THE ECONOMIC RELATIONS, ANATOMY, AND LIFE HISTORY OF THE GENUS LERNAEA

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Contribution from the United States Fisheries Biological Station, Fairport, Iowa

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INTRODUCTORY.

During the summer of 1914 while working at the Bureau of Fisheries station at Fairport, Iowa, many new species of copepods parasitic upon fresh-water fish were obtained, and interesting bionomic relations between these parasites and mussel glochidia were discovered. The results of these investigations have already been published.[a]

Among the new species was one belonging to the genus *Lernæa*, which proved to be of exceptional interest, since larvæ were found in various stages of development. But not enough were obtained to give anything like a complete life history, and consequently this was left until the following summer, 1915. At that time additional larval stages were found and the entire development was carried up to the adult form.

Two new species were discovered and those already described were carefully reviewed, so that the entire genus might be placed upon a sound and substantial basis. Specimens of the adults of various species were sectioned and the entire internal anatomy was reconsidered, together with the oogenesis, in the light of the series thus obtained. And it is vastly to the credit of those old observers that all the wonderful advance in technique since their day has only been able to supplement, and not to supplant, their painstaking work. The larvæ were also sectioned and their anatomy was fully worked out.

Material was thus provided for both the external and internal morphology of the larva as well as the adult, for much of the histology, and for the entire life history, all of which have been incorporated in the present paper.

This work, especially the life history, is one of the most important factors in determining the systematic position of the genus, which ought now to be fairly well established.

With the two new species here presented the number now recognized in the genus reaches 17, more than half of which are American.

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[a] Bulletin, Bureau of Fisheries, vol. 34, 1914, p. 331–374, pl. 60–74.

HISTORICAL.

The genus *Lernæa* was founded by Linnæus in 1758, in the tenth edition of his "Systema Naturæ," with the three species, *cyprinacea*, *asellina*, and *salmonea* (p. 655).

The species *asellina*, a salt-water form, has since become the type of the genus *Medesicaste*, while the species *salmonea*, a fresh-water form, is the type of the genus *Salmincola*. The species *cyprinacea*, another fresh-water form, thus becomes the type of the original genus by elimination as well as by priority.

In 1822 [a] Blainville founded his new genus *Lernæocera*, and gave as his first or type species *branchialis*, which had been included by Linnæus in his genus *Lernæa* in the twelfth edition of the "Systema Naturæ." Blainville also included in his new genus a second species, *cyclopterina*, which later became the type of the genus *Hæmobaphes*. His third species was new to science and he named it *surriraiis* for Dr. Surriray of Havre, who sent him a specimen. But his description gave the egg strings as uniseriate, which would exclude it from the genus, and in all probability it was identical with *Lernæenicus sprattæ*. Of course Blainville had no right to add, as his fourth and last species, *cyprinacea*, the type of Linnæus' genus *Lernæa*.

We thus have the genus *Lernæa* established by Linnæus in 1758, with *cyprinacea* as a type and including the species *branchialis* (1767), and the genus *Lernæocera* established by Blainville in 1822, with *branchialis* as a type and including the species *cyprinacea*.

Curiously enough, in endeavoring to straighten this muddle, subsequent authors have reversed the genera, and *branchialis* has come to be accepted as the type of the genus *Lernæa*, while *cyprinacea* was formally declared to be the type of *Lernæocera* by Cunnington in 1914. [b]

But *Lernæa* is the oldest genus amongst the parasitic copepods, and its ancient prestige must be restored by giving it again its original type species and making it a fresh-water instead of a salt-water genus.

In 1832 [c] Nordmann published a more complete description of *L. cyprinacea*, but failed as Blainville had done to find the swimming legs.

His paper was of great value, however, because it contained the description and figures of a newly hatched nauplius larva, the first and the best that have ever been published.

In 1833 [d] Burmeister presented a second description of *L. cyprinacea*, illustrated by good figures; he also showed that the species described by Nordmann was not *cyprinacea* at all, but a species new to science, which he named *esocina* from its host. But he regarded the two pairs of antennæ as the anterior and posterior rami of a single appendage, and he added one more to the list of those who had failed to find the swimming legs. The swimming legs were first discovered by Brühl in 1860 on a species which he named *Lernæocera gasterostei*, but which was evidently the same as the one described by Nordmann, viz, *esocina*.

In the following year Claus confirmed Brühl's discovery upon two specimens sent him by Prof. Leuckart and called by the latter *Lernæa gobina*, but which Claus after examination believed to be identical with Brühl's species. In addition he corrected a mistake common to all previous investigators, by whom the two pairs of antennæ had been transposed, the anterior pair having been called posterior and the posterior pair

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[a] Jour. Physique, vol. 95, p. 372–380, 437–447.

[b] Proc. Zool. Soc. London, 1914, p. 819–829.

[c] Mikrogr. Beiträge, pt. 2, p. 123.

