupy a position at the base of the branchial crown. The telotroch is not affected by metamorphosis and it persists long after the metamorphosis. On the fourth setiger the uncinus first appears in pair ventral to the notopodial bristles. The ànus is now opened on the dorsal surface of the pygidium just posterior to the telotroch. The larva does not feed at all during metamorphosis. During further development shrinkage of the head, development of the branchial crown, disappearance of the head and anal vesicles and addition of the neuropodial bristles take place concurrently. Fig. 17, Pl. XXII and Fig. 29, Pl. XXIV represent the larvae a day later old. The degenerated head remains only as a small club-shaped protuberance just anterior to the mouth. The branchial lobes elongates markedly, with three branches on each side. All of these branchiae are ciliated along the ventral surface with a number of stiff hairs at their terminal portions. The prototroch is fallen off excepting a patch of cilia locating immediately posterior to the mouth. At the anterior end of the achaetous segment a wedge-like depression appears to form V-shaped ventral lips. These lips are densely ciliated, each one provided with one or two long cilia beating slowly. A pair of eyes shifts back on the anterior dorsal portion of the first achaetous segment. The collar rudiment is not still apparent. The head vesicle still remains, but becomes much smaller in size. The body has six segments between the region from the head to the pygidium. There are few chaetigerous segments as shown in the pelagic stage. During metamorphosis the uncini are newly added, while a number of notopodial bristle bundles remain unchanged. The clavate ventral bristles appear on the second and third setigers. The worm begins to secrete a thin-walled tube of mucus in which they move for themselves about by means of their bristles.

A day or later the worm completes the metamorphosis and begins to feed. The total time taken to metamorphose is about three days. In the present stage the rudiment of the head or snout is entirely disappeared. It has not been determined whether the snout is thrown off or absorbed. The anal vesicle also disappears. The ventral lip of the mouth is gradually prolonged. By the time the fourth pair of branchial filaments is added to the former three pairs and it immediately gives rise to a short filament which bends ventrally. A pair of so-called labial palps is also formed within the branchail crown at this stage. It is branched from the inner base of the dorsalmost filament. The palp and the fourth filament seem to be appeared simultaneously. The worms acquires the fifth chaetigerous segment. The rudiment of the collar is indicated as an obscure thickening of the ectoderm on the dorsal surface near the eye-spots. The anus opens just behind the telotroch on the dorsal surface. The tube when first formed is semitransparent, the walls of which are later thickened by further additions of mucus. In the meantime the small sand grains are very loosely knit together, leaving large irregular gap between them through which the worm can be seen. The young is able to retract the branchial crown into the anterior portion of the tube.

5. *Juvenile stages.* During the further development after metamorphosis the main changes are confined largely to steady development of the branchial crown and elongation of the trunk by addition of segments at its posterior end just in front of the pygidium. At the same time the faecal groove begins to appear. When the larva has been provided with six setigers a continuous ciliary band running along the median dorsal line from the anterior extremity to the telotroch appears (Fig. 20). This row of cilia represents the dorsal part of the adult faecal groove. When the ninth setiger has been formed, the intersegmental groove between it and the eighth setiger becomes ciliated on both sides. The young with ten setigers shows that the dorsal faecal groove shares the branches downwards to both sides at the posterior margin of the eighth setiger, surrounding the intersegmental groove. The ciliated grooves thus descended from both sides become united together at the ninth setiger leading backwards as far as the telotroch (Figs. 21–22). In the young with about fifteen setigers, however, the faecal groove does not bifurcate at the eighth setiger, but runs always from the dorsal surface to the ventral on the right side of the body across the eighth and ninth segments as shown in the adult. During the pelagic stage the branchiae first arise as a pair of bud-like protuberances simultaneously on either side of the head just in front of the prototroch and gradually increase in length. At the beginning of metamorphosis each branchial process is represented by two short branches of subequal length. Soon after a third pair of branches is formed the so-called labial palps are derived from the inner side of the first branches. When metamorphosis is com-

plete, the four primary branches excepting the palps are present, of which the fourth one depatches from the third branch. In *Branchiomma* the palp of the adult appears on the anterior ventral part of the lobe as a third and smaller bud. Out of the four branches three ones early formed grow steadily longer and bud off pinnule-like branches. Pinnules first appear near the base and on the inner side of the first filament. Subsequently additional pair is developed above the first pinnules on the opposite side (Fig. 20). In this figure the fourth branch derived from the third branch is beginning to bud off a short branch from the base, and these two branches do not bud again during the subsequent development so far as the young worms have been reared. When the branchial crown is expanded, the most posterior, i.e. ventral or fourth pair of filaments bends ventralwards. The branchial rudiments become ciliated soon after their first appearance. All the branchial filaments are supported by the cartilageous or skeletal cells. While the branchia grows, the trunk elongates by addition of segments at its posterior end. The eight setigers first formed have the thoracic characteristics, with dorsal bristles and the ventral uncini while the ninth and the succeeding ones bear dorsal uncini and ventral bristles. The neurotroch is first fallen off when the young acquired ten setigers. The persistence of the neurotroch for a considerably long period is quite characteristic of this species. Correlated with the growth of the trunk the collar membrane also develops gradually. The collar-folds are brought about to the surface of the first achaetous segment and ultimately become joined to each other owing to the outgrowth of a median fold originated from the ventral ectoderm. In the young worm the first achaetous segment is distinctly demarcated from the succeeding chaetigerous one, but the segmentation between them becomes indistinct as the collar membrane grows and finally disappears entirely in the adult.

6. *Formation of bristles.* Two pairs of the dorsal bristle bundles are first developed. Each bundle contains two bristles, one longer tapering and winged (Figs. 39–40) and the other shorter fine needle-like. During the metamorphosis the larva acquires four pairs of the dorsal bristles. The uncinus first appeared on the fourth setiger of the early metamorphosing larva, well resembles in shape the dorsal uncini found in the abdominal region of the advanced larvae (Fig. 33). It is pectinate in shape bearing five or six minute teeth above a main fang. A short time later the uncini of the second and

third setigers appear, all of them being hook-shaped with three teeth above the main fang as shown in Fig. 43. The uncini of the fifth setiger have the similar form to those of the fourth. Except the second and third setigers all of the succeeding ones belonging to the thoracic region have uncini of the pectinate form as usually shown in the abdominal region of the adult worm. When the young acquired twelve or more chaetigers these larval uncini found in the thoracic segments are subsequently lost and are replaced anew by hook-shaped thoracic uncini. The fact is very interesting compared with the development of certain young Serpulid worms. In the development of Serpulid worms it takes often place that the fourth and the succeeding setigers are beset with dorsal uncini and ventral bristles. After thus the several abdominal setigers have been formed the anterior ones are transformed into the thoracic form with dorsal bristles and ventral uncini. In the present species there never occurs the transformation of the abdominal segments into the thoracic ones. The first setiger is entirely devoid of an uncinus. The dorsal notopodial bristles of the thoracic segments are composed of two types; one spatulated (Figs. 49 and 53) and the other longer, slender and winged (Figs. 43–46). In the abdominal segments the ventral bristles are slender, limbate and the dorsal ones are pectinate having five or six rows of teeth above a main fang. The bristles with small broad wings and long whip-like tips are confined to the thoracic segments. The first setiger bears long wing-like bristles only (Figs. 43–44), being destitute of the short spatulate ones as shown in the succeeding thoracic segments.

7. *General accounts.* Concerning the larval development of the Sabellid worms there is a few literature available, the most comprehensive account being that of Wilson (1936). The earliest account on the Sabellid larvae was given by Claparède and Mecznikow in 1868. They described briefly the development of *Dasychone lucullana*. Roule (1885) also treated the same species, but he gave only a brief sketch of the external features of the development. Recently Wilson (1936) studied in detail the development of *Branchiomma vesiculosum*. In the same paper he described the early larvae of *Sabella pavonina*. A comparison of the larvae of *Chone teres* and *Potamilla myriops* with those of *Branchiomma* described by Wilson may throw some light on the development of this family. *Branchiomma* does not lay the eggs inclosed in mucus as in *Dasychone* or *Chone*. In

early stages the larva bears the prototroch with three bands of cilia, leaving a gap on a dorsal side. In the three-days-old larvae the prototroch consists ventrally of five bands of cilia, of which the second one is broadest and has the longest cilia. The early larva of *Potamilla* has also the prototroch with three discontinuous bands of cilia leaving a narrow dorsal gap. In *Sabella* the prototroch is composed of four rows of cilia as shown in *Chone*. As to the asymmetrical occurrence of the eyes Wilson gave no mentions. In *Branchiomma* the head and anal vesicles develop in a similar manner with those of *Chone* and *Potamilla*. In *Sabella*, however, the head vesicle is double instead of being single. The telotroch as is shown in *Chone* does not appear in other Sabellid worms throughout the early development. In the larva of *Chone* it is characteristic that the telotroch is not only present but also persists after metamorphosis. The sensory cilia on both anterior and posterior ends of the body are poorly developed in all the members of the Sabellids so far studied. The absence of long provisional bristles and specialized locomotive cilia seems to be due to the short pelagic life. The larva of *Branchiomma* ready to metamorphose has a pair of small lobes, which indicates the rudiment of the future collar, on each side of the body a short distance behind the prototroch. In *Chone* the collar rudiment first appears in the metamorphosed worm. As regards the fate of the larval head and the development of the branchial crown during metamorphosis the both species are, in general, well related to each other. The formation of a snout or a proboscis due to a shrinkage of the larval head is one of the interesting characteristics found in the development of the Sabellid worms. In *Branchiomma* the bristles and uncini appear at much earlier stage than in *Chone*. When the larva of *Branchiomma* has been provided with three setigerous segments, the uncini begin to appear in all but the first setiger. In the fourth setiger an uncinus is, however, formed preceding the bristles. In *Chone* the uncini always begin to appear later than the bristles in the fourth setiger during metamorphosis. In *Branchiomma* there is no special modification of the thoracic uncini as in *Chone*. When the eight anterior setigers with dorsal bristles and ventral uncini have been formed the position of the bristles and uncini in the ninth and the following segments is reversed, i.e. the ninth and succeeding setigers are provided with dorsal uncini and ventral bristles as shown in the abdominal region of the adult worm. In this respect *Chone* agrees well with *Branchiomma*. In *Chone* the provisional, pectinate uncini develop in the fourth and the following thoracic segments as already stated. During the course of the Serpulid development it has hitherto been convinced the several anterior segments bearing the dorsal uncini and ventral bristles are transformed into the thoracic segments with dorsal bristles and ventral uncini. Recently Segrove (1941), however, observed in the development of a Serpulid worm, *Pomatoceros triquator*, that all adult thoracic segments are formed before any abdominal ones appear, and accordingly there is no transformation of the segments of the abdominal type with dorsal uncini and ventral bristles to the thoracic one with dorsal bristles and ventral uncini as generally shown in the Sabellid development. In the Serpulid larvae three thoracic setigers are formed simultaneously, not subsequently as usually shown in Sabellid larvae.

As regards the several structures appeared during the course of the developments in the Sabellidae and Serpulidae there are many points to show close affinity between these two families. In particular, the features which are common to the Serpulids and Sabellids, as shown in the development of the branchial processes, in the occurrence of head and anal vesicles, and in the mode of the metamorphosis may serve to reveal the close relationship between the two families.

XIII. Development of *Spirorbis spirillum* Linné

(Plates XXV–XXVI)

1. Breeding habits of S. spirillum and S. nipponicus. Mature individuals of both species can be obtained during the greater part of the year in Akkeshi Bay except the winter season from December to March. The worms live in the small spiral tubes of lime attached to some foreign bodies such as stones, shells and various sea-weeds growing in the littoral zone. In one breeding season the worm spawns the eggs more than two times at least. The larvae attaining the maturity in two months are capable to breed once more in the same year. I observed that the young newly settled down at the beginning of July began to breed in the middle of September. From the early spring to the early winter ripe eggs were found within the parents' bodies.

In *S. spirillum* the eggs are laid side by side along the inner surface of the tube outside the parent's body. They are arranged in short strings composed of one to four longitudinal rows containing eggs from ten to twenty in number. Thus the total number of eggs found in one tube is greatly variable, from ten to eighty. Each egg enclosed in a thin capsule is invested and knitted together by a very thin transparent membrane which forms a common sac. These eggs are more or less flattened against the inner wall of the spiral tube to allow room for the worms which lie internal to them. This can clearly be seen when calcareous matter of the shell is dissolved in Bouin's fluid. The early stages of the larva are passed while the eggs are thus enclosed.

A few individuals of *S. nipponicus* spawn in March, but the spawning activity reaches the maximum from May to September. All finished spawning in late November. During the breeding season the cylindrical body formed at the upper end of the trumpet-shaped calcareous plate of the operculum serves as a brood-pouch. The eggs are laid inside the operculum which protects the larvae from injury and so it was easy to see which worms had spawned. Each egg is enclosed in a capsule, but there is no common membranous sac binding eggs each other as shown in the former species. The eggs are laid from ten to forty in number per one brood-pouch. The larval stage is passed through within the operculum. In both species the eggs in these positions are all fertilized and in almost equally developed. The worms lived well in the laboratory and could be used for observation for a considerable time after collection. All observations were made by removing eggs and larvae from either tube or operculum. The early stages of segmentation have not been studied.

2. *Development within tube.* The eggs newly laid are generally orange in colour, and sometimes variable from faint violet to yellowish orange. They are opaque and densely granulated, when seen by reflected light a pale violet patch is seen. The eggs are ovoid in shape, slightly flattened against the wall of the tube, 140μ long and 95μ wide on the average. They are covered with thin transparent egg-membranes. The germinal vesicle of the unfertilized egg disappears by fertilization, and the egg becomes equally dense exclusive of the central small semitranslucent round area. The development within the tube is completed in about five days, and the larva does not feed at all during that period. Cleavage stages were seen on several occasions, but when the embryos were removed to finger bowls with sea-

water, the cleavage became abnormal. Therefore observations were made on embryos and larvae freshly taken from the tube. The trochophore seems to be formed about twenty-four hours after the first cleavage. The trochophore is ellipsoid in outline, longer than broad, 150μ long and 110μ in the maximum breadth. The entire body is finely granulated and considerably opaque, and the central area is denser than the rest. The prototroch consists of two rows of fine and short cilia encircling the body, of which the anterior being longer. An oval ectodermal depression in the median ventral line indicates the future mouth; the posterior area to the mouth is a little flattened and is beset with a transverse row of short cilia. Although the larva at this stage may be called a trochophore, it differs from the typical one in the absence of the functional mouth and anus. These organs are never complete in any stages of the early larval history, and it is only at the stage of the metamorphosis that the gut opens and animal begins to feed. A pair of the lateral bulges just behind the prototroch indicates the rudiment of collar membrane. As the trochophore develops, yolk cells of the gut become better marked and the ectodermal invagination of the stomodaeum becomes also distinct.

About twenty-four hours afterwards the larva rotates inside the egg-membrane and moves actively when it is taken out from the membrane. The egg-membrane is ovoidal and thin, 160μ long and 140μ wide. The larva measures 150μ long and 110μ at the widest portion. Due to the formation of the collar membrane the entire body can be divided into three-regions; anterior cephalic, middle collar and posterior thoraco-abdominal regions. The cephalic portion is rounded. A tuft of the short apical hairs first appears at the median terminal portion. A pair of the ventral eyes is distinct and is present at the posterior portion of the cephalic region. The anterior dorsal eyes are not still formed. On the lateral side just below the ventral eyes there occurs a pair of rather long flagelliform cilia beating slowly. The movement of this cilia is independent of that of the cilia of the prototroch. The prototroch consists of the anterior row of long and rather strong cilia measuring about 60μ long and of the posterior one of shorter cilia, about 20μ long. The mouth is indicated as a round invaginated area beset with a number of fine cilia. A narrow transverse row of short cilia directed posteriorly is located just behind the mouth. The collar membrane is now well formed, overlapping the whole ventral surface of the middle body region. The posterior border of the collar membrane is smooth, being devoid of a median incision as shown in *S. nipponicus* described later. On the dorsal surface the collar membrane is widely separated by a median broad gap. The thoraco-abdominal region occupies one-third the entire length of the body and does not show any segmentations. At this stage the neurotroch first appears. It consists of four narrow separate bands, each one composed of short cilia extending transversely across the ventral surface of the trunk. They beat actively. The anus is densely beset with short cilia. At the posterior extremity of the body a pair of long stiff sensory cilia projects backwards. The anal vesicles at the posterior extremity are translucent, structureless bodies filled apparently with fluid. The gut becomes distinct from the rest of the body as an opaque sac-like organ.

