On an Ampharetid Worm, *Schistocomus sovjeticus* Annenkova, with some Notes on its Larval Development[1)]

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(*With two Textfigures*)

Colonies of *Schistocomus* are found in several places below the low-water mark to a considerable depth in the vicinity of the Akkeshi Marine Biological Laboratory. The animals live each in tough membranaceous tubes which are found together with a lot of tubes of *Potamilla myriops* on muddy ground with shells and pebbles. The tubes, of which the major portion lies embedded in mud, get narrowed as they pass deeper into soil. They vary in size, measuring 8–12 cm long, and are considerably longer than the worms lodged within. In the exposed portion of the tubes various extraneous objects such as fragments, small pieces of the calcareous algae and sandy particles are plastered to the surface.

We have hitherto nothing whatever about the development of Ampharetidae, so that a brief account of the reared larvae from eggs to the stage just prior to the metamorphosis was here given for the first time. Though the exact limits of the breeding season remain unknown, the majority of the worms collected during the summer months, July–August, were found carried the fully ripe eggs and spermatozoa within the body cavities. In nature the worms do not collect their eggs in gelatinous masses, which afford both food and protection to the developing larvae, but seemingly scatter the eggs in water.

The genus *Schistocomus* was first created in 1919 by Chamberlin,

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for an Ampharetid found at Laguna Beach, California, and named *S. hiltoni*. In 1932 Fauvel gave a full description of the same species collected at Madras coast, India. More recently Annenkova (1937) described a new species which belongs undoubtedly to the same genus from Peter the Great Bay, Sea of Japan, under the name *S. sovjeticus*. As described later the species reported by Annenkova is closely related to the Chamberlin's species, a main point which distinguish it being the structure of the neuropodium of the abdominal region. The genus *Schistocomus* was defined by Chamberlin as follows: "Like *Phyllocomus* in lacking tentacles and postbranchial spines, in bearing fifteen pairs of fasciae of capillary setae and four pairs of branchiae. It differs from that genus in having the branchiae of two types, one pair being of the ordinary, smooth, simple, subulate form and the other three with the edges divided, two pinnately, bearing two close series of lamellar branches, and one with an essentially single series of branches in the genotype". As was pointed by Chamberlin this genus is well characterized by the presence of the pectinate gills, recalling those of an Amphictenid worm, *Pectinaria*, and the entire absence of the paleae and the postbranchial hooks. Fauvel, in the diagnosis of *S. hiltoni* from India, stated that "the buccal tentacles are very likely lacking; both Chamberlin and I failed to find any". The buccal tentacles are easily retracted into the mouth, and in the preserved specimens none of them is generally exserted, though they are clearly recognizable in a living state as shown in Fig. 1, c. Such being the case, it seems quite probable that both Fauvel and Chamberlin have overlooked the presence of the buccal tentacles. In his description of *S. sovjeticus*, Annenkova made also no mentions as to the occurrence of the buccal tentacles. The genus *Schistocomus* approaches most nearly to *Amage* and *Phyllocomus* in the reduction of the head and its appendages such as paleae and postbranchial hooks. It shows also certain affinity with the Amphictenidae in the possession of the pectinated branchiae. In the following the full descriptions of the Japanese specimens were given.

The body is inflated and widest in front, tapering backwards to a slender caudal region. It measures 35–45 mm by 0.5–0.7 mm at the broadest portion. The number of segments varies from 61 to 70. The buccal tentacles are crowded and retractile. They are smooth