[d] Acta Acad. Caes. Leop. Carol. Nat. Cur., vol. 17, p. 309.

anterior. Again, in 1867,[a] he published a description of *Lernæocera esocina*, in which he mentioned both *gobina* and *gasterostei* as distinct species, and added many details of external and internal structure. In 1863 Krøyer added three new species, *catostomi*, *pomotidis*, and *phoxinacea*, to the genus, the first two of which were from the Mississippi River. In 1865 Heller added another species, *lagenula*, obtained during the voyage of the *Novara*.

In 1870[b] Hartmann published the description of a species which he named *barnimii*, together with excellent figures which included the eggs and the development up to the metanauplius stage. This is by far the best paper upon any species of the genus, and it included as much of the internal structure as could be made out without sectioning.

Meanwhile here in the United States Le Sueur had established in 1824[c] the first American species, *cruciata*, upon material obtained in Lake Erie. After a long interval he was followed by Kellicott with two other American species, one, *tortua*, from New York State in 1881,[d] and the other, *pectoralis*, from Michigan in 1882.[e]

With these 10 species the genus remained until 1914,[f] when Cunnington published a short paper including a "List of described species" and three from the Tanganyika region in Africa that were new to science.

In spite of its brevity and omissions this paper proved to be of considerable value because it summed up all the described species and presented a key for their identification. Among other things, with reference to the genus, Cunnington stated, "A careful study of these forms has given me the impression that two or three of them may merit separation as distinct genera" (p. 822), but he wisely concluded not to do this at present. On the next page he said: "The appendages appear to show comparatively minor differences within the limits of this genus, and have not been appealed to for the purpose of establishing new species."

The appendages certainly are remarkably similar in all the species examined by the author, but this very fact precludes the establishment of new genera, for which there must be characteristic differences in the appendages as well as in body form.

Cunnington mentioned Krøyer's *catostomi* and *pomotidis*, Heller's *lagenula*, and his own *diceracephala* as possible candidates for the prospective new genera.

The first three are shown to be good Lernæans in this paper. With reference to Cunnington's species the chief distinctive feature mentioned is "the existence of only two cephalic horns—apparently the dorsal pair—instead of four." But it may be noted that the ventral pair in another of his species, *temnocephala*, are hardly large enough to be called horns rather than spines, the ventral pair in *variabilis* and *tenuis* are also often very minute, and in *anomala* they have entirely disappeared.

These species certainly belong to the present genus in spite of considerable variation in the number and structure of the horns, and the same is probably true of *diceracephala*. Unless in addition to the lack of ventral horns or the presence of a dorsal horn there were also well-marked differences in the appendages, it would be manifestly inadvisable to establish any new genus.

ECOLOGY.

The parasites belonging to this genus are immovably anchored in the tissues of the host's body. Consequently we should expect to find, as in the Lernæopodidæ, consid-

[a] Sitzungsb. Gesellsch. Beförd. ges. Naturw. Marburg, p. 5–12.
[b] Arch. Anat. Physiol., p. 726–752.
[c] Jour. Acad. Nat. Sci. Phila., vol. 3, p. 286.
[d] Proc. Amer. Soc. Micros., vol. 2, p. 41.
[e] Loc. cit., vol. 4, p. 75.
[f] Proc. Zool. Soc. London, 1914, p. 819–829.

erable sexual dimorphism, a loss of the powers of locomotion, and modified means of prehension. But the peculiar life history greatly modifies these characters and even does away with some of them.

Sexual dimorphism.—Since the females attain a length in some species of more than 20 mm. we would naturally look for a much smaller male, with marked differences between the sexes. But a study of the development convinces us that there is no sexual dimorphism for the following reasons: There is no disparity in size up to the close of the copepodid stages, at which time both sexes become mature and their union takes place. After this union the male either dies at once or becomes a free swimmer for a short time and then dies. And while the female subsequently seeks out a final host and undergoes upon it marvelous changes in size and form, we can not in fairness compare her altered proportions with those of the male before his death, and hence there is no real dimorphism.

Locomotion.—The adults are incapable of locomotion, but the nauplius, metanauplius, and copepodid larvæ are exceedingly active and move about constantly and vigorously. When placed in a watch crystal of water the copepodid larvæ swim around in search of something to which they can cling.

If there is a fragment of a gill filament present they all congregate upon it and remain there. Every now and then they leave in search of a better location, but finding none return to the filament.

If there is nothing present to which they can fasten they swim about until tired, then come to rest upon their backs on the bottom of the watch glass, and may remain there an hour or more. They can be kept alive in this way for several days. When swimming or when moving about over the gills the motion of the larva is jerky and spasmodic. They swim with the back downward, darting for a short distance in almost any direction, sometimes in a straight line, sometimes in a wide curve, stopping wherever it happens, usually in a horizontal position, and then sinking slowly to the bottom.

But they also have the ability, possessed by many of the free swimmers, of holding themselves suspended from the surface film of the water by means of their antennæ, their bodies hanging in a vertical position, and they often come to rest in this manner and remain for some minutes.