The larva gradually increases in length and girth, and undergoes several changes about twenty four hours afterwards. The larva elongates attaining about 200μ in length and 100μ at the broadest portion of the collar region. The cephalic region is slightly broader than long. A pair of the small oval eyes is newly added on the dorsal surface in front of the posterior eyes. At this stage the rudiments of the operculum and branchia first appear at the base of the cephalic portion. The rudimentary branchia arises as a slight swelling on each side dorsal to the eye and immediately anterior to the prototroch. A small oval lobe on the right side just above the prototroch indicates the rudiment of the operculum. An apical tuft and the prototroch elongate in their length. A pair of fine cilia is found at the posterior margin of the collar membrane. In this stage the segmentation between the thorax and abdomen becomes first discernible. In the thorox three pairs of bristles are formed simultaneously. The abdomen is short, club-shaped, and is destitute of any segmentation. There is a pair of fine cilia protruded from the anterior dorsal surface of the abdomen as is shown in the foregoing stage. A pair of the anal vesicles becomes more prominent. It is only after metamorphosis that the vesicle disappears and the anus shifts to the terminal portion. Of the four neurotrochal cilia groups the first one belongs to the thorax and is situated between the second and the third chaetigerous regions, and the other three bands are located in the abdominal region. The mouth and the anus are little changed. In the entire body are distributed numerous violet orange granules. The digestive tract ending anteriorly in the prototrochal region is orange brown and more or less translucent in the posterior portion.

Fig. 11 shows the oldest larva that could be found inside of the parent's tube. The larva is very active, and wriggles about within the egg-membrane. The abdominal region lengthens and is obscurely segmented. The apical tuft is composed of several stiff hairs. The ventral posterior eyes are irregularly V-shapd. Between the ventral eyes and the prototrochal ciliary band occurs a pair of stiff hairs as shown in the previous stages. A collar membrane extends considerably towards the anterior and dorsal directions, and now it envelops the anterior half of the thoracic region. Just .posterior to the collar membrane the first group of neurotrochal cilia is located. In the abdominal region two pairs of digit-form processes are found on both lateral sides of the fourth group of neurotrochal cilia. These ectodermal foldings help the movement of the young worm after they settled down. The posterior extremity of the larva is densely ciliated and bears a pair of slender stiff hairs.

About twelve hours afterwards the larva emerginates from the egg capsule and commences a free-swimming life.

3. Pelagic stages. The larva just liberated from the parent's tube is about 260μ in length, excluding cilia, and 110μ in breadth at the maximum width across the collar region. The head shows slight difference from that of the larva hitherto described, and is still separated from the trunk by a conspicuous thickened belt of the prototrochal cells. The apical sensory tuft, the longest one measuring 30μ in length, consists of several slender stiff cilia beating actively. The two pairs of eyes are fully developed; the anterior dorsal eyes small and oblong, while the posterior ventral ones large, obliquely elongated and constricted in the median portion. In this species the posterior eyes have no marked hyaline lens-like bodies at the terminal ends as shown in *S. nipponicus*. In the dorsal cephalic portion the rudiments of the operculum and the branchiae are more well developed and raised up as ectodermal elevations. On the left side of the head there are two branchial rudiments and on the right side are a single branchial and an opercular rudiments. In *S. borealis* an unpaired operculum first grows from the left side of the neck. Two stiff sensory cilia are projected from the terminal portion of the branchial rudiments. The collar membrane is well developed overlapping the surface of the ventral thoracic region. The thorax is now three segmented and demarcated from the abdomen at about two-thirds the length of the entire body. Each thoracic segment bears a pair of short, hair-like bristles. The abdomen is narrowly elongated and segmented three. Neurotrochal cilia are still present. A pair of digit-form adhesive processes at the posterior abdominal region becomes conspicuous; the internal margin of these processes is glandular and striated. From the dorsal surface of the second abdominal segment a pair of long stiff cilia is protruded. The anal opening is fringed with a number of cilia and a pair of long lateral sensory cilia. Anal vesicles elongate much longer than broad. The digestive tract is well formed and may be divided into two regions. No marked calcareous shell glands are as yet present. The duration of pelagic life of the larvae seems to be variable to some extent; in some cases it continues as long as two or three hours, but sometimes twelve or twenty hours. The larvae swim freely in sea-water for about five or six hours, and then begin to settle down and to form the tube. Metamorphosis is initiated by the retrogression of locomotive cilia and by the tube-building operation.

4. *Metamorphosis and early bottom stages.* When the young worms attain the stage at which they are ready to enter the sedentary life, the majority of them become attached to the wall of the vessel. The free swimming larvae often do not immediately settle to the bottom previous to the secretion of the shell in which they live. Upon the surface of the culture vessel containing sea-water I found a multitude of small white bodies, which on close examination were found to be the *Spirorbis* larvae just secreting the shells. They float on the surface for a short time but soon afterwards sinks to the bottom. The case or shell of the larva formed at first is not coiled, but slightly curved, horn-shaped, with less solid walls at the narrow posterior extremity. The tube when first formed is semitransparent and appears to be composed of mucus partially impregnated with calcareous matter. Fig. 16 and 17 represent the larvae of the early bottom stage; the head and collar are half protruded outside the cavity of the case. It is quite difficult to draw accurately the outline of the larva at this stage, since the movement is so quick in retracting itself into the case, and the young is quite sensitive to any slight motion in the vicinity. The head is now markedly degenerated to a triangular rod-shaped process which is directed ventrally below the head appendages. The branchial processes are now distinctly marked out. They are oblong club-shaped, bearing a number of stiff hairs near the

terminal ends. There are four branchial appendages on the left and two on the right side. The trumpet-shaped operculum arising from the base of the right branchial appendage is well developed. A grated plate of the operculum is also formed. A pair of the small anterior eyes is now disappeared and that of the posterior ones alone is retained at the base of the branchial crown. An apical tuft and the neurotroch are now thrown off, and while the prototroch and telotroch persist for a considerable time in the degenerated condition. In the present stage the prototroch remains only on the ventral surface and consists of a single row of cilia instead of two as is shown in the free-swimming stage. The transverse ciliary band previously found just below the mouth now entirely disappears. At the posterior extremity there is still present a band of short cilia encircling the anus and a pair of short stiff hairs. The flap-like, thin transparent collar membrane is fully formed overlapping the thoracic region. On the dorsal surface the membrane is divided into two large round lips by a median deep incision. These dorsal fan-shaped flaps cover about the half posterior portion of the branchial crown. On the ventral side the membrane hangs on the thoracic region and wraps the outside of the tube when the anterior body of the worm is extruded from the case. The outer surface of the collar membrane rolled back over the lip of the tube is beset with a few stiff cilia. The oesophagus is slender, finely ciliated along the inner border, and the dark gut is represented by a spacious cavity terminating posteriorly. A pair of the anal vesicles is still retained at this stage. Only three pairs of the bristles occur on the thoracic region, each one being consisted of two wing-like slender bristles. The most remarkable change takes place in the posterior body region. When the body is well extended both the posterior lateral portions are protruded backwards to form a pair of massive foot-like appendages. Each of these appendages terminates posteriorly to a digit-form adhesive process which is in contact with the inner wall of the tube and supports the body firmly. When the body is withdrawn into the case, these foot-like protuberances are immediately contracted to the level of the anal region. Such a movement of the foot-like appendages with the terminal adhesive processes as described above reminds us that of leech. By means of this 'foot' the worm can locomote within the tube. The tube is thin, delicate, semitransparent and is membranous at the posterior end. About two days later than the foregoing stage the anterior portion of the tube begins to bend to the right side. Due to the deposition of the calcareous matter the general appearance of the tube becomes harder and more steady. The branchiae are now finely ciliated along the outer surface. The remainder of the larval head is much decreased in size and is only discernible as a small ventral knob. The prototroch is still well developed at the ventral portion. On the dorsal surface the collar membrane is now divided into the right and left flaps as shown in the adult worms. There are three pairs of bristles, each one bearing three bristles. No uncinus as yet appears. The minute cilia found near the anal region were lost. The young worm quickly contracts the body into the case by means of the adhesive processes.

Comparison with *S. nipponicus* will be afforded in the following section.

XIV. Development of *Spirorbis nipponicus* Okuda

(Plates XXVII–XXVIII)

1. Development within operculum. The egg laid newly are reddish brown in colour, and each enclosed with a thin transparent membrane. The eggs of an early stage is shown in Figs. 3 and 4, Pl. XXVII. It is oval, measuring about 160μ long and 140μ wide at the broadest portion, and opaque, reddish brown with yolk; by transmitted light the central yolky endoderm cells are seen dark yellowish brown. At the anterior one-fourth of the body, there is a narrow tract of short cilia encircling the entire body surface. It is a prototroch which consists of two bands of cilia, the anterior one of which having longer cilia measuring 15μ long. Below the prototroch there is a broad round depression at the median ventral portion, indicating the future mouth. No eyes are descernible. The central endodermal cell mass is prominent. The larva rotates slowly within the egg-capsule. A day later the larva increases in length and width. It measures 180μ long and 170μ wide. The central mass indicating the gut is very dense and granulated, but the surrounding tissues are more or less transparent. The larva is rounded dorsally, but less so ventrally. Two pairs of eyes soon appear; an anterior dorsal pair being approximately small and circular, but a posterior pair roughly kidney-shaped. The posterior eyes are situated more ventrally. The prototroch is similar to that of the foregoing stage, but becomes stronger. A single transverse row of cilia just below the mouth now appears. The collar membrane indicated as a lateral and ventral protuberance of the body-wall occupies the half posterior portion behind the prototroch. As shown in Fig. 4 the posterior margin of the collar rudiment is markedly protruded in the posterior ventral region. As the larva develops, the yolk cells of the gut become marked better and the ectodermal invagination of the stomodaeum becomes distinct. Behind the collar rudiments there occurs four neurotrochs along the mid-ventral line, each one havnig a single transverse row of short cilia beating activeiy. At the end of the posterior part, there are a band of fine cilia and a pair of stiff, long cilia. The larva moves sluggishly within the egg-membrane.

Figs. 5 and 6, Pl. XXVII indicate the larvae about twenty four hours afterwards. In the present stage several important changes take place in the body. The body of the larva is now divided into three regions; anterior or cephalic, central and smaller posterior regions. The anterior and the central body regions are separated to each other by a ring of prototroch, the central and posterior by the collar. Slight swellings appear on each side dorsal to the anterior eye and immediately anterior to the prototroch. They enlarge rapidly to the conspicuous lobes which subsequently give rise to the branchial and opercular rudiments. A folded ectodermal mass on the right side indicates the future operculum. A group of rather stiff cilia forms the apical tuft. On both lateral sides of the body just behind the prototroch a pair of oblong mass of cells is formed. This vacuole-like vesicle is a shell-gland which is white in colour by a reflected light. The mouth leads to a ciliated vestibule, immediately posterior to which is present a transverse row of cilia. The collar membrane is now well developed and represented by two prominent flap-like projections on the right and left sides of the body. At this stage three pairs of bristle bundles first appear, each with a single needle-like bristle. The neurotroch becomes conspicuous. The posterior body lengthens and bends ventrally. The whole larva is transparent; the gut is bluish yellow. There are two pairs of eyes. The posterior pair situated ventrally is larger, oblong in shape terminating in a lens-shaped hyaline body. The larva is still enclosed in its capsule, and it was observed to push continually the envelope with the spines. Figs. 10 and 11 show the oldest larvae that could be found inside of the operculum of the mother. The larva leaves the brood-pouch within the following five or six hours. The larva just before hatching measures 280μ in length and 160μ in breadth. The head remains unchanged, except an addition of a pair of stiff tactile hairs borne on the ventro-lateral region above the posterior eyes. The opercular rudiment on the dorsal right side of the cephalic region enlarges in size. The branchial lobe on the left side becomes also folded. The shell gland is almost circular. The swimming cilia of the prototroch are long and curled along the sides of the head when not in use. The posterior abdominal region behind the collar membrane is now segmented by a faint constriction. A pair of digit-form adhesive processes is formed at both lateral ends of the last neurotroch. The anal region with two stiff tactile hairs is densely ciliated. The digestive tract is packed with dark bluish yellow granules at the anterior half portion and is nearly translucent in the posterior region.

2. *Liberation of larvae from operculum.* The egg-capsule surrounding the larva is liable to be broken off by a slight mechanical shock just before hatching, and the larva thus liberated swims about within the brood-pouch. Owing to the swimming larvae the brood-pouch on a trumpet-shaped calcareous plate is now split off along the upper dorsal margin. Through the passage newly opened the larvae emerge from the brood-pouch and set in the pelagic life. It takes only five or six minutes before the larva swims out the brood-pouch. The empty brood-pouch evacuated falls off before long, but sometimes it remains in situ for a considerable length of time until the new one is formed (Fig. 13, Pl. XXVII). The brood-pouch filled with just fertilized eggs is often constructed anew on the older one containing the advanced larvae.

3. *Pelagic stages.* After liberation from the brood-pouch the larvae swim actively in large glass dishes with sea-water, and in a few hours a good number of larvae are found on the side of the bowl nearest to the light. Figs. 15 and 16 represent the larvae about two hours after liberation. The body measures 370μ long and 140μ wide at the broadest portion. The length from the anterior end to the prototroch is 70μ. A tuft of the apical sensory hairs falls off at the end of the pelagic stage just before the metamorphosis. The prototroch and the neurotroch are as in the foregoing stage, but become stronger. The lens-like terminal body of the posterior ventral eyes is prominent, half-moon shaped. The rudiment of the operculum is now

markedly protruded and folded. The shell glands situated just posterior to the prototroch are well developed attaining at their maximum size, and extend as far as half the length of the thoracic region. These glands are filled with white calcareous substance. The collar membrane is greatly elongated on both lateral sides and clothed with a tuft of fine cilia at its posterior lateral margin. Along the median dorsal line both the lateral flaps are shifted upwards leaving a broad, deep median incision. The abdomen now lengthens and has four segments. The neurotroch consists of four groups of fine cilia: one belongs to the thoracic region and the remaining three to the abdomen. The anal region is closely beset with minute cilia. A pair of sensory tactile hairs becomes longer than before. Three pairs of bristle bundles are found on the thoracic region as shown in the previous stage. Each one of them has a needle-like bristle with more or less spatulated terminal portion. The oesophagus extends backwards as far as the midway of the thorax, and continues to the enlarged stomach, which is packed with a number of deep bluish fine granules. The gut then gradually narrows towards the anus.

The larvae in the pelagic stage are positive in phototropism, and swim across a dish directly towards a source of light, frequently slowly rotating on their longitudinal axes. Sometimes they swim in circles about one place.

4. *Metamorphosis and early bottom stages.* The duration of the pelagic life varies in wide ranges. The larvae reared take five to six hours before they are ready to metamorphose. Actual process of metamorphosis is not easy to follow, as the larvae soon secrete mucus, thence the observation being difficult. At the end of the pelagic life they crawl about the water surface for a short time and then they settle down to the bottom by mucus secreted. They now appear to be no longer affected by light. At first a quantity of transparent mucus-like secretion is supplied from the shell glands. Fig. 17, Pl. XXVI represents the larva just metamorphosed living in the thin, soft tube. The branchia and operculum are now turned outwards and forwards. The operculum projecting from the right dorsal side is trumpet-shaped. Just ventral to the operculum there are three branchial masses, two of which are large and bottle-shaped and the others are small and round. On the left side there are three large and a single small branchial rudiments. On the terminal portion of the branchial rudiments there occur a number of rather stiff cilia.

Two pairs of eyes are still present, but each of the anterior pair stands closer to one another than in the earlier stage. Except a part of the prototroch and the anal ciliary band all other cilia shown in the previous stage are now entirely fallen off. The prototroch does not form a continuous band of cilia, but it leaves a spacious gap at the dorsal and ventral median portions on both lateral sides of the neck. A pair of the shell glands are now in use to form a tube. The collar membrane is rolled back over the upper lip of the tube, enveloping almost its entire outer surface. The secreted substance from the shell glands is at first deposited in the space between the body and the flap-like collar membrane. And thus the collar membrane acts as a protecting sheath during the development of the tube. The posterior body is still naked, and a pair of the adhesive processes remains unaltered. The anal region is ciliated. The sensory cilia borne on the posterior end of the body are fallen off. The pygidial region of this species is not specially deformed as is shown in *S. spirillum.* The posterior body bends forwards and ventralwards. The tube first formed does not take a horny shape as shown in *S. spirillum,* but it is always constructed spirally from the beginning. A day later the tube becomes harder and longer as the calcareous materials are gradually deposited, and consequently it envelops a body of the young worm completely. Sometimes the tube is coiled erectly as is shown in Fig. 21, Pl. XXVIII. The length of time during which a young settles down and forms a tube is much shorter than in *S. spirillum.* Within about a fortnight all the larvae either died off or settled down and there metamorphosed.