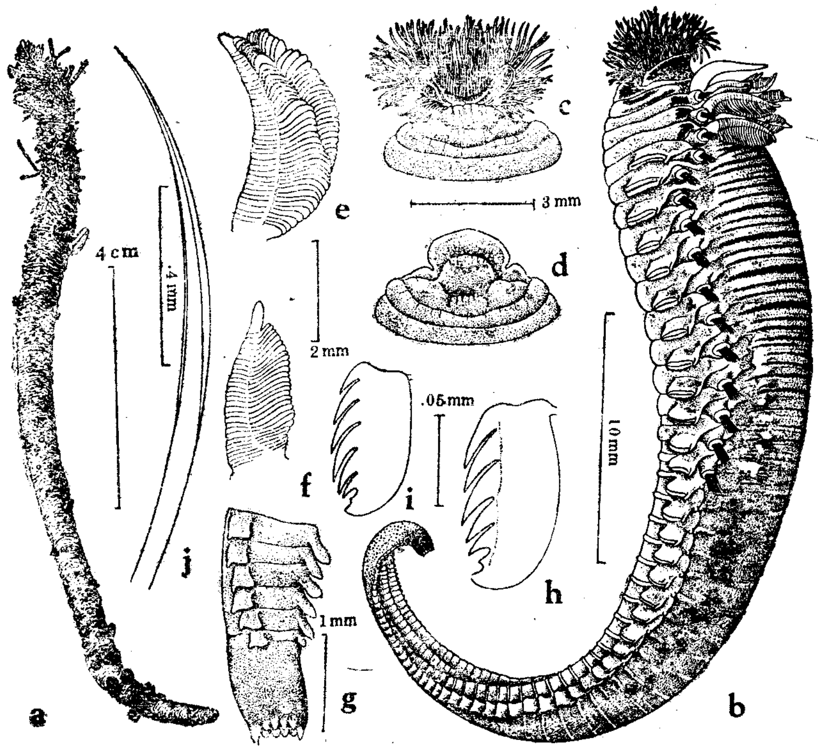

Fig. 1. *Schistocomus sovjeticus* Annenkova. a, Tube; b, Entire worm, side view; c, Ventral view of the anterior end to show the everted buccal tentacles; d, The same, the buccal tentacles being retracted into mouth; e, Gill with double rows of lamellae from the 4th segment; f, Gill with a single series of lamellae from the 3rd segment; g. Pygidium, ventral view; h, Uncinus from thorax; i, The same, from abdomen; j, Capillary winged seta.

and slender cirriform arising from the V-shaped tentacular membrane. The prostomium extends as a prominent upper lip above the mouth. The peristomium is feebly developed in the dorsum and it forms ventrally a lower triangular lobe with a convex anterior margin. No eyes were detected. The dorsal surface of the prostomium and peristomium is longitudinally wrinkled. The second segment is achaetous. There are 15 thoracic setigerous segments with dorsal winged capillary setae. The first notopod appears on the 3rd segment. The neuropod begins on the 6th segment (4th setigerous segment) and is continued to the end of the body. The paleae and the postbranchial hooks are entirely absent. There are four pairs of branchiae. The first two pairs are situated dorsally on the 3rd segment (1st setigerous segment), i.e. a pair of the outer subulate, smooth branchiae and two inner ones with a single series of the pectinate lamellae. The third pair is borne on the 4th segment just dorsal to the second notopod, while the last or the fourth pair on the 5th segment. The third and fourth branchiae are both provided with the double rows of triangular lamellae (Fig. 1, e & f). Excepting the fourth branchiae, which are distinctly separated from others, the remaining ones are fused at their basal portions to one another. The notopodium is well developed, cylindrical in shape, bearing a bundle of the winged capillary setae as generally shown in other Ampharetid worms. The neuropodium is square with straight truncate distal edge, but in going caudad it becomes reduced to a slight tubercle. Each one of the neuropods bears a blunt cirriform process at the upper dorsal corner in the thorax as well as in the abdominal region. There occur no marked changes in structure between the thoracic and abdominal neuropodia as Fauvel described in *S. hiltoni.* In *S. hiltoni* the neuropodial pinnules in the abdomen become more elongated than those of the thorax, and the processes at the dorsal corners also lengthen and become cirrus-like. A small round knob (a reduced notopodium?) arises at the dorsal base of each neuropodium in the abdominal region. The uncinus is a rhomboidal plate with 5 or 6 large bent teeth above the lower curved process which bears also a small spur (Fig. 1, h & i). The uncini in the abdominal portion are smaller than those of the thorax and bear generally 6 large teeth. The small conical nephridial papillae is situated at the base of the notopodium on the 6th and 7th segments. The pygidium is cylindrical rod-shaped body with a pair of the longer lateral cirri and 4–6 bluntly conical papillae on both dorsal and ventral sides (Fig. 1, g). In living state the body colour is light greenish yellow with reddish violet bands traversed across the anterior ten or twelve segments. The prostomium and the peristomium are also densely speckled with the violet pigments. In the middle and the posterior body excepting the pygidium a number of the small violet dotts are scattered on the dorsal body surface. The pygidium is deeply coloured with dark violet pigments as shown in the head. During the breeding season the female is chocolate brown and the male pale white in colour due to the containing sexual products.