On the gills of the fish they always move about with their ventral surface next to the filament, using the swimming legs for locomotion and the second antennæ and maxillipeds for prehension. They catch hold of the filament and kick themselves free with a jerk that helps to send them forward. When resting the first antennæ are extended horizontally, the two being in the same straight line, while the second pair are turned ventrally and parallel to each other. The maxillipeds also stand out ventrally at right angles to the surface of the head, ready for use. During locomotion the posterior half of the body is often inclined ventrally, the flexure occurring between the fourth and fifth-sixth (fused) thorax segments. After the short rest at the surface or the long rest on the bottom the larva moves about as actively as ever, and this alternate motion and resting is kept up until a host is found.

Prehension.—The organs of prehension are the second antennæ and the maxillipeds; these are similar in both sexes and are the only means of prehension possessed by the male. The larvæ never develop a frontal filament like that of the Lernæopodidæ and the other Lernæidæ, but continue to move about freely during their entire larval life.

But the female, after she has sought out her final host and fastened herself to it by means of the second antennæ and maxillipeds, develops an entirely different method of attachment. She first burrows through the skin of the host and into the underlying tissues by means of her second antennæ, her powerful maxillæ, and her maxillipeds, until the anterior half of the body is entirely buried. The segments of the thorax then begin their final lengthening and transformation, and at the same time processes or horns, two, three, or four in number, grow out laterally from the cephalothorax into the surrounding tissue and anchor the head securely in place. Once formed, the function of prehension is entirely assumed by these horns for the remainder of the creature's life. The only subsequent use for the second antennæ and maxillipeds is to pull the mouth into contact with the food; for this purpose they retain to the full their form and powerful musculature.

Specimens of *variabilis* have been found which did not burrow through the skin, but were fastened to one of the fish's scales. In such instances the horns are still developed, but instead of penetrating the tissues they are flattened out upon the scale and more or less fused with it. Here also, therefore, the horns assume the function of attachment to the host, but there is more work left for the second antennæ and maxillipeds in the procuring of food.

As a result of the burrowing usually practiced by the larva we find that the tissues of the host are profoundly modified; those in immediate contact with the head and neck of the parasite harden into a tough, leathery skin which helps to hold the creature in place, and which is usually found enveloping the head and anterior end of the parasite after it is removed from its host. There is often also a swelling of the surrounding tissues, so that a good-sized lump or tumor is formed, perforated through the center and with the posterior part of the parasite projecting from the perforation. Sometimes the head and neck of the parasite work about so much within the burrow that it keeps the flesh of the host raw and bleeding, similar to the sores on the sunfish (*Mola mola*) occasioned by various species of the Caligidæ. Le Sueur and Kellicott mentioned such sores in connection with the species obtained by them.

Location.—The larvæ are always found upon the gills, either clinging to the filaments or to the skin covering the arches. After mating when the female copepodid larva seeks out her final host she fastens to the outside of the body instead of the gills, in the place where she is to be transformed into an adult. Mating and the attachment of the spermatophores has entirely changed her choice of a location and she now seems to prefer the vicinity of one of the fins, usually the dorsal.

And when six or eight specimens are found upon the same fish they are arranged in a row alongside this same dorsal fin. But they never burrow through the flesh into the body cavity, and hence do not, like some of the other Lernæidæ, attack the heart, the liver, or any other vital organ.

Relation to mussel glochidia.—It has been found by the author that there is a well-defined antagonism between mussel glochidia and parasitic copepods belonging to the Ergasilidæ.[a]

The same antagonism evidently exists between the glochidia and the copepodid larvæ of the present genus.

During the summer about 150 short-nosed gars (*Lepisosteus platostomus*) were examined for these larvæ. These fish were obtained in "Patterson Lake," "Drury Lake," and similar slews, which the fishing crew visited regularly and the fish of which they infected artificially with mussel glochidia. Gars were often obtained in the

[a] Bulletin, United States Bureau of Fisheries, vol 34, 1914, p. 345.

seine along with other fish and were infected the same as the rest. Of the 150 specimens examined 53 had been thus artificially infected with glochidia, a trifle more than a third of the whole, and upon these not a single copepodid larva was found.

In many instances both infected and uninfected gills were removed and placed together in a jar of water over night. The gills that had no glochidia were well covered with copepodid larvæ and many specimens were obtained from them on the following morning. But none of these larvæ would fasten on the gills that were already occupied by glochidia.

In wandering about the aquarium the larvæ necessarily came in contact with both kinds of gills, but would not fasten on those that had glochidia. Hence there must be something in connection with the glochidium-infected gill that becomes manifest to the copepodid larva and exerts upon it an antagonistic influence. What this is it would be very difficult to decide, but it would seem as if it must influence the larva through sensations corresponding either to smell or taste.

And the antagonism is not all in one direction; the presence of copepodid larvæ proves fully as distasteful to the glochidia as does that of the glochidia to the larvæ. On the gills above mentioned that were well infested with copepodid larvæ no glochidia were found, or if present they were in such small numbers (one to four) as to prove the general statement still more forcibly. Some of these fish must have had the same chance as the others to become artificially infected with glochidia; the very fact that they were caught and brought in for examination proved this.

Finally to complete the evidence about a dozen fish were found with a respectable infection of both glochidia and copepodid larvæ, about half a dozen of each. This would seem to indicate that the antagonizing influence, whatever it may be, can not be spread over the entire gill by a few parasites of either kind, but that it requires a dozen or more.