5. *Juvenile stages.* After metamorphosis the changes taken place during the juvenile stages are confined mainly to the growth of the branchial crown and the operculum, and an addition of the segments. As already mentioned the branchial and opercular rudiments arise as a mass of large prominences on either side of the head anterior to the prototroch. For a short time during early metamorphosis each branchial process acquires three pairs of short branches of unequal length. Soon a fourth branch develops near the base of the second one, and accordingly there are four pairs of the primary branchial filaments formed. On the right side one of these branches is replaced by an operculum. Throughout the succeeding stages the third branch remains short, unbranched and ultimately forms a so-called palp of the adult. The other three branches on the left side

and two on the right become steadily longer, and each one buds off the paired pinnule-like branches. Each branchia bears a number of stiff cilia at the end and is densely ciliated along its innerside. The shell-glands discharge wholly their contents during the metamorphosis for tube-formation, and they remain as empty cases which disappear before long. A pair of small eyes is present immediately behind the branchia. There are three pairs of bristle bundles in the thorax. Each bundle contains two capillary and winged bristles. The uncini of the second and third setigers appear later than the bristles. As shown in Fig. 10, Pl. XXVII the uncinus takes a similar form to that of the adult. The base of the uncinus is distinctly trifurcated.

6. *General accounts.* Pagenstecher appears to have been the first to record eggs and development of *Spirorbis*. In 1863 he published a paper dealing with the development of *Spirorbis spirillum* from the egg to metamorphosis. Afterwards the species observed by him has been shown by several writers to belong to another species, *S. pagenstecheri*. The worm incubates the egg within the operculum as shown in *S. nipponicus*. Before hatching from the operculum the larvae acquire already four pairs of bristles. The fact greatly differs from the observation on other Serpulid worms, in which arise three setigers simultaneously. The neurotroch figured by Pagenstecher is seemingly represented by a continuous ciliary band extending from the mouth as far as the posterior extremity of the body. A pair of the shell-glands is well developed during the early larval stages, and they are described as "ovalen gelben Fleck neben dem Magen rechts und links". The large posterior eye is provided with a cup-shaped lens. In 1866 Agassiz described the larva of *S. spirillum*. In this species the eggs are found in strings arranged in two rows within a mother's tube. According to him the eggs are considerably advanced within the body of the mother before they are transferred to the cavity of the tube. So far as my observation on the same species goes, it was unable to observe the larvae in the stages developing in the body of the mother. The larvae of *S. spirillum* observed by Agassiz have the ocular spots always limited to two, instead of being four as is generally shown in other *Spirorbis* larvae. Moreover, the tentacle develops at first on the right side, and next the corresponding tentacle appears on the left, and subsequently the rudiment of odd opercular tentacle occurs covering the right tentacle. In my observation on the same species the operculum was the first

to appear as a cephalic appendage on the right side. In 1868 Claparède and Mecznikow figured and described briefly the larva of *S. pagenstecheri*. Willemoes-Suhm in 1871 gave also a brief account on the early larvae of *S. nautiloides* which is synonymous with *S. borealis*. Goette (1882) mentioned some accounts on the early development of *S. nautiloides*. He alluded mainly on the problem of the gastrula formation. In 1885 Fewkes traced the larval development of *S. borealis* belonging to the sub-genus *Leiospira*. Compared his observations with the development of two species treated here, both belonging to *Dexiospira*, a most obvious difference between these subgenera lies apparently in the mode of the opercular development; i. h. the opercular rudiment of *S. borealis* appears on the left side of the cephalic region, not on the right side as usually shown in *Dexiospira*. The operculum of *S. borealis* does not serve a purpose of a brood-pouch as *S. spirillum*. Schively (1897) also described the segmentation and the larval development of *S. borealis*. According to him the eggs fallen into the body cavity are fertilized and then emerge from the opening of the operculum and are placed along the mid-dorsal furrow of the tube. Since that time no further work on *Spirorbis* larvae has been published.

Larvae of the genus *Spirorbis*, so far investigated by several authors, agree with each other in possessing a rather short pelagic life. The larvae liberated either from the operculum or the parent's tube settled down to the bottom in a few hours, and therefore it frequently happens during a night that smooth sides of the vessel are completely covered with small calcareous tubes formed by the *Spirorbis* larvae hatched before evening. The larvae of other Serpulids, such as *Pomatoceros* observed by Segrove (1941), show, on the contrary, a considerably protracted pelagic existence. As Segrove supposed justly the larvae developed from small eggs which were poorly supplied with yolk enter a pelagic life in earlier stage and move about actively for collecting food for long time before metamorphosing into the adult worm. On the other hand, the larvae developed from large eggs with plentiful yolks are independent of external food supply, and hence pelagic life is of less importance. The larvae of *Spirorbis* may be classified into the latter category. The head and anal vesicles are conspicuous organs of vesicular structure and are found in the head and pygidium of the larvae among a number of the Polychaete larvae. Of these vesicles the anal ones are most well developed in Sabellidae and Serpulidae. As to the occurrence of the anal vesicles in the *Spirorbis* larvae no mentions have been given by the previous authors. The characters to distinguish the larvae of *S. nipponicus* from those of *S. spirillum* can be briefly tabulated as follows.

S. nipponicus	*S. spirillum*
1. The larva before pelagic stage is incubated within the operculum.	1. The larva before pelagic stage is incubated within the tube of parent.
2. No special sensory cilia on the ventral cephalic region.	2. On ventral cephalic region a pair of long stiff cilia is present just above prototroch.
3. Shell glands appear in early stages and well developed.	3. The presence of shell glands is quite indistinct.
4. Posterior eyes are provided with conspicuous lens.	4. Posterior eyes have no lens.
5. Presence of anal vesicles is rather indistinct.	5. Anal vesicles are well developed.
6. Posterior body remains unaltered throughout the development.	6. During metamorphosis posterior body is deformed specially.

In *S. spirillum* the tube first formed is translucent and horn-shaped, and it takes a considerably long time before the spiral tube is completed, while in *S. nipponicus* the tube is constructed spirally from the beginning of the development and is formed completely in twenty-four hours. The uncini of *S. nipponicus* are appeared in the earlier stage than *S. spirillum*.

XV. Résumé and Conculusions

Family Eunicidae

1) Larvae of *Lumbriconereis latreilli* Audouin et M. Edwards were reared from the egg to the young worm through metamophosis.

2) The eggs are laid in jelly-mass attached to sea-weeds, such as *Zostera* and *Sargassum* etc. The early development takes place inside of the jelly and the larval history is much abbreviated.

3) The trochophore stage and the free-swimming phase are both omitted from the larval development. The early metatrochophore is provided with akrotroch, prototroch, paratroch and telotroch.

4) The larvae emerge from jelly-mass at the stage with two to seven chaetigerous segments and set immediately in a creeping life.

5) The succession of the bristles is described.

6) Spawning habits and previous references of Eunicid larvae have been discussed.

The larvae of Eunicidae may be characterised by possession of an extremely broad preoral band of short cilia, retaining the typical protrochophore, and lack the true trochophore stage. The neurotroch does not develop in the early larvae. According to Häcker (1896) the polychaete larvae which pass through the early stages of development in a gelatinous capsule tend to omit the true trochophore stages from their life-history. In a number of Eunicid worms, in which the eggs are laid in the gelatinous mass, the omission of the free-swimming stage from the larval life is not usual. *Marphysa gravelyi* and *Diopatra variabilis* are both known to have no free-swimming stage. These habits are due to the eggs supplied with a large amount of food yolk and to the fact that the early development of these larvae takes place under the protection of a gelatinous capsule. In the Eunicidae the chaetigerous segments appear successively and not simultaneously as usually shown in the larvae of Nereidae.

The larvae of *Lumbriconereis latreilli* have a more complex ciliation than other Eunicid larvae. Disregarding the presence of the broad prototroch of short cilia characteristic of the Eunicid protrochophore, the occurrence of akrotroch and paratroch have only been observed in the larva of *Lumbriconereis* here considered. Such a complexity of the larval ciliation in *Lumbriconereis* is rather interesting in considering the facts that the adult structures of this worm are more simplified than other Eunicid worms. Some larvae belonging to the Nereidae, e.g. *Nereis pelagica,* have three pairs of paratroch at the stage corresponding to the metatrochophore stage, and the akrotroch is also added later after hatching. The neurotroch is entirely absent from both the Eunicid and Nereid larvae.

Family Nereidae

1) The development of *Neanthes* sp. from the atrochal stage to the young worm with sixteen chaetigerous segments is described.

2) The eggs are laid in a hardened silk-like capsule attached firmly to the leaves of *Zostera marina*. They are densely yolked. The early development takes place within the spawn-mass.

3) There are no trochophore stage and no free-swimming phase. The larval cilia are much reduced and apparently absent. The

larvae in an early stage possess already three chatigerous segments. A pair of the large provisional eyes is distinct during the stage before hatching.

4) The larvae creep out of the spawn-mass bearing three chaetigerous segments when the tentacles and tentacular cirri have appeared.

5) The first pair of the parapodia loses the bristles, and a lobe grown between the noto- and neuropodial chaeta-sacs becomes the third posterior pair of tentacular cirri.

6) In the earliest stages bristles are mainly homogomph falcigers with short appendices: afterwards are added the bristles of the adult form. The acicular bristle appears first in the eighth setiger and in the succeeding three or four. No provisional bristles.

7) A comparison of the larva was made with other Nereid larvae previously known.

The larvae of Nereidae, whatever the mode of their early life may be, will be characterised by the precocious development of the certain structures of the adult. As a rule, the larvae of Nereidae possess three chaetigerous segments in an early stage, and these setigers are formed simultaneously. Though the first three segments are formed in the early metatrochophore stage, the development of the succeeding segments is supressed until the several appendages of the primary segments are completely formed. The facts that the early developmental activities are centered at first in a definite number of the primary segments may be related with the special cephalisation shown in the adult. The similar phenomenon is also taken place in other allied families such as Phyllodocidae and Aphroditidae, in which the free-swimming trochophores show already well-marked larval structures revealing the characteristics of the family. The transition of the first parapodia to the tentacular cirri is also regarded as one of the characteristics seen in the Nereid larvae. At the early bottom stage the middle lobes of the first pair of the parapodia markedly lengthen and shift forwards and give ultimately rise to a third pair of tentacular cirri. When the fourth setiger is developed, the larvae, both pelagic and non-pelagic, commence their bottom life. The development of the ciliation and the bristles is much abbreviated in the larvae lacking the free-swimming stages. The larvae of *Neanthes* develop from the atrochal stage to the non-ciliated metatrochophore directly, and thus there is neither trochophore stage nor free-swimming life.

Family Ariciidae

1) The development of *Nainereis laevigata* (Grube) and *Haploscoloplos kerguelensis* (McIntosh) are described from the egg to the young worm about sixty days old in the former, and to the young metamorphosed individuals in the latter.

2) In *Nainereis laevigata* the eggs are laid in a ribbon-shaped mass of mucus attached to the muddy ground near the *Zostera*-region. *Haploscoloplos kerguelensis* collects the eggs in a pear-shaped mass of jelly supported by a long stalk.

3) The prototroch of *Nainereis laevigata* consists of a single complete band of short cilia and that of *Haploscoloplos kerguelensis* of three incomplete bands leaving a dorsal gap.

4) The gastrotroch is only found in *Haploscoloplos kerguelensis*. The paratroch of the achaetous second segment is present in the both species, forming a complete ring of cilia in *Nainereis* and a discontinuous band in *Haploscoloplos*.

5) The bristles first appear when the larvae of *Nainereis* are equipped with six segments, and those of *Haploscoloplos* are not discernible untill ten segments are completed. *Haploscoloplos* has three pairs of branchiae when the metamorphosis is just furnished, while *Nainereis* shows no sign of the branchiae at the corresponding stage.

6) The occurrence of the dorsal segmental organ and the nototroch is characteristic of *Nainereis laevigata*, in which the former first appears on the sixth chaetigerous segment of the nine-setiger larva. The larval eyes of the both species are provided with the well-developed lens-like hyaline bodies.

It has been quite unknown whether the free-swimming larvae of the Ariciidae do or do not bear the provisional long bristles as usually shown in the allied family Spionidae. So far as the present investigation goes the larvae of this family entirely lack any bristles during the pelagic life, and they swim about by means of the locomotive cilia only. In *Haploscoloplos kerguelensis* the larva hatches out from jelly about three days after fertilization and enters the pelagic life, which lasts generally no more than one day or two. *Nainenreis laevigata* spends also a shortened swimming stage. Owing to such concised pelagic existence the development of the long provisional bristles which help the swimming movement may be suppressed in the Ariciid larvae. The bristles first formed are normal, making their appearance at the metamorphosing larvae. Except the absence of provisional bristles there are some resemblances in ciliation between the larvae of the Ariciidae and Spionidae. The gastrotroch found in pairs in the larvae of *Haploscoloplos* is also present in the majority of the Spionid larvae. The nototroch found in the advanced larvae of *Nainereis* occurs likewise in the larvae of Spionidae, such as *Scolecolepis fulgida* and *Polydora hopulura*. It is interesting to notice that the early larvae of *Nainereis laevigata* agree well with those of Eunicid larvae, *Lumbriconereis latreilli*. Though the former only has the neurotroch both the Ariciid and the Eunicid larvae considered here have the similar ciliation as shown in the distribution of akrotroch, paratroch, telotroch and prototroch. As to the general characteristics of the Ariciid larvae the short notes have already been given in the previous section.

Family Spionidae

1) The development of *Spio filicornis* (O. F. Müller) is described from the egg to a very late planktonic stage.

2) The eggs are collected in an ellipsoidal mass of jelly with a slender long stalk.

3) The larvae emerge from the jelly mass at the stage with three chaetigerous segments and enter a long pelagic life.

4) In early stages the prototroch and telotroch are separated into several groups of cilia.

5) The larvae have the complicated vestibules surrounding the mouth, with special sensory cilia. A pair of the round ciliated swellings is found on the head and on the body segments in the swimming larvae.

6) A pair of well-developed anal vesicles is present in the metatrochophore.

In general the larvae of the Spionidae are well adapted to prolonged free-swimming life, and, accordingly, the locomotor cilia of the prototroch are well developed, and the feeding cilia are also formed. The occurrence of extremely elongated provisional bristles which assist in floating, as do the spines of diatoms, may be also related with the prolonged pelagic life. The formation of a vestibule in the metatrochophore is also the common characteristic shown in the Spionid larvae. The prototroch and telotroch are generally separated into several groups of cilia. The specialised interparatroch is found in the advanced larvae. In Spionid larva all the segments are developed in series, as in Eunicid larvae. In the larvae of the Chaetopteridae and Magelonidae, which are both classified into the Spioniformia, no vestibule is found during the development. Gravely (1909) supposed that the funnel-like mouth sbown in the early larva of *Chaetopterus* was deduced from an exaggeration of the vestibule as found in other Spioniform larvae. As already stated, the presence of the anal vesicles in *Spio filicornis* is quite remarkable as such a structure which is unknown in the Family, though the similar vesicular bodies are generally found in the larvae of the Sabellidae and Serpulidae.

Family Cirratulidae

1) Larvae of *Cirratulus cirratus* (O. F. Müller) were reared from the egg to the young worm through metamorphosis.

2) The eggs are laid in a fusiform gelatinous mass attached to the muddy bottom by two narrow ends. The early larval stages are passed through within the jelly mass.

3) The larvae are yolky, having a broad prototroch, akrotroch and telotroch. A tuft of apical cilia is well developed.

4) During metamorphosis most of the cilia disappear. The neurotroch is little affected by metamorphosis, and it remains still in the advanced larva with six setigers.

5) The bristles appear for the first time a few days after metamorphosis. A pair of the crescent nuchal organs appears at the same stage. The first branchial filament appears when some five setigers have been formed. Following to the development of the branchial filament a tentacular filament also makes its appearance on the posterior margin of an achaetous segment.

The larvae of the Cirratulidae have rather complex ciliation during the early stages. An apical tuft consists of several long cilia. The prototroch is represented by a broad band of fine cilia, and the telotroch as well as the akrotroch is completely formed. In spite of the presence of such well-developed locomotor cilia the larvae spend quite short pelagic life and do not feed at all before metamorphosis. The early larvae of the Cirratulidae well resemble those of some Capitellid worms, such as *Notomastus latericeus*. In both larvae the disappearance of the prototroch during metamorphosis is gradual and takes place in stages. The neurotroch is the last to disappear. In Terebellid larvae the neurotroch also remains for a considerable time after metamorphosis. In the Ariciid larvae the first branchial bud appears always on the definite segment while in the Cirratulid larva the position of the first branchial filament is variable to some extent in different individuals. In the latter the relative length of branchiae is extremely irregular; it is neither alike on two side of one individual nor on even same side of any two individuals. A metatrochal ciliary band as shown in the Ariciid larvae is not found in the Cirratulid larvae.