Apart from Annenkova's statement that the ventral processes (neuropodium) begin at the fifth chaetigerous segment instead of the fourth, the Japanese specimens fit well with *S. sovjeticus* described by him from Peter the Great Bay. Annenkova treated only single incomplete specimen and it appears to me probable that his statement may be based on faulty observation. In *S. hiltoni* the first neuropodium appears also on the fourth chaetigerous segment. Neither Fauvel, Chamberlin nor Annenkova said anything about the nephridial papillae. The Japanese specimens have two pairs of small nephridial papillae on the 4th and 5th chaetigerous segments. *S. sovjeticus* is closely related to *S. hiltoni* recorded from warm waters. The only point to separate these two species rests on the structure of the abdominal neuropodia. In *S. hiltoni* the neuropodium of the abdominal region carries slender rather long dorsal cirrus and triangular blunt lobe above the pinnule.

Notes on the Development

There is no difficulty in separating the males and females carrying ripe sexual products, for the former are whitish with blue tint while the latter are russety on the dorsal surface. Although apparently ripe worms have been kept under sea-water circulation in the laboratory, non has ever induced to spawn naturally. The females were cut open, and the eggs shaken out into clean sea-water were successfully fertilized by simply adding the sperm, though it is necessary to rinse the eggs later to rid them of the superfluous spermatozoa. The larvae were reared in a plunger-jar filled with open sea-water which had been filtered through fine bolting silk.

The unfertilized egg obtained directly from the body cavity was irregular in outline and had a conspicuous germinal vesicle. After fertilization the egg becomes nearly spherical and about 150μ in diameter (Fig. 2, b). The general colour is russety by both transmitted and reflected light. The egg is enclosed in a thin membrane consisting of at least three layers. The membrane is separated from

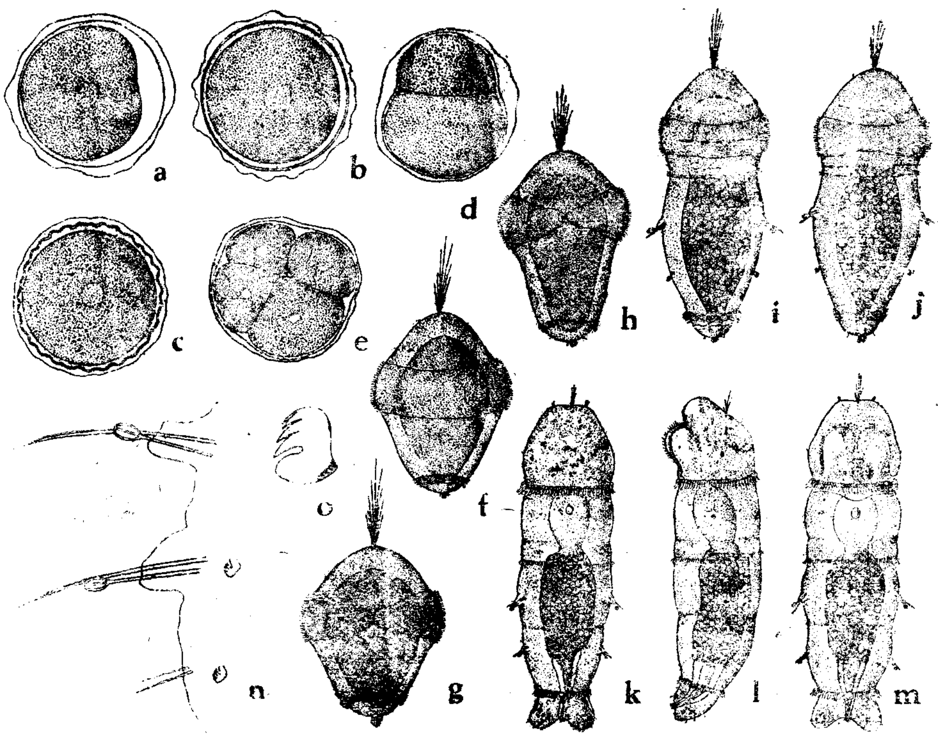

Fig. 2. Development of *Schistocomus sovjeticus* Annenkova. a, The egg just fertilized; b, The egg half an hour after fertilization; c, The same one hour after fertilization; d, The 2-cell stage; e, The 4-cell stage, viewd from animal pole; f, Dorsal view of larva 18 hours after fertilization; g, Ventral view of the same larva; h, Larva 24 hours after fertilization, viewed from ventral side; i, Dorsal view of larva 48 hours after fertilization; j, Ventral view of the same; k–m, Larvae about 70 hours old; k, dorsal view; l, lateral view and m, ventral view; n, Outline of paradodium of right side, viewed from ventral side, of a larva 4 days old; o, Uncinus.