When the smaller number is present the antagonism is incomplete and both kinds may be found upon the same gill, but when the larger number is present the antagonism becomes complete and one kind of parasite occupies the gill to the exclusion of the other.

Two conclusions naturally follow from these observations, the one being the reverse of the other:

1. If conditions occur which are peculiarly favorable to the copepods and they increase so as to be present in considerable numbers on the gills of all the fish, then artificial infection with mussel glochidia will be seriously hindered and may even be a failure.

2. But evidently this artificial infection with glochidia and any natural infection that may occur will operate as a preventative against the increase of the copepod parasites, and if persisted in might reduce their numbers almost to extinction. At all events among fishes kept for the purpose of breeding mussel glochidia there will be very little danger of such an epidemic of copepod parasites as often occurs in trout ponds and aquaria, due to excessive development.

Geographical distribution of species.—Of the 17 species here enumerated 9 (53 per cent) are from our North American rivers and lakes, 4 (24 per cent) are from Africa, 3 (17 per cent) are from Europe, and a single one (6 per cent) is from South America. The following list gives the names of the species found on the respective continents:

North America: *anomala*, n. sp., *catostomi*, *cruciata*, *dolabrodes*, n. sp., *pectoralis*, *pomotidis*, *tenuis*, *tortua*, *variabilis*.

Africa: *barnimii*, *diceracephala*, *haplocephala*, *temnocephala*.

Europe: *cyprinacea*, *esocina*, *phoxinacea*.

South America: *lagenula*.

Cunnington stated: "So far as I am aware, the existence of the genus in Africa has never been put on record before" (1914, p. 819).

But *barnimii* was captured in 1860 at Dabbeh on the River Nile in Nubia. The single South American species is probably not a fair representation of the genus on that continent, but simply means that there has not been very much search for these parasites upon South American fishes.

Similarly, the nonappearance of Asia in the above list must not be interpreted as excluding the genus from that continent. Practically none of the fresh-water fishes belonging to that region has ever been examined for parasites, and there is no obvious reason why the genus should not be represented there as well as elsewhere.

Hosts.—This entire genus and the single known species of the genus *Sylvestria* are the only Lernæans which infest fresh-water fishes, but they are widely distributed amongst the different families of fishes, as can be seen from the table which follows.

Moreover, it will be noted that if the larvæ thus far discovered can be taken as typical of the entire genus, every species of *Lernæa* has at least two hosts, widely differing from each other. One of these serves as the temporary host of the copepodid larvæ, the other as the final or permanent host of the adult female. Our knowledge of the larvæ of the different species is at present too limited to enable us to draw any general conclusions with reference to the relations between the temporary and permanent hosts. But it is worthy of comment that both kinds of hosts include fish which frequent the surface, others which frequent the bottom, and a third class which may be found at almost any depth.

Probably later investigation will discover some general relation between these; it would at least seem reasonable that the two hosts of the same species should be fishes that frequent similar localities.

Host species.	Parasite species.
Ambloplites rupestris (redeye)	*cruciata*, adult female.
Ameiurus nebulosus (bullhead)	*tortua*, adult female. *pomotidis*, copepodid larvæ.
Aplodinotus grunniens (sheepshead)	*tenuis*, adult female.
Barbus bynni (fish of River Nile)	*temnocephala*, adult female.
Catostomus nigricans (hog sucker)	*tortua*, adult female.
Clarias mossambicus (fish of River Nile)	*diceracephala*, adult female.
Cyprinus carassius (carp)	*cyprinacea*, adult female.
Esox lucius (pike)	*cyprinacea*, adult female. *esocina*, adult female.
Eupomotis gibbosus (sunfish)	*cruciata*, adult female.
Gasterosteus aculeatus (stickleback)	*esocina*, adult female.
Labeo niloticus (fish of River Nile)	*barnimii*, adult female.
Lepomis pallidus (bluegill)	*variabilis*, adult female. *dolabrodes*, adult female. *pomotidis*, adult female.
Lepisosteus platostomus (short-nosed gar)	*variabilis*, copepodid larvæ.
Lota vulgaris (burbot)	*esocina*, adult female.
Micropterus salmoides (largemouth black bass)	*cruciata*, adult female. *anomala*, adult female.
Moxostoma macrolepidotum (large-scaled sucker)	*cruciata*, adult female. *catostomi*, adult female.
Notropis cornutus (shiner)	*pectoralis*, adult female.
Perca fluviatilis (perch)	*esocina*, adult female.
Phoxinus marsilii (minnow)	*phoxinacea*, adult female.
Polypterus birchir (fish of the White Nile)	*haplocephala*, adult female.

Host species.	Parasite species.
Polypterus congicus (fish of Lake Tanganyika)	*haplocephala*, adult female.
Polypterus senegalis (fish of the White Nile)	*haplocephala*, adult female.
Rutilus rutilus (European roach)	*esocina*, adult female.
Stizostedion canadense (sauger)	*cruciata*, copepodid larvæ.