Family Terebellidae

1) *Lanassa nuda* has been reared for the first time from the egg through the metamorphosis to early bottom stages.

2) The orange eggs are laid in wrinkled oval mass of jelly attached to the bottom by a short stalk. The early larva has a broad prototroch, a narrow telotroch and a neurotroch.

3) During the early metatrochophore stage a rudiment of median tentacle appears. Bristles first develop before metamorphosis.

4) Metamorphosis proceeds gradually and the neurotroch remains to exist until the early bottom stage.

5) There is no free-swimming stage. When they are ten days old the larvae begin to settle down and secrete around themselves a thin mucus tube. Tentacles appear in succession.

6) A number of eye-spots appear in the advanced young worm with fifteen setigers. Notopodial bristle bundles in ten pairs. Provisional bristles are shedded off and replaced by wing-like bristles at the same stage.

The Terebellid worms show a certain degree of resemblance to the Ampharetids in the body divided into thorax and abdomen, and in the form of the parapodia, bristles and uncini. And so the usual position of the Terebellidae next to the Ampharetidae in systematic works is not, at present, questioned. Owing to meagreness of the development of the Ampharetid worms, it is impossible to discuss further the affinity between the Terebellidae and Ampharetidae by the present study on the development of the former family. The early Terebellid larva has a rather broad prototroch which does not act as a locomotor organ for the pelagic life. The bristles are formed in succession during the stages before metamorphosis. As shown in the Cirratulid larvae the neurotroch is less affected by metamorphosis, and it is fallen off in a considerably later stage. *Lanassa* belongs to the sub-family Polycirrinae including several other genera such as *Polycirrus, Lysilla* and *Amaea* etc., all characterised by the entire absence of the branchiae on the first segment. The development of the branchiae in the Terebellid larvae takes place gradually, e.g. in *Loimia medusa,* the first pair of the branchiae appears at first at the stage with about twelve pairs of bristle bundles and about seventeen pairs of uncinigerous processes.

Family Arenicolidae

1) The larvae of *Arenicola claparedii* Levinsen were reared from the eggs to the post-larval stage with a full number of segments of the adult worm.

2) The eggs are deposited round the parent's body living in the burrow, forming a tube-like cylindrical layer. The early developmental stages are passed through within the spawn-mass.

3) The larvae emerge from the 'egg-tube' when the first pair of the bristle bundles has completely been formed. Apart from the rather poorly borne prototroch and wing-like bristles the larva has no special locomotor apparatus for the pelagic life. After metamorphosis the young worm begins to feed. About three days after liberation the larvae begin to metamorphose and have the five setigerous segments.

4) During metamorphosis the larvae sink to the bottom and secrete a thin gelatinous envelope within which they creep about.

5) A pair of nuchal grooves first appears at the three-setiger larva. A number of refringent yellow brown globules are accumulated at both ends of the body.

Benham (1896) placed the Arenicolidae in his suborder Scoleciformia which contains six families. In this suborder the Arenicolidae stands more closely to the Scalibregmidae, having less affinities with the Opheliidae and the Maldanidae. The Arenicolidae agree with the Scalibregmidae in the general shape of the body, sub-division of segments into annuli, small lobed prostomium, and the presence of gills of the similar type. At present, however, we have nothing whatever about the larval development of the Scalibregmidae, Opheliidae and Chloraemidae, and there are only imperfect accounts on the early larva of the Maldanid worm. According to Wilson (1882), who has studied the segmentation and early larvae of *Clymenella torquata* and *Arenicola cristata*, the early cleavage stages of *Arenicola cristata* so closely resemble those of *Clymenella* that one set of figures might almost answer for both. The early larva of *Clymenella* figured by Wilson resembles also in general features that of *Arenicola*. In both of them the ciliary bands are rather ill-developed, and the segmentation is also indistinct. In *Arenicola* larva the bristles appear at much earlier stage than in *Clymenella* larva.

No mentions have been given as to the mode of metamorphosis and the development of the later stages of *Clymenella*. The Capitellid larva, *Capitellides giardi* Mesnil observel by Day in 1936, shows some resemblances to the Arenicolid larva in the ciliation and in the fate of the prototroch during metamorphosis. *Capitellides* is sheltered within the tube of its parent till the metamorphosis, and hence there is no free-swimming stage. During metamorphosis the cilia of the prototroch do not disappear simultaneously. The comparison of the larvae of *Arenicola claparedii* with those of other species has been given in the foregoing section. The spawning habit of *Arenicola claparedii* is quite remarkable among the Polychaete worms, as already stated.

Family Sabellidae

1) The developments of *Chone teres* Bush and *Potamilla myriops* Marenzeller were described from the egg to the young worm through metamorphosis.

2) In *Chone teres* the eggs are inclosed in a semi-fluid gelatinous mass of ovoid shape with a narrow, short peduncle, by which the spawn-mass is attached to the opening of the parent's tube. In *Potamilla myriops* the eggs are pelagic, and discharged freely in the sea-water.

3) The early larva of *Chone teres* is provided with a broad prototroch, a neurotroch and a telotroch, of these the occurrence of

the telotroch is quite characteristic of this species. *Potamilla* larva has no telotroch as usually shown in other Sabellid larvae. In the both species there are a large head vesicle and a pair of anal vesicles. A pair of statocyst appears in early larva of *Chone teres*.

4) The bristles first appear during the pelagic life, and a pair of eye-spots is also formed.

5) The metamorphosing larva of *Chone* settles on the bottom and secretes for itself a tube of mucus. During metamorphosis the number of segments is not added newly, and the main change takes place in the head structure and ciliation.

6) The branchial rudiments appear as a pair of the lobed swellings at the last pelagic stage and begin to branch before metamorphosis.

When we compare the larval development of Sabellidae with those of other families it becomes quite clear that the Sabellid larvae have more closely affinities with the Serpulid larvae than with the larvae of other neighbouring families. The anal vesicles are conspicuous in structure and in most well-developed condition in the Sabellid and Serpulid larvae. The branchial crown also develops in the similar way in both the families. It develops as a pair of the ectodermal thickenings on the sides of head and becomes soon three-lobed. In the development of the thoracic membrane the larvae of both families show a close similarity. Though the telotroch is generally absent in most of the Sabellid and Serpulid larvae, it may eventually be found to occur in the Sabellid larvae as shown in *Chone teres*, and accordingly it can not be considered that the absence of the telotroch is one of the valid characters to prove the affinity between the Sabellid and Serpulid larvae as Wilson (1936) assumed. There are also, however, some points of differences between these two families. In the larva of *Spirorbis* the neurotroch is not formed as a continuous band of cilia as shown in the Sabellid larvae, but is separated into several groups of cilia. In the Sabellidae the first three thoracic setigers develop in succession, while in the Serpulidae these setigers appear simultaneously. In majority of the Serpulid larvae, with the exception of *Pomatoceros triquator*, the segments added to the first three thoracic setigers are of the abdominal type, with dorsal uncini and ventral bristles, and afterwards anterior several segments of the abdominal type are transferred to the thoracic segments. In the Sabellid larvae the segments of abdominal type first appear after the full number of thoracic segments of the adult form has been formed. As already shown in the Nereid larvae the Sabellid larva also tends to postpone the development of the body segments during the formation of the head appendages.

Family Serpulidae

1) The larvae of *Spirorbis spirillum* Linné and *S. nipponicus* Okuda were reared through the metamorphosis to early bottom stages.

2) *S. spirillum* lay their eggs side by side within the tube and *S. nipponicus* in operculum which serves as a brood-pouch. The larvae of these species liberate the shelter after first three thoracic setigers have been formed.

3) In both the species the early larvae have well-developed apical tuft and prototroch. The neurotroch is not continuous but forms four separate groups. The first three setigers begin to appear simultaneously.

4) In *S. spirillum* the larval eyes carry a large lens. Two pairs of adhesive processes develop during the pelagic stage. The development of the branchial crown and the operculum takes place in the similar way in both the larvae. These rudiments appear as a pair of the lobed swellings in front of the prototroch. The opercular rudiment is homologous with the branchial bud and is located always on the right side. Behind the prototroch the rudiments of the collar membrane are protruded as an outgrowth of the body wall.

5) In *S. spirillum* the presence of the anal vesicle is quite distinct, but it is more or less obscure in *S. nipponicus*. The head visicle is absent in both species.

6) The tube of *S. spirillum* newly formed is horn-shaped, rather straight, and afterwards it bends spirally. In *S. nipponicus* the tube is formed spirally from the beginning.

7) After settling-down the abdominal portion of the young worm of *S. spirillum* is particulary projected to form a pair of the foot-like protuberances.

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Explanation of Plates

Plate XII

Development of *Lumbriconereis latreilli* Audouin et M. Edwards

Fig. 1. Egg-mass laid on a gulf-weed, *Sargassum* sp.
Fig. 2. Two-cell stage.
Fig. 3. Four-cell stage, viewed from animal pole.
Fig. 4. Eight-cell stage, viewed from above.
Fig. 5. Transition from sixteen to thirty-two-cell stage, from upper pole.
Fig. 6. Early embryo 20 hours after two-cell stage.
Fig. 7. Spherical embryo about 24 hours older than the one shown in Fig. 6. Dorsal view.
Fig. 8. Early metatrochophore. Dorsal view.
Fig. 9. The same. Ventral view.
Fig. 10. Dorsal view of larva four days old. First bristle bundles are appearing. Dorsal view. Actual length approx. 350μ.
Fig. 11. Metamorphosing larva three days after early metatrochophore. Ventral view. Actual length approx. 440μ.
Fig. 12. Later metamorphosing larva with two chaetigerous segments taken from egg-mass.
Fig. 13. The same. Ventral view.
Fig. 14. Recently metamorphosed larva seven days old. Ventral view.
Fig. 15. The same. Dorsal view.
Fig. 16. Dorsal view of larva eight days old.

Plate XIII

Development of *Lumbriconereis latreilli* Audouin et M. Edwards

Fig. 17. Larva with five setigers. Dorsal view.
Fig. 18. Dorsal view of young worm twelve days old. Actual length approx. 1 mm.
Fig. 19. Young worm with ten setigers. Dorsal view. Actual length approx. 1.3 mm.
Fig. 20. Young worm found creeping on the tube of *Potamilla*. Dorsal view. Actual length approx. 3.4 mm.
Figs. 21–23. Bristles of the larva as shown in Fig. 10.
Fig. 24. Maxilla first appeared in larva with five setigers.
Figs. 25–27. Bristles of larva with five pairs of bristle bundles.
Fig. 28. Bristle bundles from second parapodium of young worm with eight setigers.
Fig. 29. Crochet of young worm with ten-setigers.

Plate XIV

Development of *Neanthes* sp.

Fig. 1. Cocoon-shaped egg-mass laid on leaf of *Zostera*.
Fig. 2. Egg-mass cut open to show the clusters of eggs.
Fig. 3. Another egg-mass.
Fig. 4. Recently spawned fertilized egg. Actual length approx. 280μ.
Fig. 5. Larva about five days after fertilization. Lateral view. Actual length approx. 340μ.
Fig. 6. The same larva viewed from frontal side. A pair of provisional eyes quite distinct.
Fig. 7. Ventral view of the same larva.
Fig. 8. Larva of the same stage as shown in Fig. 5. Dorsal view.
Fig. 9. Larva about six days old. View of left side. Three pairs of bristles are first appeared.
Fig. 10. Frontal view of the same larva.
Fig. 11. Larva just before hatching. Dorsal view. Actual length approx. 460μ.
Fig. 12. Dorsal view of larva recently hatched out from egg-mass. Two pairs of ordinary eyes are appearing.
Fig. 13 Larva about seven days after hatching. Actual length approx. 800μ

Plate XV

Young worms of *Neanthes* sp.

Fig. 14. Chaeta-sac containing bristle bundles from the same larva as shown in Fig. 9.
Fig. 15. Homogomph falciger with a few serrations on upper piece. Taken from the same larva as shown in Fig. 11.
Fig. 16. First parapodia from the larva with three setigerous segments.
Fig. 17. Dorsal view of the third tentacular cirrus which was in the previous stage was the first parapodia, from the same stage as shown in Fig. 13.
Fig. 18. Ventral view of the same.
Fig. 19. Degenerated falciger found in transitional tentacular cirrus as shown in Fig. 18.
Fig. 20. Heterogomph falciger from larva with six setigers.
Fig. 21. Homogomph falciger from the same larva.
Fig. 22. Homogomph falciger with rather elongated terminal piece from the same larva.
Fig. 23. Heterogomph falciger from the same.
Fig. 24. Homogomph falciger with a few terminal teeth. This falcate seta is only found on first one or two parapodia of larva with six setigers.
Fig. 25. Right maxilla from larva with six setigers.
Fig. 26. Acicular bristle found in certain middle parapodia of young worm.
Fig. 27. Heterogomph falciger with shorter terminal piece from young worm of sixteen-setiger stage.

Fig. 28. Heterogomph falciger of young worm bearing sixteen pairs of parapodia.
Fig. 29. Heterogomph spiniger of young worm with sixteen setigers.
Fig. 30. Homogomph spiniger of the same.
Fig. 31. Young worm with eight setigerous segments. Ventral view. Actual length approx. 1.5 mm.
Fig. 32. Dorsal view of the same larva.

Plate XVI

Development of *Nainereis laevigata* (Grube)

Fig. 1. Fertilized egg. Actual length approx. 250μ in diameter.
Fig. 2. Trochophore, thiry-two hours after fertilization. Lateral view. Actual length approx. 300μ.
Fig. 3. Dorsal view of the same larva.
Fig. 4. Larva forty-six hours after fertilization. Dorsal view. Actual length approx. 370μ.
Fig. 5. Ventral view of the same larva.
Fig. 6. Lateral view of the same.
Fig. 7. Larva about four days old. Lateral view. Actual length approx. 700μ.
Fig. 8. Dorsal view of the same larva.
Fig. 9. Metamorphosing larva. Paratroch and telotroch are fallen off.
Fig. 10. Later metamorphosing larva. Lateral view. Actual length approx. 1 mm.
Fig. 11. Ventral view of head of the same larva as shown in Fig. 10.
Fig. 12. Recently metamorphosed larva ten days old. Dorsal view. Actual length approx. 1.5 mm.
Fig. 13. Young worm about sixty days after fertilization. Dorsal view. Actual length approx. 4.5 mm.
Fig. 14. Young worm with forty-three setigers. Dorsal view. Actual length approx. 6 mm.
Fig. 15. Posterior end of the young worm with sixty-three setigers.
Fig. 16 and Fig. 17. Crochets from the sixth parapodium of ten-setiger larva.

Plate XVII

Development of *Haploscoloplos kerguelensis* (McIntosh)

Fig. 1. Spawn-mass.
Fig. 2. Fertilized egg. Actual length approx. 200μ in diameter.
Fig. 3. Larva twenty four hours after fertilization. Dorsal view. Actual length approx. 220μ.
Fig. 4. Larva thirty two hours after fertilization. Dorsal view. Actual length approx. 250μ.
Fig. 5. Lateral view of the same larva.

Fig. 6. Larva about two days after fertilization. Dorsal view.
Fig. 7. Lateral view of the same larva.
Fig. 8. Dorsal view of anterior region of the same larva as shown in Fig. 12.
Fig. 9. Lateral view of anterior region of the same.
Fig. 10. Ventral view of the same.
Fig. 11. Larvae with nine segments, about fifty hours after fertilization.
Fig. 12. Free-swimming larva with eight pairs of bristle bundles.
Fig. 13. Early metamorphosing larva. Lateral view. Two pairs of branchiae are appearing.
Fig. 14. Recently metamorphosed larva. Dorsal view.
Fig. 15. Posterior end of the same larva to show the branchiae.
Fig. 16. Larva with twelve setigers. Dorsal view. About fourteen days after trochophore stage.