the egg surface before the first cleavage. When half an hour after fertilization had elapsed, the outermost membrane lifted far off the surface while the inner one which presumably consisting of two layers is much wrinkled (Fig. 2, c). About two hours after the fertilization the first cleavage furrow is fully formed. The first furrow is meridional and runs all round the egg at about the same time. It divides the egg into two blastomeres of remarkably unequal size, A-B and C-D. In about thirty minutes these two cells are divided nearly simultaneously into four cells, though the larger (C-D) is formed sometimes a little in advance (Fig. 2, e). The direction of cleavage is left oblique. The cell D of 4-cell stage is considerably larger than the other cells. All four cells undergo an almost synchronous right oblique cleavage, and an 8-cell stage results. The first trochophore becomes active and begins to swim less than eighteen hours after fertilization (Fig. 2, f & g). It is about 170μ long, roughly top-shaped and more or less flattened dorsoventrally. The colour is brown with a darker area where the gut is foreshadowed by the presence of yolk granules. The prototroch is a broad band of short cilia, arranged in a single row. It is almost a complete ring, but a slight ventral gap is present on the mid-ventral line where the broad ciliary band shifts upwards leaving a triangular space. An apical tuft of long and short fine cilia, often twisted together and directed forwards, arises at the anterior end. The stomodaeal invagination is visible as a depressed area just posterior to the prototroch on the mid-ventral line. The telotroch is a band of cilia and forms a complete ring dorsoventrally. There are a few sensory cilia at the posterior end. The larvae are positively phototropic and swim across a dish towards a source of light in an almost straight line. They swim frequently rotating clockwise on their longitudinal axes. Sometimes they swim in circles about one place. As the trochophore develops the body increases in length, and as the yolk in the gut is absorbed the lumen of that organ as well as the ectodermal invagination of the stomodaeum become more evident. Both the apical and the prototrochal cilia decrease in length gradually.

In about two days after fertilization the body is indistinctly segmented and two pairs of the notopodial bristle bundles are formed (Fig. 2, i & j). The first bundle, projecting from the conical ectodermal outgrowth, contains two bristles, one longer, winged capillary and the other spatulate having a round head. The second bristle bundle bears a single spatulate seta exclusively. No uncini are still formed. The body measures about 250μ long and 85μ wide at the broadest portion. The head is bluntly conical. The prototroch becomes narrow and the ventral gap as shown in the foregoing stage is indistinguishable. A narrow metatroch of short cilia, about 5μ in length, appears immediately behind the prototroch. It encircles the body completely. A pair of eye-spots composed of small reddish brown pigment is now well marked out. Each eye-spot is situated laterally just anterior to the prototroch. An apical tuft is still well extended, but becomes gradually short. An irregular row of the yellow refringent ectodermal globules is present on the anterior and posterior portions of the prototroch. Similar globules are also scattered on the prototroch and the pygidium. A rudiment of the floor of the buccal tentacles may be indicated as a faintly elevated outgrowth just anterior to the prototroch. From the mid-ventral portion of the telotroch a narrow band of fine short cilia leads backwards to the posterior extremity. There are two or three very fine sensory cilia near the anus.

The larva at 70 hours after fertilization is about 260μ long (Fig. 2, k-m). The head is oval with a more or less depressed terminal end. The long apical cilia are fewer in number and are probably falling. The prototroch remains only as a very narrow band of fine short cilia. A pair of the club-shaped processes, a thickening of the floor of the buccal tentacles, appears distinctly on the ventral portion anterior to the prototroch. An unpaired small swelling at the base of these protuberances is probably a rudiment of the buccal organ. All these foldings are finely ciliated along their outer margins. The body posterior to the prototroch is now distinctly segmented into three regions. The first segment is achaetous and the second one carries a metatroch of narrow ciliary band and a first pair of the notopodium. A pair of the neuropodium first appears on the third segment. Each neuropod bears a single pectinate uncinus with three teeth above a main fang. The dorsal seta sacs of the second and third segments are cylindrical, each carrying one winged capillary seta and a spatulate one. The occurrence of the provisional spatulate seta is characteristic of the early stages of development. The mouth has a cleft appearance and leads into the pharynx. The yolk cells still fill up the most of the intestinal portion. The larva continues to elongate and the segmentation becomes more distinct. In the larva 4 days old, about 280μ in length, the third chaetigerous segment is newly added. The uncini are present in all but the first segment. The disappearance of the prototroch is gradual and apparently takes place in stages. The metatroch and neurotroch still persist, though much narrowed. With the growth of the larva the food yolk is gradually used up and the gut becomes transparent. The larvae are now ready to metamorphose and they can crawl actively on the bottom of the plunger-jar. The more advanced larvae did not survive much longer and no later stages were obtained.

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