Food.—Whatever discussion there may be as to the food of copepod parasites belonging to other families, it would seem as if there was no room for any question among the Lernæidæ. When a parasite breaks through the skin of its host and burrows into the underlying tissues, we can only conclude that it is in search of suitable food. Moreover, since the tissues themselves are not destroyed, the blood and the lymph which bathes the tissues are the only possibilities left, and these make up the food of the present genus.

Economic relations.—The deliberate burrowing of the parasite into the flesh of the host must cause the latter keen torture, and it will be noted that the list of hosts includes many of our game fishes. If this genus ever became abundant it would furnish a serious menace to our fresh-water fisheries. But fortunately it is held in check in many ways, so that there is little danger of its accomplishing much harm.

During the two free-swimming periods the larvæ are a part of the plankton and are subject to all its dangers and vicissitudes. The first of these periods includes both the nauplius and metanauplius stages, while the last includes the final copepodid stage, or so much of it as is occupied in the search for the final host. Thus the entire time during which the larva swims about freely is much longer than in the Lernæopodidæ and approaches closely to that of the Caligidæ.

Again the necessity for two hosts operates against the genus; if it is difficult to find one host it is twice as difficult to find two. And the ratio is increased by the possibility that the larva may be carried by the first host where it can not find the second one. The more complicated the life history the more numerous are the chances of failure. And the species of the present genus, together with the other Lernæans, have the most complicated development amongst all the parasitic copepods. All these things operate so much against them that they are the least numerous of the parasites; one may often examine hundreds of fishes without finding a single specimen of the genus. And they never occur in any considerable numbers upon a single fish; one specimen to each host is by far the most common mode of distribution.

EXTERNAL MORPHOLOGY.

The morphology of the genus has already been well worked out by Brühl, Claus, Hartmann, and others, but they used only what could be seen through the body wall or discovered by ordinary dissection.

So far as known no investigator has ever employed serial sections or double staining. These agents bring out many additional facts, explain others that have heretofore seemed obscure, and modify considerably some of the interpretations that have been given. In order that the present account may form a complete whole the substance of what was published by the above-named authors is here included in a condensed form and to it are added the new facts and explanations.

General body form.—The body of the adult female is made up of three parts or regions—the cephalothorax, the free thorax, and the abdomen. (See fig. 69, pl. XIV.)

Dorsally the head is well differentiated from the first thorax segment, but ventrally the two are completely fused. From the sides and sometimes from the dorsal surface of the (fused) first thorax segment soft horns, more or less branched, extend outward and serve to anchor the parasite in the tissues of the host. The free thorax starts as a slender neck, which increases gradually in diameter backwards, making the trunk of the creature club-shaped. At the posterior end the dorsal portion of the thorax passes insensibly into a short abdomen, which is much narrower than the thorax, bluntly rounded, and tipped with a pair of tiny anal laminæ.

On the ventral side the thorax is abruptly narrowed to the diameter of the abdomen, leaving a bluntly rounded protuberance for which Cunnington has proposed the name of "pregenital prominence."

The egg cases are attached to the ventral side of the thorax just in front of the base of the abdomen; they are oval or elliptical in outline and much shorter than the body. The eggs are large, spherical, and not flattened; they are multiseriate, but have no definite arrangement.

Torsion.—During the process of burrowing into the fish's tissues the body of the parasite usually becomes twisted upon its longitudinal axis, so that the pregenital prominence, instead of being on the ventral surface with the mouth and the appendages, is turned to one side and may even be carried through 180°, so that it apparently lies on the opposite or dorsal surface of the animal.

Quidor has described this arrangement in a recent paper on some of the other Lernæidæ and has named it torsion. He called the torsion direct when it turns from the left over toward the right, looking at the animal from the anterior end, and inverse when it turns from the right over toward the left. He claimed that one kind of torsion was shown when the parasite was attached to the left side of the fish and the other kind when it was attached to the right side, and that the amount of torsion was constant for a given species. The author has disproved this claim for other genera in the Lernæidæ,[a] and the few data available for this genus are all against it.

The first adverse fact is the existence of altogether too many full-grown adults without any torsion at all. An occasional specimen of this sort would only furnish the usual exception that occurs with every rule. But in the data given below 8 specimens of *cruciata* out of 20 showed no visible torsion, namely, 40 per cent of the whole.

Claus in dealing with *L. esocina* noted that young forms 3.50 mm. long possessed straight bodies on which the four pairs of swimming legs were in the same straight line and that the twisting took place gradually during subsequent growth[b] Evidently it frequently happens that there is no subsequent twisting, for every one of the eight specimens just mentioned was 15 to 20 mm. long and carried egg strings.

In the second place, specimens obtained from the same fish do not show the same torsion. A single 9-inch largemouth black bass, *Micropterus salmoides*, was obtained at Fairport, Iowa, which was infested with eight specimens of *L. cruciata*, two on the right side, five on the left, and one on the median line behind the dorsal fin. Of the first two one showed direct torsion of 180° and the other inverse torsion of 150°; the single parasite on the median line showed an inverse torsion of 180°; of the remaining five, two showed direct torsion of 135° and 180°, respectively; and the other three inverse torsion of 150°, 180°, and 180°. Thus neither the amount nor the kind of torsion was constant, but it might be objected that the maximum difference is only 45° and that five out of the eight specimens did show a torsion of exactly 180°. But even three out of eight, 37 per cent, is still too large a number to be treated as mere exceptions, and this proportion is greatly increased in the following data.