Plate XVIII

Development of *Cirratulus cirratus* (O. F. Müller)

Fig. 1. Spawn-mass. Actual length approx. 40 mm.
Fig. 2. Fertilized egg. Actual length approx. 100μ in diameter.
Fig. 3. Larva twenty four hours after fertilization. Actual length approx. 110μ.
Fig. 4. Larva about forty hours after fertilization. Dorsal view. Actual length approx. 130μ.
Fig. 5. Larva three days old. Dorsal view. Actual length approx. 180μ.
Fig. 6. Ventral view of the same larva.
Fig. 7. Larva four days old. View of left side.
Fig. 8. Ventral view of the same larva.
Fig. 9. Dorsal view of the same.
Fig. 10. Metamorphosing larva. Dorsal view. Actual length approx. 440μ.
Fig. 11. Larva with three setigers. Dorsal view. Actual length approx. 650μ.
Fig. 12. Lateral view of the same larva.
Fig. 13. Later metamorphosing larva with tentacular buds. Dorsal view. Actual length approx. 1 mm.
Fig. 14. Ventral view of the same larva. Neurotroch still remains.
Fig. 15. Posterior end of ten-setiger larva.
Fig. 16. Bristles of the same larva as shown in Fig. 11.
Fig. 17. Serrated capillary bristle of young worm with twenty-one setigers.

Piate XIX

Development of *Cirratulus cirratus* (O. F. Müller)

Fig. 18. Crochet of the young with twenty-one setigers.
Fig. 19. Larva about forty days old. Dorsal view. Actual length approx. 2.6 mm.
Fig. 20. Anterior body of young worm about sixty days old. Dorsal view.

Fig. 21. The same with different number of branchiae.
Fig. 22. Bristles from first neuropodium of young worm as shown in Fig. 20.
Fig. 23. Bristle from first notopodium of the same young worm.
Fig. 24. Bristle bundles of the twelfth neuropodium of the same worm.

Plate XX

Development of *Lanassa nuda* (Moore)

Fig. 1. Spawn-mass. Actual length approx. 18 mm.
Fig. 2. Fertilized egg within egg-sac. Actual length approx. 170μ.
Fig. 3. Early embryo twenty-four hours after fertilization. Dorsal view.
Fig. 4. Larva two days old. Dorsal view.
Fig. 5. Larva three days old. Dorsal view. Actual length approx. 280μ.
Fig. 6. Lateral view of the same larva.
Fig. 7. Dorsal view of larva four days old.
Fig. 8. Metamorphosing larva seven days old. Actual length 450μ.
Fig. 9. Larva with eight setigers. Lateral view. Actual length approx. 500μ.
Fig. 10. Anterior end of larva as shown in Fig. 6.
Fig. 11. Winged bristle from larva with four setigers.
Fig. 12. Spatulate bristle from the same larva.
Fig. 13. Uncinus from the same larva.
Fig. 14. Winged bristle from the larva with thirteen setigers.
Fig. 15. Spatulate bristle from the same larva.
Fig. 16 and Fig. 17. Uncini from the same larva.
Fig. 18. Ventral view of anterior end of larva shown in Fig. 19.
Fig. 19. Recently metamorphosed larva with ten setigers.
Fig. 20. Young worm thiry days old. Dorsal view.
Fig. 21. Lateral view of the same young worm.
Fig. 22. Young worm with thirteen setigers. Lateral view. Actual length approx. 1 mm.

Plate XXI

Development of *Arenicola claparedii* Levinsen

Fig. 1. Spawned egg-tube around the female body.
Fig. 2. A portion of egg-tube. Fertilized eggs within egg-case.
Fig. 3. Early metatrochophore. Dorsal view.
Fig. 4. Later metatrochophore. Dorsal view. Actual length approx. 320μ.
Fig. 5. Rotating larvae just before hatching in chorion of egg-tube.
Fig. 6. Larva shortly after hatched out. Dorsal view. Actual length approx. 400μ.
Fig. 7. Lateral view of larva with three setigers. Crochets are appearing.
Fig. 8. Metamorphosing larva with four setigers. Dorsal view.
Fig. 9. Provisional spatulate bristle from two-setiger larva.

Fig. 10. Bristle from three-setiger larva.
Fig. 11. Crochet from the same larva.
Fig. 12. Winged bristle from the same.
Fig. 13. Crochet from the larva with four setigers.
Fig. 14. Recently metamorphosed larva with six setigers. Dorsal view.
Fig. 15. Enlarged view of anterior end of the same larva.
Fig. 16. Young worm with fourteen setigers. Lateral view. Actual length approx. 1.7 mm.
Fig. 17. Young worm with full adult number of segments. No branchiae are as yet appeared. Dorsal view.

Plate XXII

Development of *Chone teres* Bush

Fig. 1. Early larva two days old. Dorsal view. Actual length approx. 220μ.
Fig. 2. Larva three days old. Lateral view.
Fig. 3. Larva a day later than stage as Fig. 4. Actual length 270μ.
Fig. 4. Dorsal view of four days old. Actual length approx. 400μ.
Fig. 5. Lateral view of the same larva. A pair of statocyst appeared.
Fig. 6. Dorsal view of larva with two pairs of bristles. Actual length approx. 500μ.
Fig. 7. Lateral view of the same larva.
Fig. 8. Larva just before hatching. Dorsal view.
Fig. 9. The same with three setigers. Lateral view.
Fig. 10. Larva recently hatched out. Dorsal view. Actual length approx. 520μ.
Fig. 11. Ventral view of the same larva.
Fig. 12. Metamorphosing larva with four setigers. Dorsal view. Actual length approx. 540μ.
Fig. 13. Lateral view of the same larva.
Fig. 14. Anterior end of the same larva as shown in Fig. 14.
Fig. 15. Still older larva. Snout becomes shorter than branchiae.
Fig. 16. Anterior end of the same larva.
Fig. 17. Later metamorphosing larva. Lateral view.

Plate XXIII

Development of *Chone teres* Bush

Fig. 18. Recently metamorphosed larva with five setigers. Lateral view.
Fig. 19. The same. Dorsal view. Telotroch still remains.
Fig. 20. Larva with six setigers. Dorsal view.
Fig. 21. Young worm with ten setigers. Dorsal view. Faecal groove is formed.
Fig. 22. Ventral view of posterior end of the same worm.
Fig. 23. Ventral view of posterior end of the young worm with fourteen setigers.
Fig. 24. Young worm with five abdominal setigers. Dorsal view. Actual length approx. 2 mm.

Fig. 25. Young worm with seventeen setigers. Dorsal view. Actual length approx. 2.8 mm.
Fig. 26. Ventral view of anterior end of the same worm.
Fig. 27. Ventral view of pygidium of the same young worm.
Fig. 28. Newly formed mucus tube of young worm as shown in Fig. 25.

Plate XXIV

Bristles of *Chone teres* Bush

Fig. 29. Ventral view of anterior end of the metamorphosing larva.
Fig. 30. Ventral view of anterior body of young worm with seventeen setigers.
Fig. 31. Dorsal view of the same.
Fig. 32. Lateral view of the same.
Fig. 33. Uncinus first formed in the larval body.
Figs. 34–36. Winged and needle-like bristles from six-setiger larva.
Fig. 37. Uncinus from the same larva.
Fig. 38. Crochet from the same.
Fig. 39. Winged bristle from ten-setiger larva.
Fig. 40. Uncinus from the same.
Fig. 41. Crochet from the same.
Fig. 42. Uncinus from seventeen-setiger larva.
Fig. 43. Winged bristle of abdominal parapodia from the same larva.
Figs. 44–45. Winged capillary bristles of first parapodia of the same larva.
Fig. 46. Winged bristle of third parapodium of the same larva.
Fig. 47 and 49. Spatulate bristles of the same.
Fig. 48. Crochet from the same larva.
Fig. 50. Crochet from thoracic region of ninteen setiger larva.
Fig. 51. Winged bristle from thoracic parapodia of the same.
Fig. 52. Winged bristle from abdominal parapodia of the same.
Fig. 53. Spatulate bristle from thoracic region of the same.
Fig. 54. Uncinus from abdominal region of the same.

Plate XXV

Development of *Spirorbis spirillum* Linné

Fig. 1. Early larva about twenty hours old. Lateral view. Actual length approx. 150μ.
Fig. 2. Ventral view of the same.
Fig. 3. Larva about two days old. Dorsal view. Actual length approx. 160μ.
Fig. 4. Still older larva than the last. Lateral view. Actual length approx. 180μ.
Fig. 5. Ventral view of the same.
Fig. 6. Larva about three days old. Dorsal view. Branchial buds three pairs of bristles are first appeared. Actual length approx. 200μ.

Fig. 7. Lateral view of the same larva.
Fig. 8. Ventral view of the same larva.
Fig. 9. Larva just before pelagic stage. Ventral view. Actual length approx. 240μ.
Fig. 10. Free-swimming larva about four days old. Actual length approx. 260μ.
Fig. 11. Dorsal view of the same.
Fig. 12. Fertilized eggs glued together in common sac of thin membrane. Each egg about 140μ in diameter.

Plate XXVI

Development of *Spirorbis spirillum* Linné

Fig. 13. A portion of parent tube cut open to show the cluster of eggs.
Fig. 14. Ventral view of the free-swimming larva about four days old. Actual length approx. 260μ.
Fig. 15. Still older larva than the one shown in Fig. 16. Anterior end of tube is bending.
Fig. 16. Recently metamorphosed larva within newly formed tube. Adhesive process of abdomen is well extended. Ventral view. Actual length approx. 320μ.
Fig. 17. Dorsal view of the same larva.
Fig. 18. A tube formed in early bottom stage.
Fig. 19. Fertilized eggs within operculum of *Spirorbis nipponicus*.

Plate XXVII

Development of *Spirorbis nipponicus* Okuda

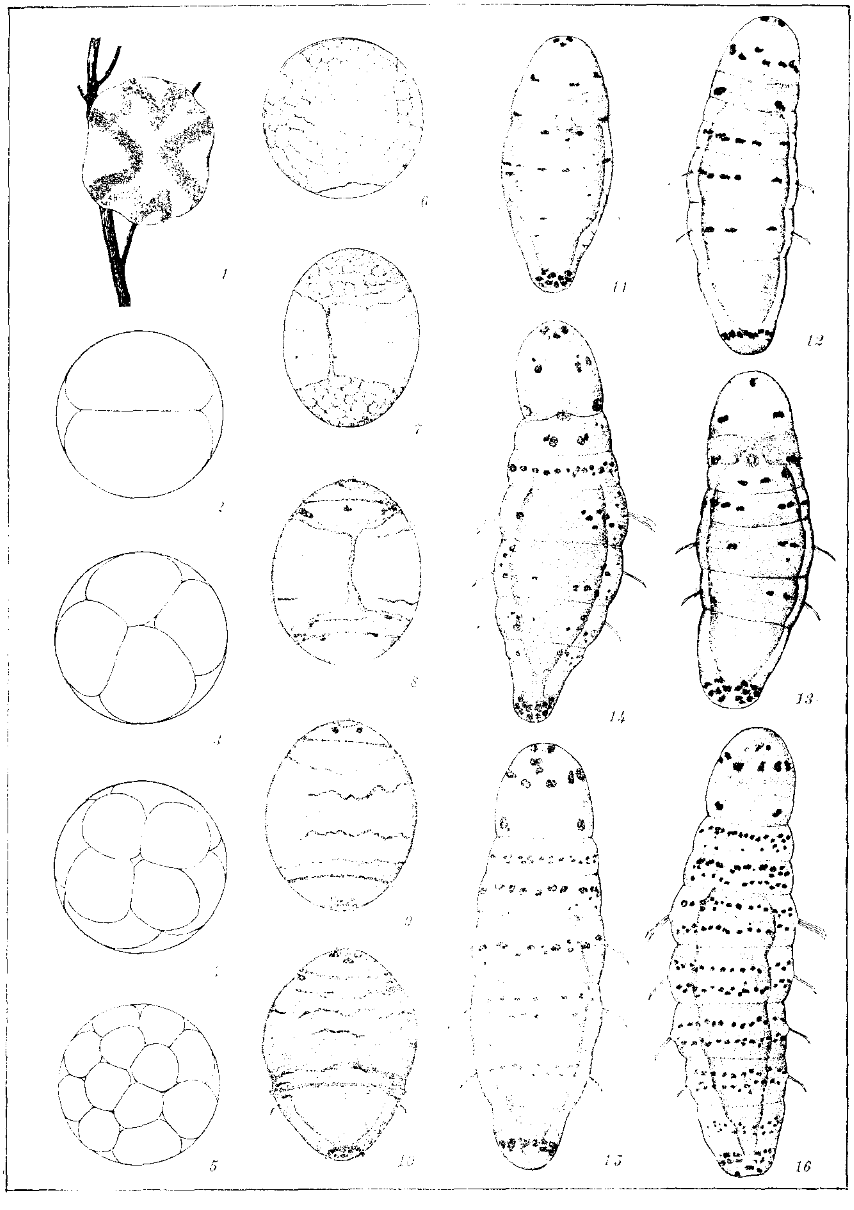
Fig. 1. Double formation of brood-pouch. Larvae within upper pouch are ready to release.
Fig. 2. Lateral view of the early larva about 24 hours old. Actual length approx. 160μ.
Fig. 3. Dorsal view of the same.
Fig. 4. Lateral view of the larva about two days old. Actual length approx. 180μ.
Fig. 5. Dorsal view of the same.
Fig. 6. Larva three days old. Dorsal view. Branchial and opercular rudiments are appearing.
Fig. 7. Lateral view of the same larva. First sign of segmentation is indicated.
Fig. 8. Ventral view of the same.
Fig. 9. Oldest larva just before hatching. Dorsal view. Actual length approx. 280μ.
Fig. 10. Uncinus with trifurcated end.

Fig. 11. Glated plate of operculum from the same young worm as shown in Fig. 20.
Fig. 12. Broken brood-pouch to show liberation of larvae as shown in Fig. 9.
Fig. 13. Brood-pouch newly formed beneath the older one.