[a] Proc. U. S. Nat. Mus., vol. 53, p. 10.

[b] Schrift. Gesellsch. Beförd. ges. Naturw. Marburg, vol. 9, supplement, p. 2, 1868.

The detached specimens in the National Museum collection were examined for the kind and amount of torsion, but of course nothing could be told as to which side of the fish they came from.

Four specimens of *L. tortua*, all from the same fish, showed torsions of 45° inverse, 90° inverse, 720° direct (two complete revolutions), and 90° inverse, respectively. Five specimens of *L. variabilis* from different fish showed respective torsions of 45° inverse, 90° inverse, 0°, 100° inverse, and 45° inverse. In 20 specimens of *L. cruciata* from different fishes, all the same size and carrying egg strings, there were 8 that showed no torsion at all, 4 that showed 180° direct torsion, 2 that showed 180° inverse torsion, while the torsions of the other 6 were, respectively, 150° inverse, 45° direct, 25° direct, 25° inverse, 100° direct, and 20° direct.

A single specimen of *tortua* from *Micropterus salmoides* at Black Creek, N. C., had its body twisted inversely in three complete revolutions (1080°) just behind the cephalothorax. (See fig. 4, pl. VI.) In view of such extreme differences, the only rational conclusion is that neither the amount nor the kind of torsion possesses any systematic value whatever.

The cephalothorax.—At the anterior end of the cephalothorax, between the bases of the anterior horns, is a small button-shaped projection, its posterior margin fused with the dorsal surface of the cephalothorax, its anterior margin projecting freely, its dorsal surface more or less strongly convex. This may be called the head or cephalon and it carries on its anterior free margin the two pairs of antennæ, which are very similar in all the species of the genus. (See fig. 5, pl. VI.) The first antennæ are three or four jointed, not including the basal protuberance to which they are attached, which is entirely lacking in some species and which is immovable when present. Every joint is heavily armed with long plumose setæ along its anterior margin. Claus and some of the older investigators ascribed five joints to these antennæ, but their illustrations show that they counted the basal projection as a fifth joint. (See fig. 42, pl. XI.)

The second antennæ are two jointed, again omitting the basal projection; the proximal joint is unarmed, while the terminal joint ends in a tuft of setæ and a single large curved claw, making these appendages uncinate and attesting their prehensile function. The same remarks apply to these appendages as to the first pair, Claus and others designating them as three jointed. (See fig. 43, pl. XI.) The anterior margin of the head projects between these antennæ as a more or less pointed rostrum.

In the center of the dorsal surface of the projecting head lies a proportionally large eye, made up as in other parasitic copepods of three parts. The paired lateral portions each surround a large spherical lens, while the unpaired anteroventral portion contains a retinal layer of dark pigment. (See fig. 2, pl. VI.) In *L. barnimii* Hartmann described the eye as located on a special flattened plate on the dorsal surface of the head; the three refractive bodies were spherical and of about the same size, and the unpaired one was posterior. In *L. esocina* according to Claus and in all the American species examined the paired lateral portions are much larger than the unpaired central one, and the latter is anterior and ventral. Often nothing can be seen of this optical apparatus in external view since it is buried some little distance beneath the skin and lies just above and posterior to the supra-œsophageal ganglion. But in preserved and cleared material as well as in serial sections it is always distinctly visible. (See fig. 65, pl. XIII.)

Below the rostrum and between the antennæ on the ventral surface of the head is a short proboscis. Here again there has been diversity of opinion among the different investigators. Burmeister and Hartmann described a proboscis, while Claus and Brühl declared that there was none present. If by the term "proboscis" is meant a rigid sucking tube constantly projecting some distance from the ventral surface of the head, Claus and Brühl were right; there is nothing of the sort. But if we may designate as a proboscis the upper and under lips and some of the soft tissue connecting them, which can be protracted and withdrawn at pleasure, then Burmeister and Hartmann were correct, for there is such a proboscis, corresponding in its general make-up to that in the genus *Lernæenicus* and some other Lernæan genera.

A careful examination of the musculature connected with this proboscis, as shown in figure 7, leaves no question as to the possibility of its protrusion and withdrawal. (See p. 179.)

Claus demonstrated a chitin framework supporting the softer parts of the mouth tube in *esocina*, and this is found also in other species. The dorsal portion of this framework is formed by the upper lip, which is comparatively broad and is attached to the front of the head between the bases of the antennæ. The rest of the framework consists of a narrow chitin ring fused on either side to the lateral margin of the upper lip and supported on the ventral surface by a pair of stout rods, which extend obliquely backwards and outwards in the integument. (See fig. 76, pl. XIV.) The lower lip is in the form of a pad, attached to the outer surface of the mouth tube and articulated with the chitin ring in such a way as to allow of considerable motion backwards and forwards. This motion is accomplished by four longitudinal muscles, which extend backwards from the lower lip along the ventral surface.

The mouth parts.—Inside the mouth tube and between the two lips lie the mandibles, each of which is one jointed and strongly curved, with a sharp spinelike point and without teeth. These mandibles were discovered, described, and figured by Claus, but have been overlooked by the other investigators. They are difficult of detection and require the previous removal of the maxillæ and maxillipeds before they can be seen. The mandible of *variabilis* is curved more strongly than that of *esocina* and is clearly shown in figure 50.

The first and second maxillæ are attached to the outside of the mouth tube between the upper and under lips. Each consists of a stout basal joint and a movable terminal claw; in the first pair the claw is single, in the second pair it is double. Both pairs of maxillæ converge inwards across the tip of the mouth tube, so that the claws meet on the median line. (See fig. 5, pl. VI.)

The maxillipeds originate some distance behind the mouth tube upon the ventral surface of the cephalothorax. Each is made up of an elongated basal joint, which carries on its inner margin at the distal end a papilla tipped with a long plumose seta, and a terminal joint armed with five curved claws and a tuft of setæ. The number of parts in these maxillipeds is apparently constant for all the species, the specific differences being confined to relative shape and size.

The swimming legs.—There are five pairs of swimming legs which are variously disposed upon the body in the different species. A table has already been published [a] showing the relative distances between the successive pairs of legs in the North American species, and that table is repeated here with the addition of the two new species.

[a] Bulletin, United States Bureau of Fisheries, vol. 34, 1914, p. 370.

In this table the entire length of the parasite, excluding the egg strings, is called 100. The distance of each pair of legs from the anterior end is reduced to the proper percentage of 100, so that a comparison of the figures one with another gives the actual relative position of any pair of legs on any species.

Species.	First legs.	Second legs.	Third legs.	Fourth legs.	Fifth legs.
Anomala	3	4	29	56	74
Catostomi	4	8	48	80	....
Cruciata	10	15	42	75	....
Dolabrodes	7.5	10	38	70	98
Pectoralis	7	13	33	60	93
Pomotidis	12	38	52	88	....
Tenuis	7.5	11	35	70	....
Tortua	5.5	7	30	70	....
Variabilis	4	8	30	70	96

These relative distances are not claimed to be constant for any given species, but probably vary within certain limits; such individual variations, however, are likely to be considerably less than the specific variations given in the table. The gradual increase in these distances from in front backward shows that in the final elongation of the body after attachment to the host every free thorax segment has a share.

The anterior segments are not elongated as much as the posterior, but each contributes something. In the other genera of the Lernæidæ the bunching of the legs just behind the head shows that the great bulk of the elongation is contributed by the fifth and sixth segments.

Of the first four pairs of legs each is biramose and made up of a broad basal joint and two slender three-jointed rami. On the inner margin of the basal joint the first legs carry a stout claw, the other three pairs a single plumose seta. There is a fifth pair of legs just in front of the external openings of the oviducts; each leg is composed of a single hand-shaped joint armed with setæ. These legs do not get broken off in the mature female as easily as in the other *Lernæan* genera, where they are all bunched closely together.

Claus first called attention to the fact that these swimming legs neither degenerate nor disappear, contrary to the usually accepted understanding of the Lernæidæ. There is no diminution in size, in the number of rami or joints, or in the plumose setæ with which they are armed. The legs simply remain exactly as they were at the close of the copepodid stages when the parasite sought out its final host. They do not develop in accordance with the enormous increase in the size of the thorax and abdomen; but neither do they lose anything, not even a single seta of their armature, and hence they can not be said to degenerate. Similarly, the only disappearance is one due to breakage consequent on the burrowing habits of the parasites, which is a very different thing from degeneration.

The swimming legs are situated in transverse shallow grooves which mark the dividing lines between the thorax segments, the anterior slope of the groove being a little higher than the posterior. Each pair of legs is joined across the median line by a transverse rib, which lies just in front of the groove and is thoroughly fused with the body wall.

Owing to the torsion of the body only the anterior pair of legs lie symmetrically upon the median line. The others are carried more and more to the right or left until the fourth pair come to lie apparently on the side of the body, or may even be twisted so far that they appear to be on the dorsal surface. Really, of course, all the legs are on the ventral surface, and we must conceive of the longitudinal axis as twisted equally with the body itself. The apparent position of the legs thus affords a ready means of measuring both the direction and the amount of the torsion. (See fig. 68, 75, pl. XIV.)

The abdomen.—This is a short blunt cone on a level with the dorsal surface of the genital segment and ending in two minute anal laminæ. (See fig. 69, pl. XIV.)

These are so tiny that they escaped the notice of all the earlier investigators but are very distinct, and each is armed with a long plumose seta with a much shorter nonplumose one on either side of it.

The abdomen shows no other processes or appendages.

INTERNAL MORPHOLOGY.

The skin.—The integument is made up of three layers, the outer one hard, the two inner ones soft. In the present genus the outer layer never becomes really chitinous, as it does in some of the other Lernæids (*Hæmobaphes*, *Lernæolophus*, etc.). It is yellowish brown in color and offers considerable resistence to the penetration of fixatives.