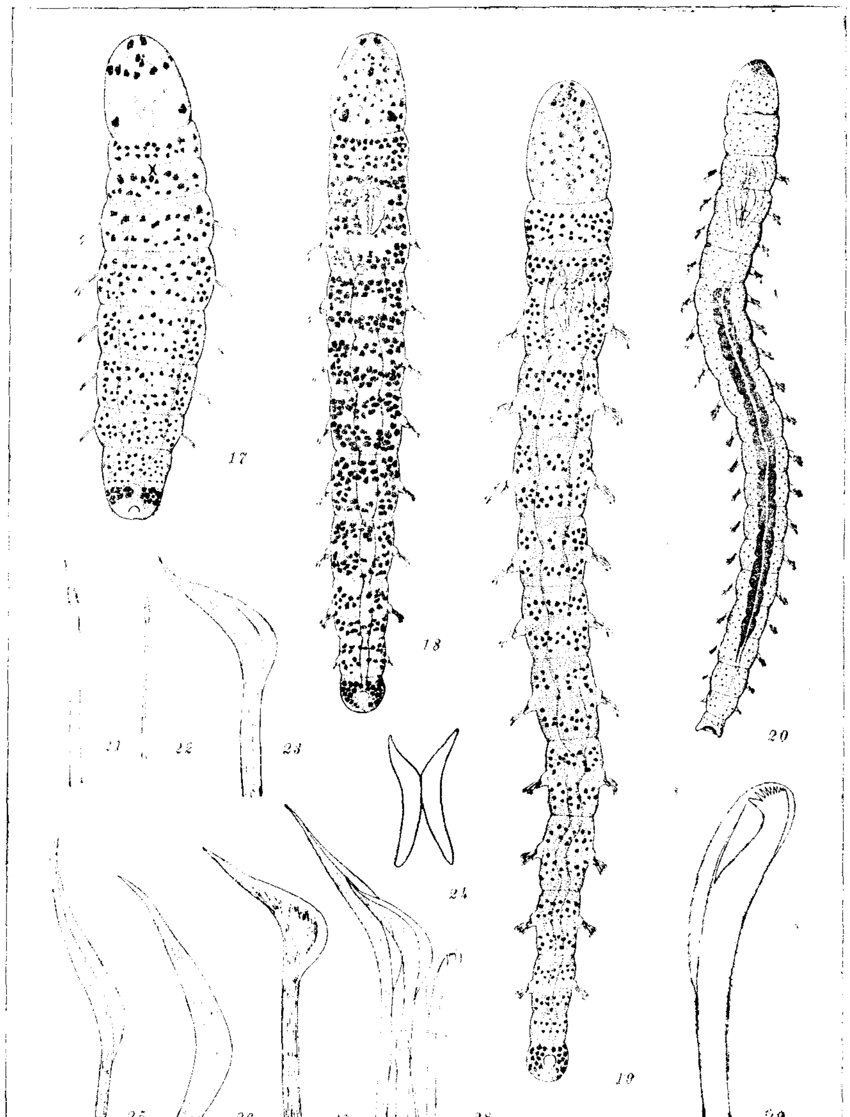
Plate XXVIII

Development of *Spirorbis nipponicus* Okuda

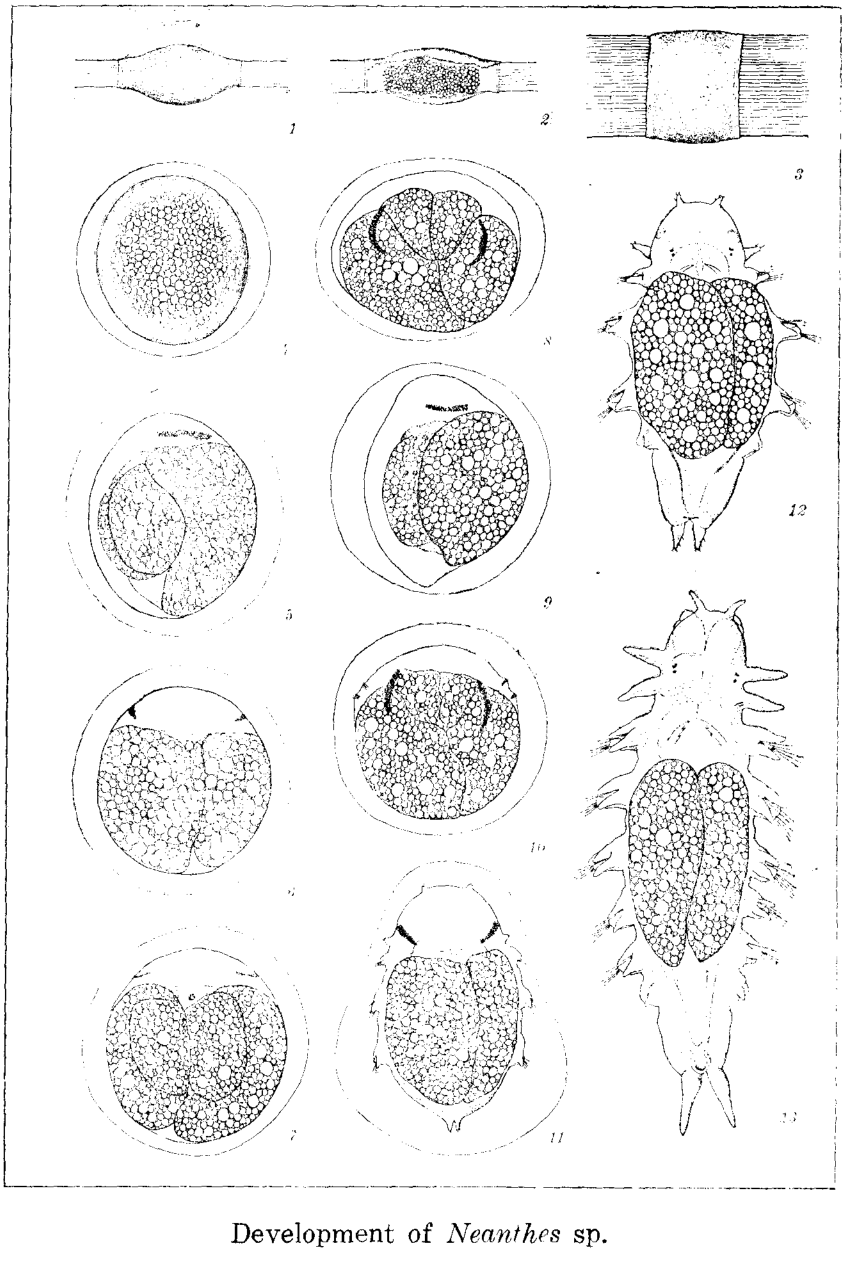
Fig. 14. Ventral view of the oldest larva just before hatching. Actual length approx. 280μ.
Fig. 15. Free-swimming larva about two hours after liberation. Ventral view. Actual length approx. 370μ.
Fig. 16. Dorsal view of the same larva.
Fig. 17. Metamorphosing young worm within transparent thin tube.
Fig. 18. Little older young worm than the last.
Fig. 19. Young worm taken from tube with branching branchiae.
Fig. 20. Young worm retracted into spiral tube.
Fig. 21. Tube spirally coiled upwards.



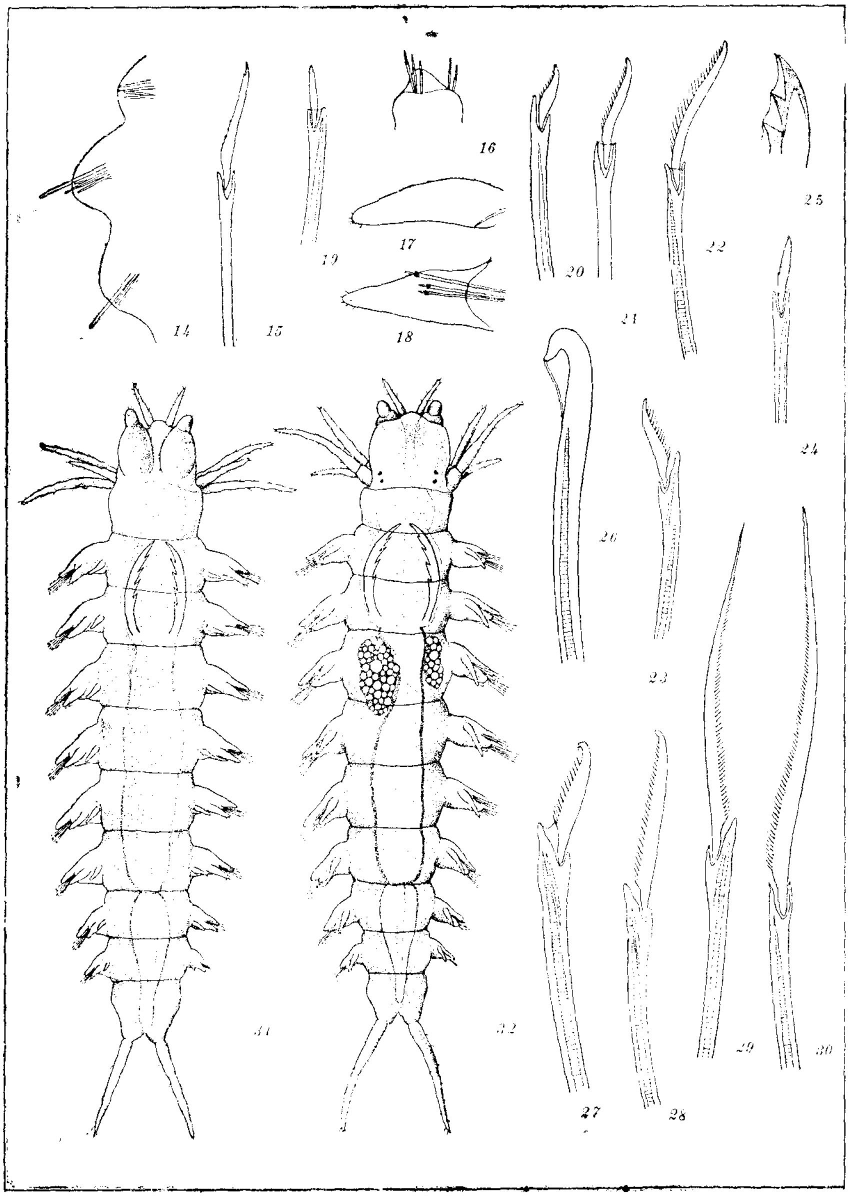
Development of *Lumbriconereis latreilli* Audouin et M. Edwards



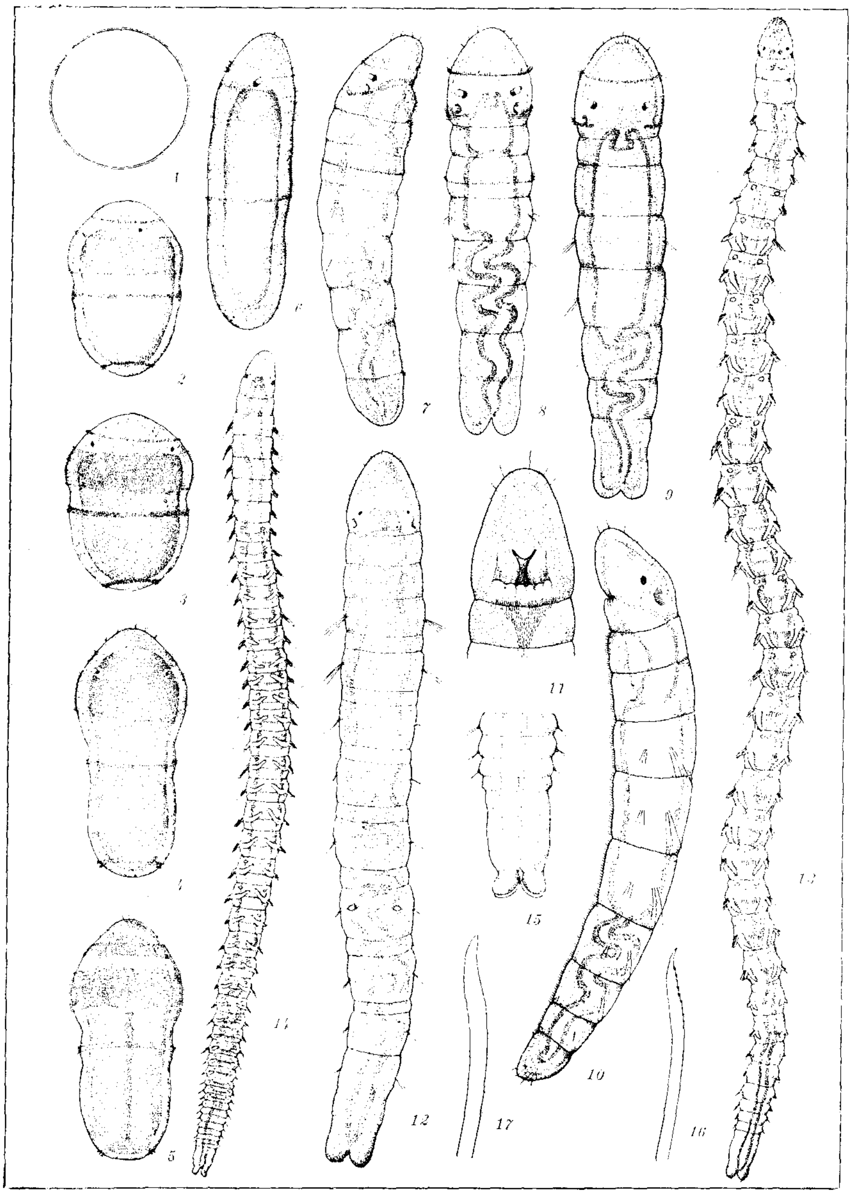
Development of *Lumbriconereis latreilli* Audouin et M. Edwards



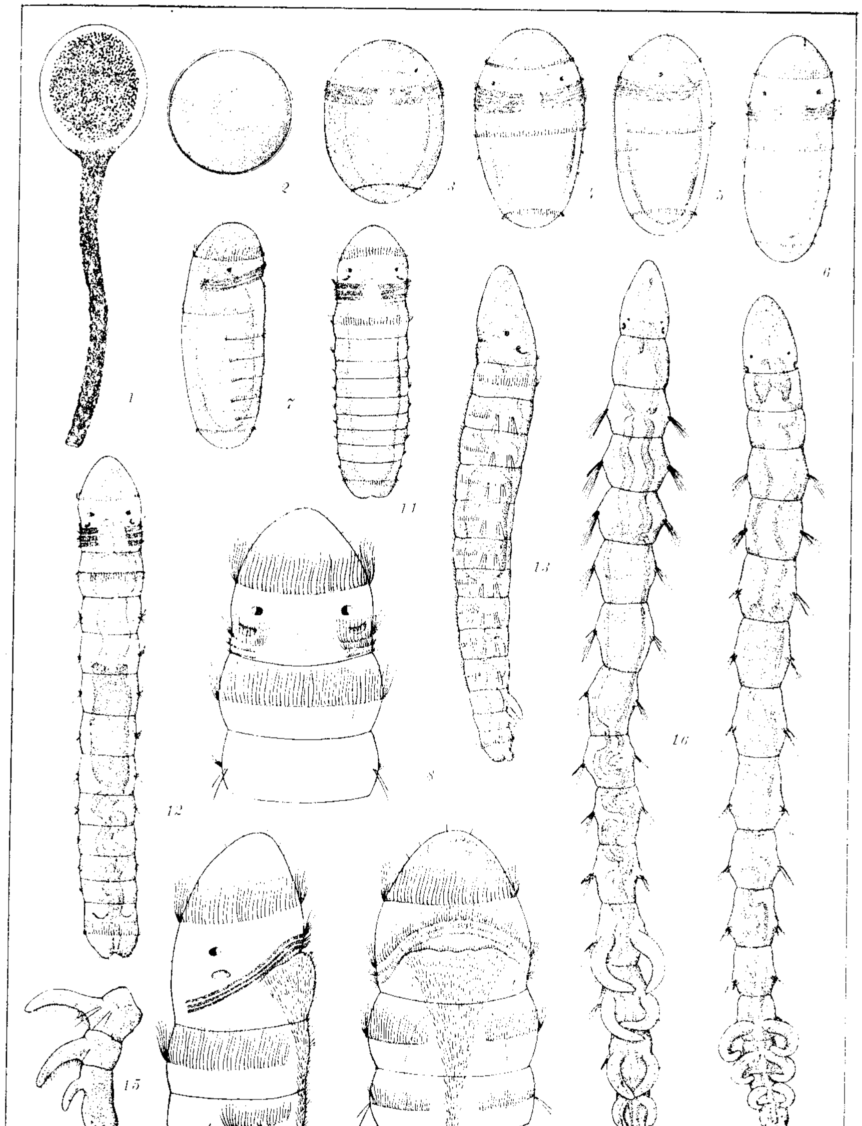
Development of *Neanthes* sp.



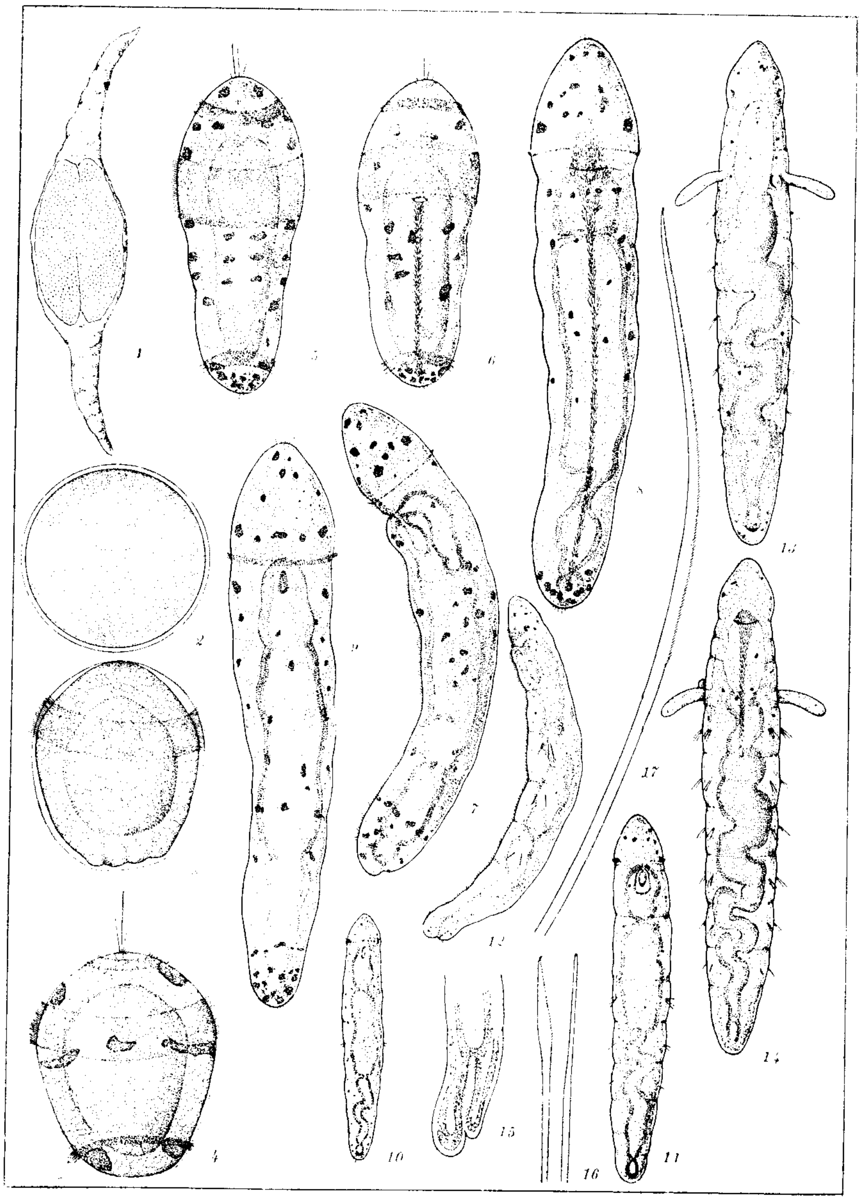
Young worms of *Neanthes* sp.



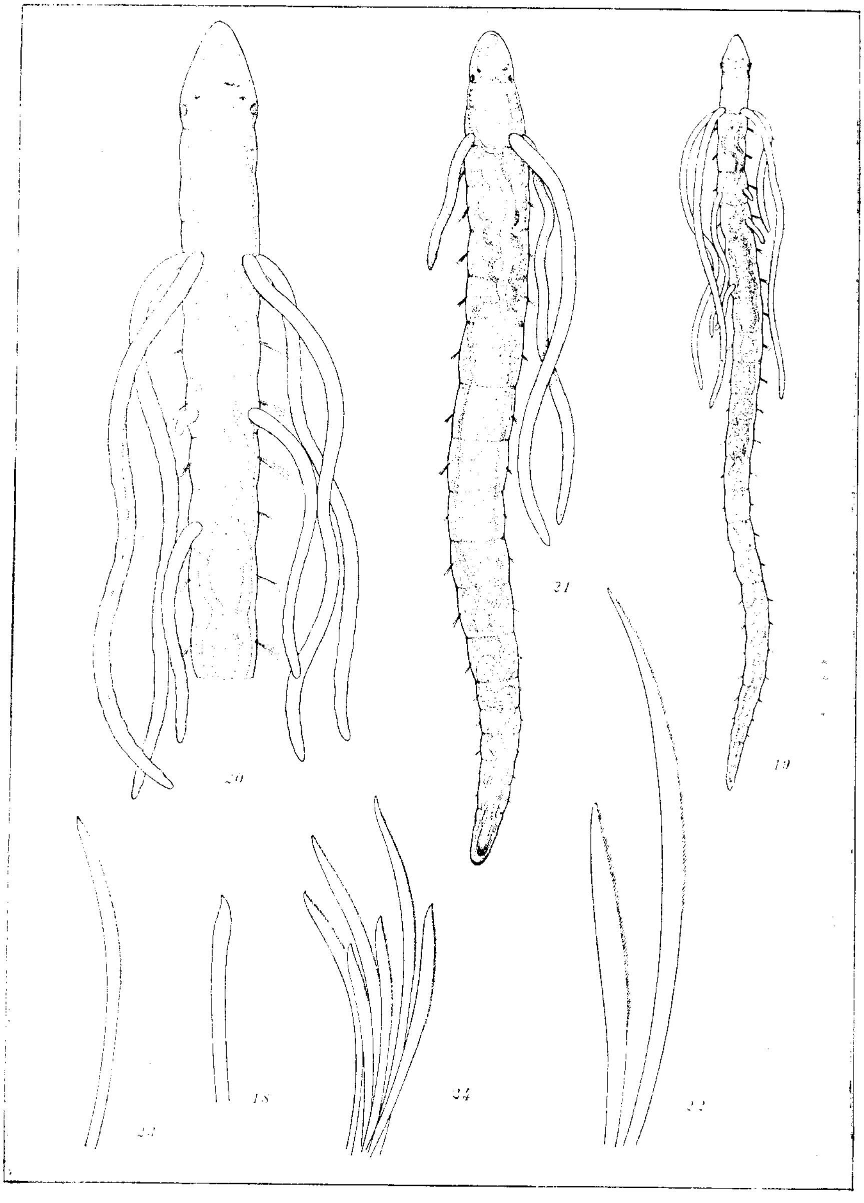
Development of *Nainereis laevigata* (Grube)



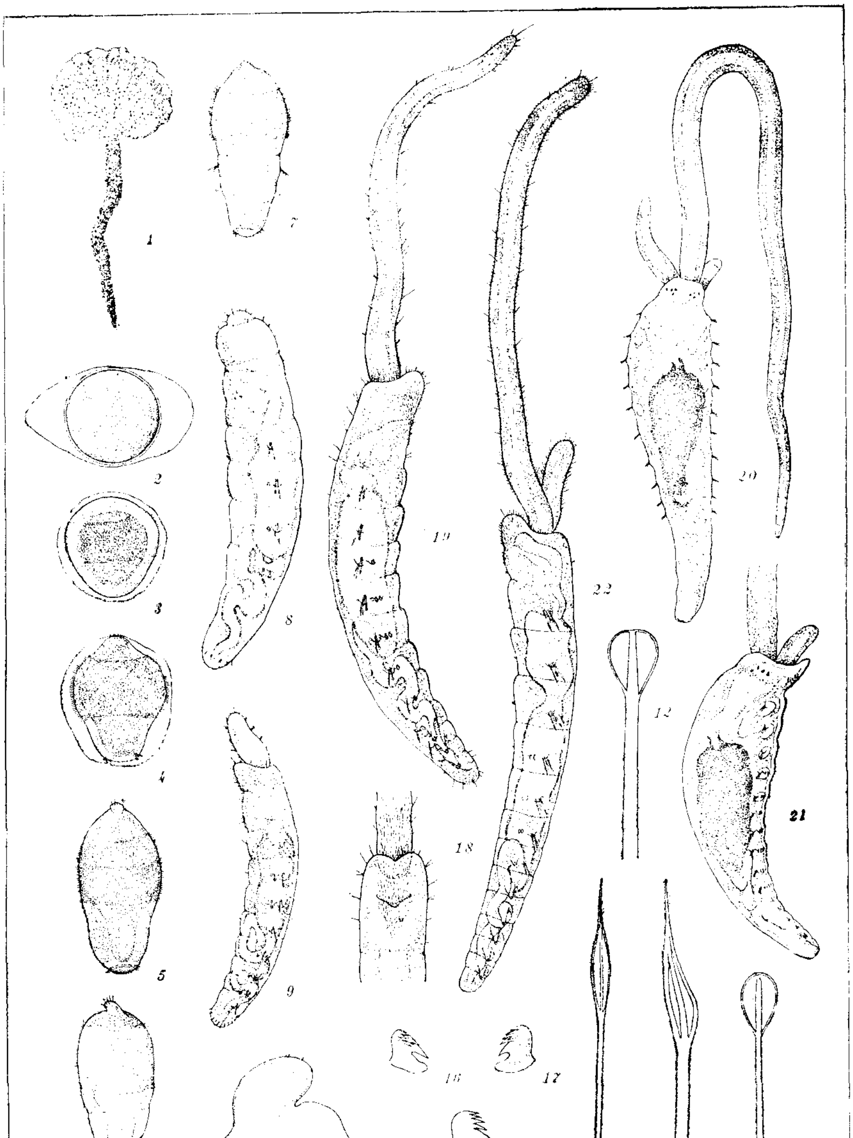
Development of *Haploscoloplos kerguelensis* (McIntosh)



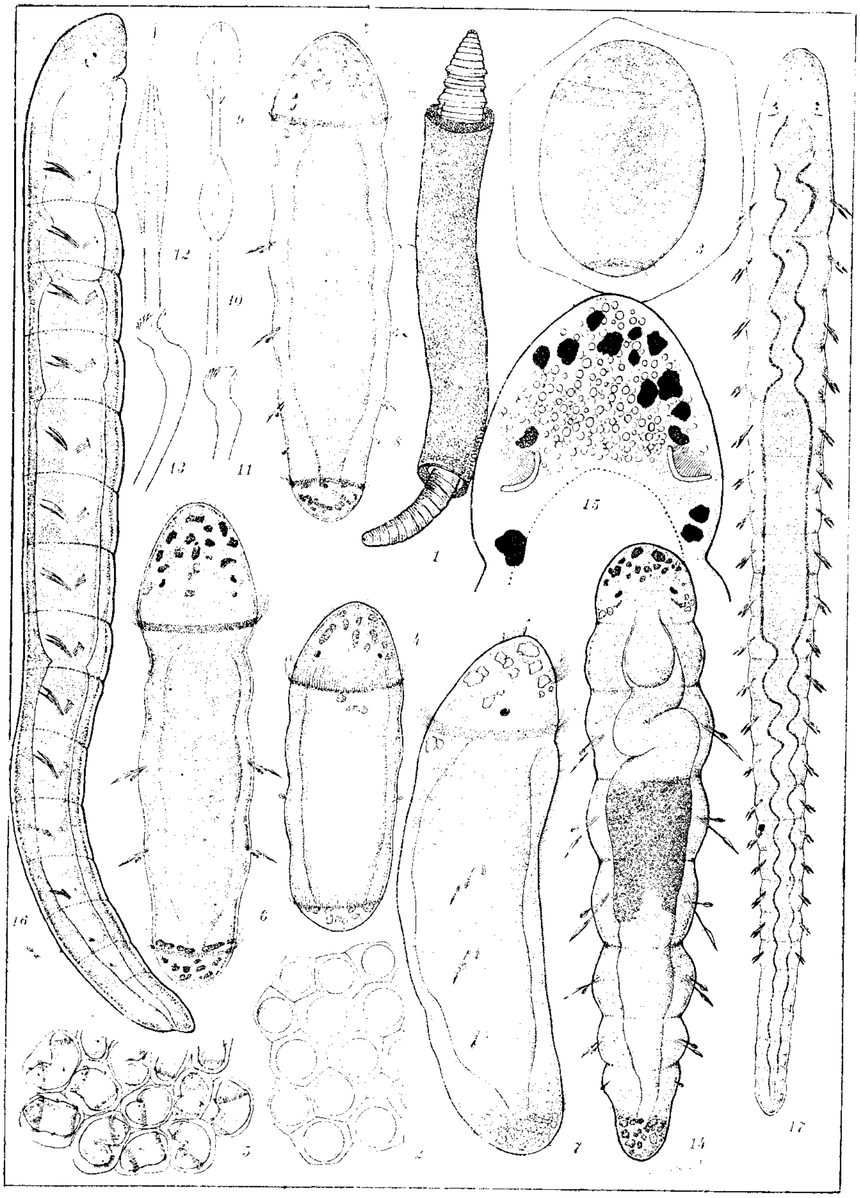
Development of *Cirratulus cirratus* (O. F. Müller)



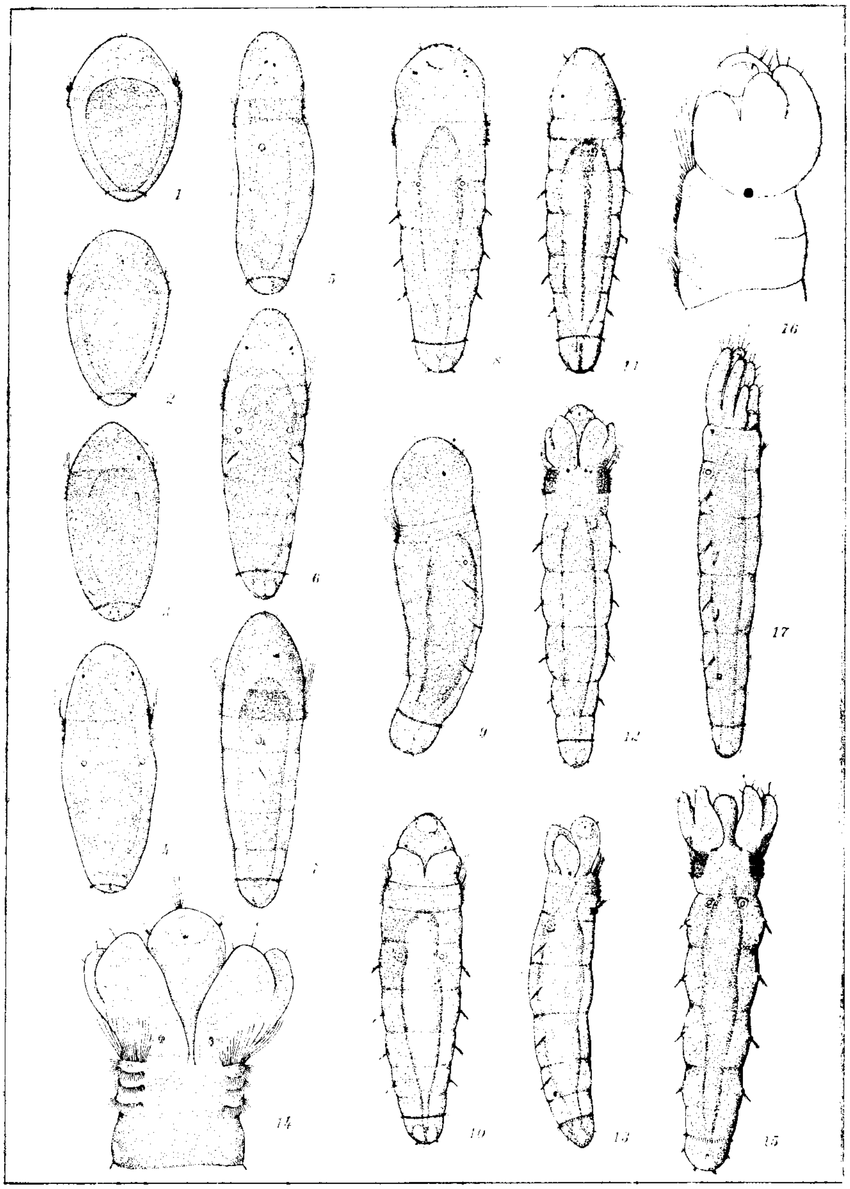
Development of *Cirratulus cirratus* (O. F. Müller)



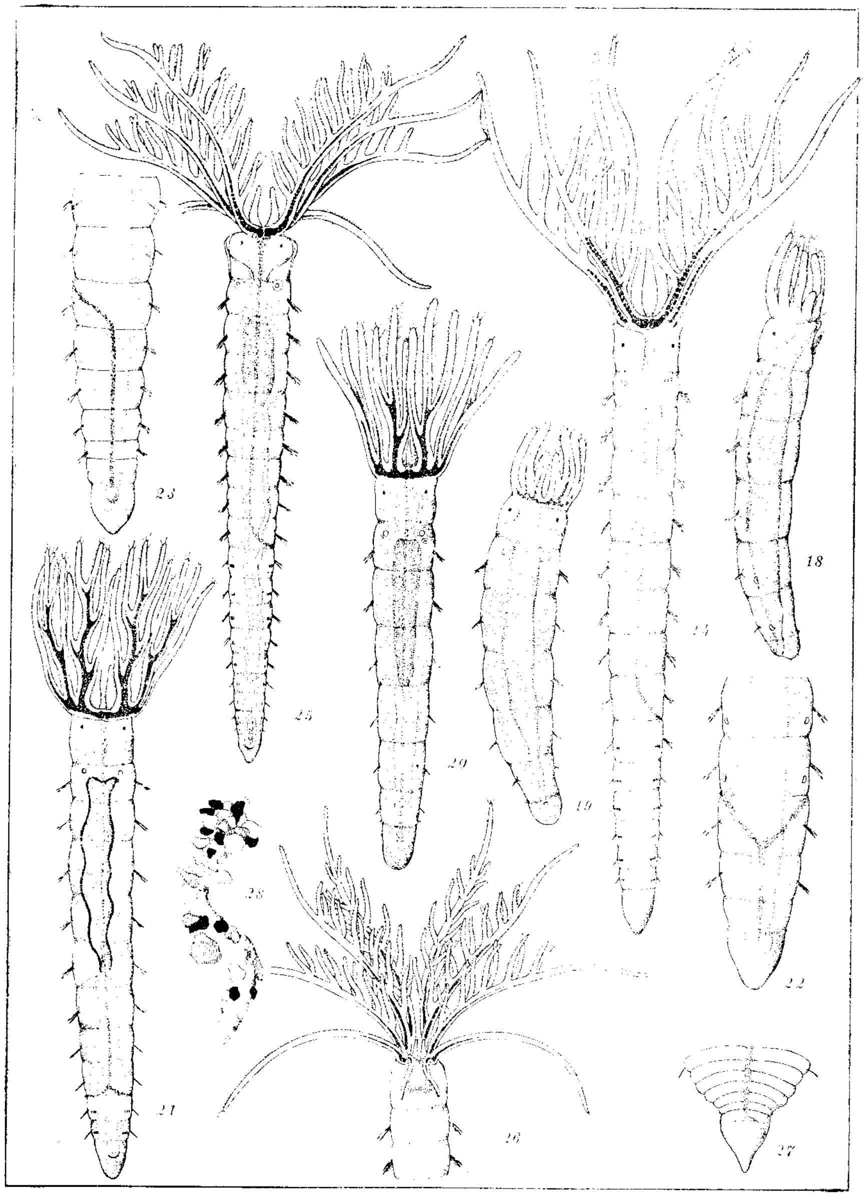
Development of *Lanassa nuda* (Moore)



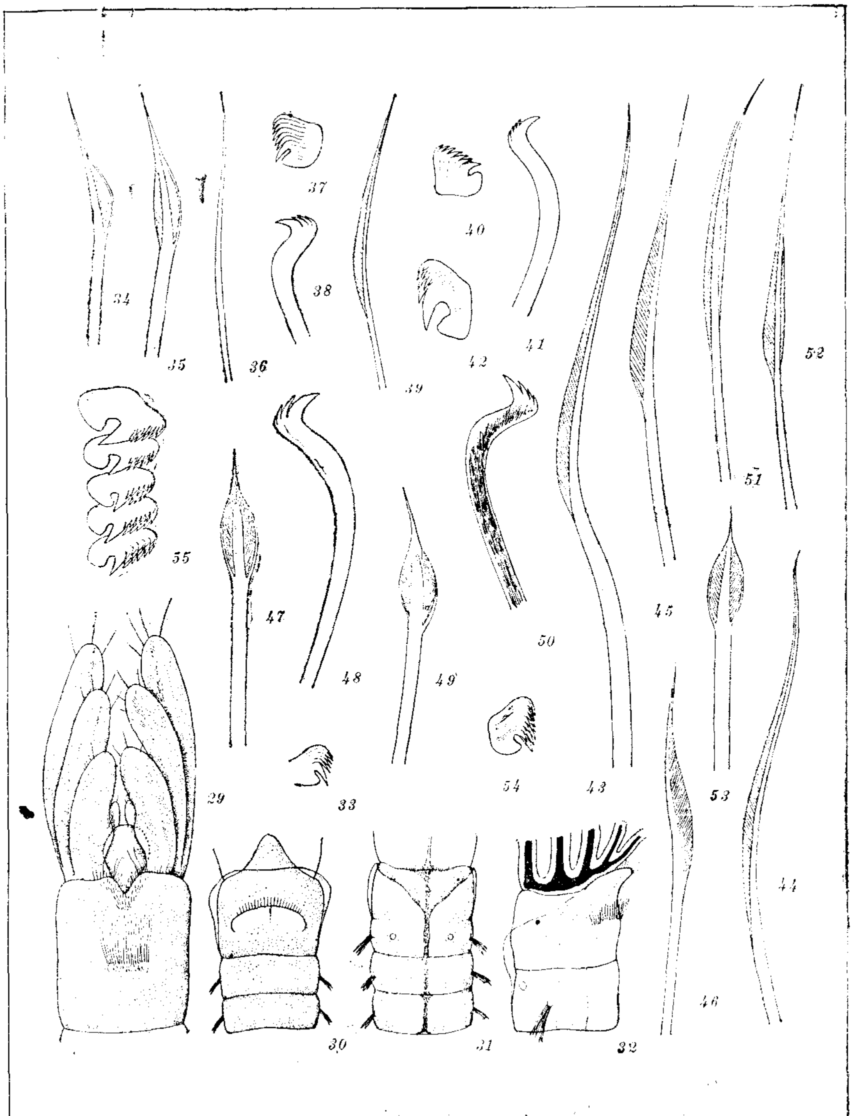
Development of *Arenicola claparedii* Levinsen



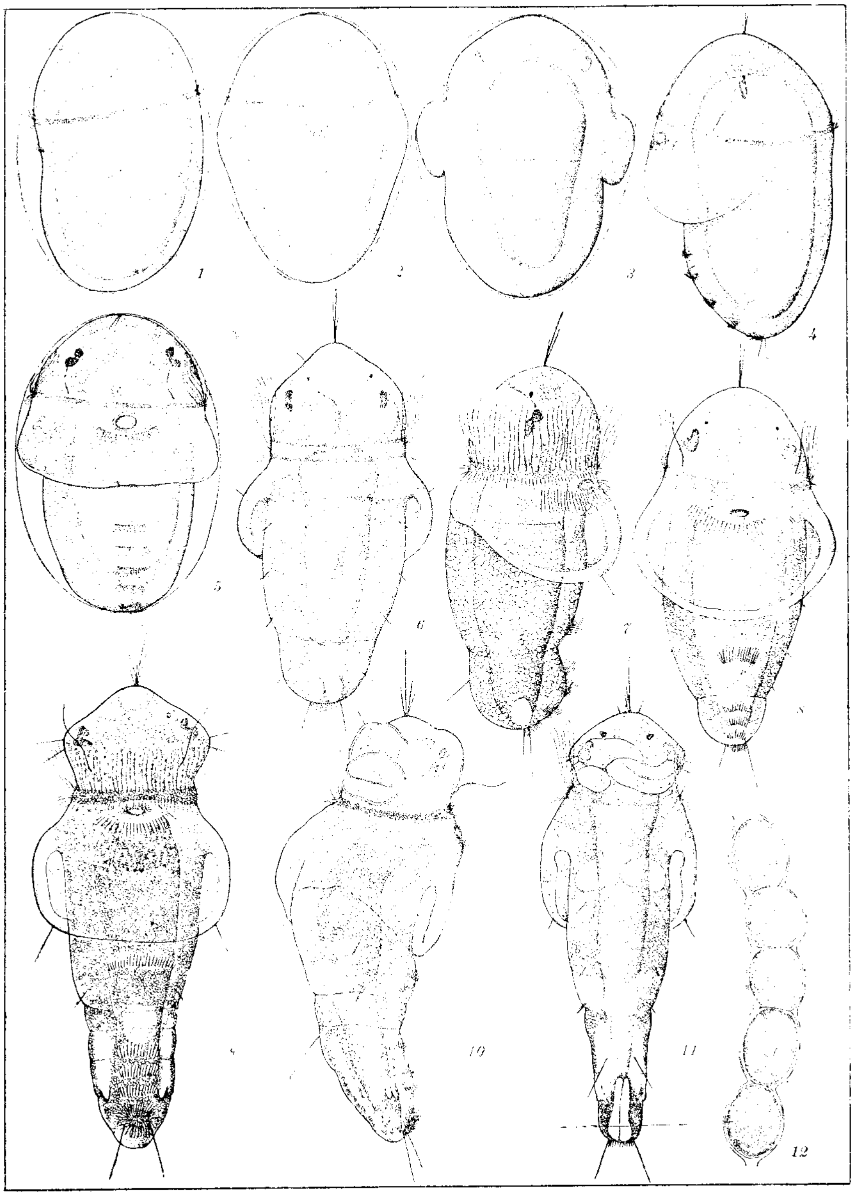
Development of *Chone teres* Bush



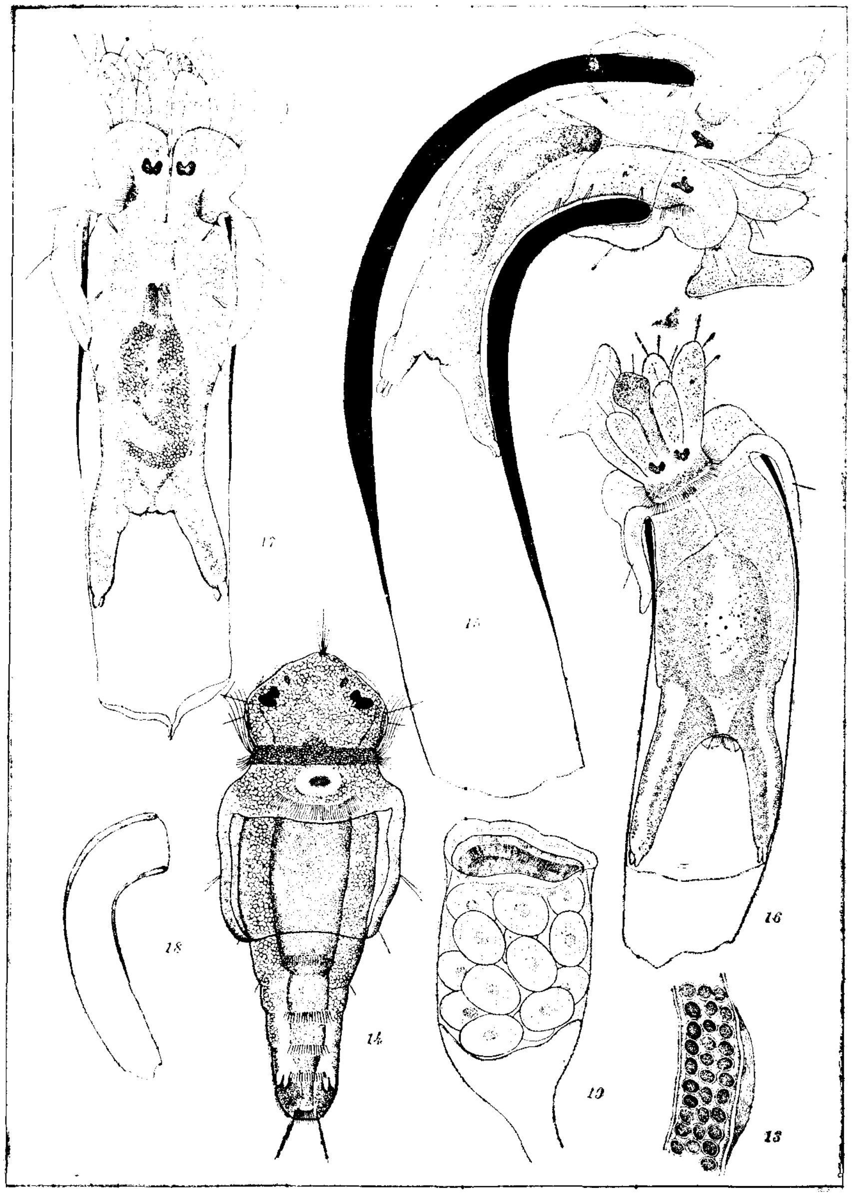
Development of *Chone teres* Bush



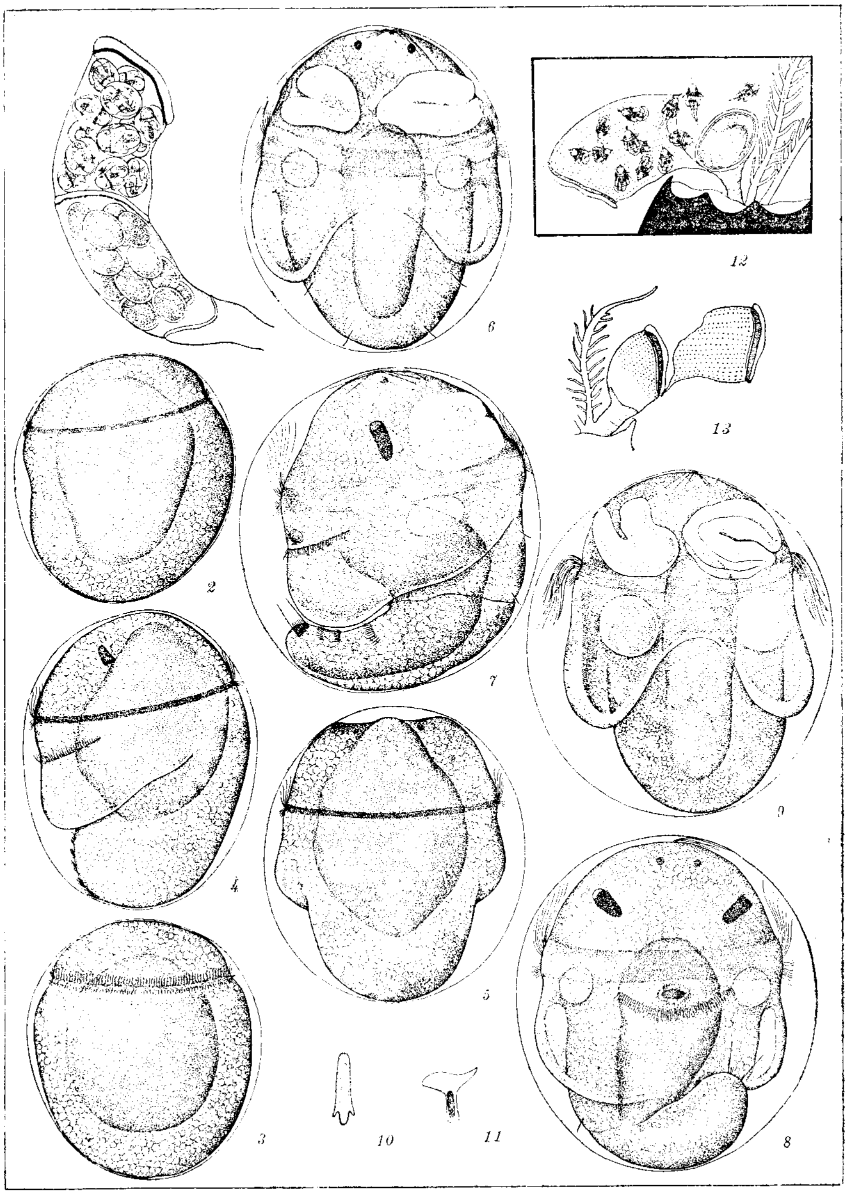
Bristles of *Chone teres* Bush



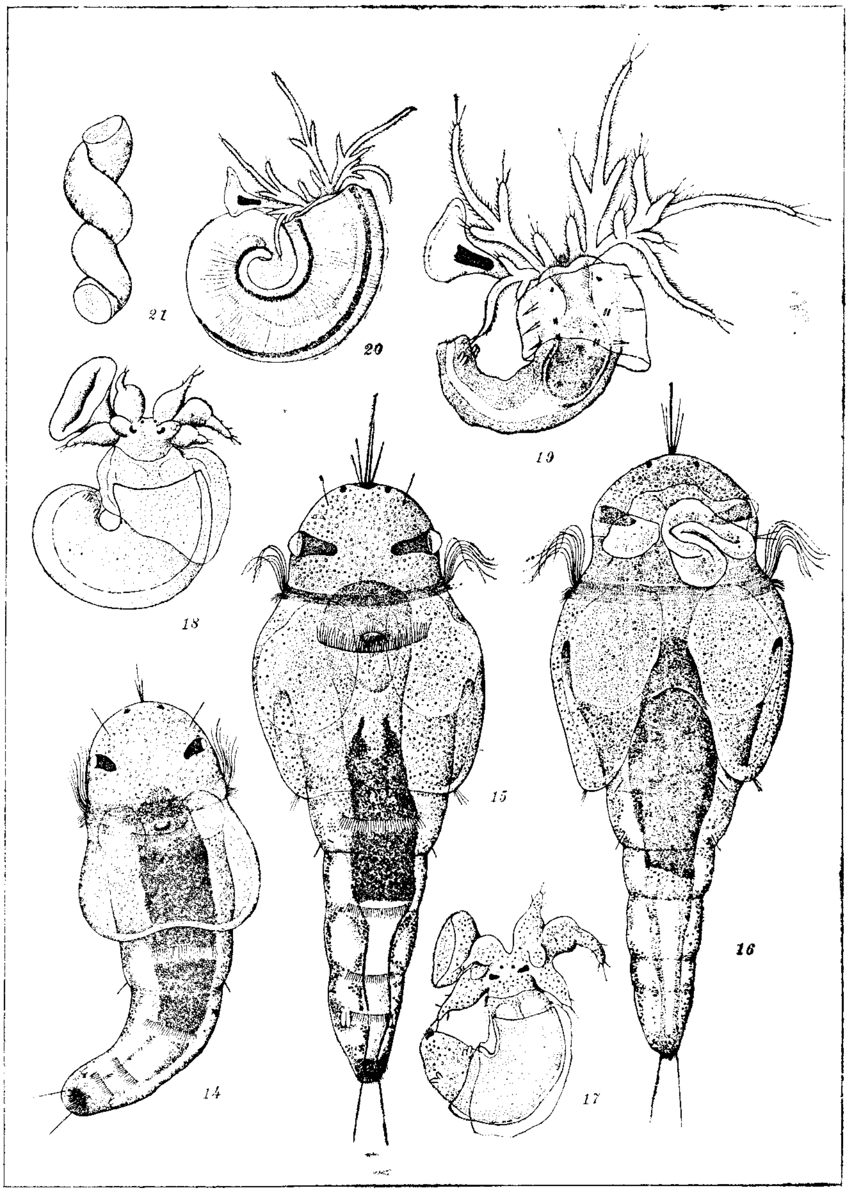
Development of *Spirorbis spirillum* Linné



Development of *Spirorbis spirillum* Linné



Development of *Spirorbis nipponicus* Okuda



Development of *Spirorbis nipponicus* Okuda