It shows in a cross section (fig. 8, pl. VII) that it is made up of thin layers of lamellæ, many (7 to 10) of which are packed together one over another. These lamellæ lie in contact with one another and show no such intervening spaces as were noted in one instance by Hartmann. Neither do any of the species examined by the present author show the delicate surface markings seen by Hartmann on the outer lamella of *L. barnimii.* But it should be added that Hartmann examined living material while in the present instance only preserved material was used.

This lamellar layer of the integument is perforated by pore canals (*pc*), which are more numerous in the center and posterior portions of the body and less numerous at the anterior end and on the horns and appendages.

Each canal is a tolerably thick-walled tube, the outer surface of the walls being finely wrinkled transversely, while the inner lumen is perfectly smooth. The outer and inner openings of the canals are slightly larger than the central lumen, and in the posterior body and horns the external surface of the canals at the outer opening forms a six-sided polygon around the circular lumen, as stated by Hartmann.

The pregenital prominence.—In lateral view this prominence forms a sort of heel, the abdomen a sort of toe, while the free thorax is the leg of the boot, as was first suggested by Nordmann. Claus stated that in *L. esocina* the posterior part of the body first assumed the boot-shaped bending at the beginning of sexual maturity. He ought rather to have said at the completion of sexual maturity, for as we can see from the life history here given sexual maturity begins and becomes so far developed as to allow of impregnation during the copepodid stage, while the boot shape is not assumed until the creature has reached its maximum length. (See fig. 68, pl. XIV.)

Inside of this external layer of the integument is a single, comparatively thin layer of polyhedral cells (*hy*), whose walls and nuclei are very clearly marked. This is the first of the inner soft layers and corresponds to the "hypodermis" of Claus or the "chitinogen layer" of Hartmann and other authors. It is much softer than the outer layer, the cell contents are fine grained, and both nuclei and nucleoli are distinctly visible.

This layer extends without change or interruption over the inner ends of the pore canals, showing that the latter are not to be regarded as ducts, each connecting with a specific glandular body, but rather the entire inner layer is probably glandular and shares all the pore canals in common. This view is strengthened by the presence, inside the hypodermis and firmly adherent to it, of the second soft layer, several times as thick, indistinctly separated into cells, and containing a coarse protoplasmic network with numerous irregularly disposed nuclei, sometimes single and sometimes gathered into bunches (*il*, fig. 8, pl. VII).

This layer has all the characters of glandular tissue and varies considerably in thickness, being thickest where the pore canals are most numerous, especially at the pregenital prominence. (See fig. 13, pl. VII.)

Here the cells are much more distinct, in fact they are usually entirely separated one from another, and each is multinucleated.

This layer is entirely lacking in the head, the arms, and the appendages, or just the places where the pore canals are fewest in number.

The digestive canal.—The mouth opens directly into the œsophagus, which is cylindrical and short, and extends diagonally downward to the stomach, from which it is separated by a powerful sphincter muscle.

The walls of the œsophagus (*oe*, fig. 7, pl. VII) are tolerably thick and are connected with the dorsal and ventral walls of the head and with the stomach walls by powerful muscles (*m*), which must be capable of widening the lumen of the œsophagus and thus producing a suction through the mouth. Such a widening would produce the so-called "crop" described and figured by Hartmann in *barnimii*, which thus becomes a temporary condition of the gullet rather than a permanent portion of the digestive apparatus. Between the horns the stomach widens and sends out a lateral lobe on either side toward the bases of the horns but not actually reaching them. It then narrows and passes insensibly into the intestine, whose anterior portion is often thrown into numerous convolutions (fig. 9, pl. VII), and which maintains a wide lumen throughout the entire body. At the pregenital prominence the intestine is abruptly narrowed into the rectum, which is spindle shaped, widened through the center, and very narrow and slitlike at the posterior end (*rc*, fig. 10, pl. VII).

The wall of the stomach-intestine is made up of an outer muscular layer and an inner epithelium, and the latter has the same structure as in other parasitic copepods, larger digestive cells being interspersed among the epithelial cells. (See fig. 62, pl. XIII.) But there are also in the epithelium of the stomach and one or two of the anterior convolutions of the intestine numerous scattered cell bodies, which are totally unlike anything found in the other families of copepods. They are spherical in shape and possess a comparatively large and very distinct nucleus and nucleolus.

The body of the cell outside the nucleus is filled with small granules, sometimes colored greenish or brownish, mixed with which are larger colorless refractive bodies. These may be spherical, angular, boat-shaped, buckle-shaped with a crossbar through the center, or simply irregular and strongly granulated. Hartmann suggested that these might be psorosperm, whose existence in the epithelial cells of the intestine was abundantly proved by Leuckart, Wagener, and Reincke.

Considering that these parasites burrow into the tissues of fish and feed upon the blood and juices found there, it would be strange if they did not obtain some psorosperm.

The transverse muscles of the walls of the intestine and rectum are comparatively powerful and produce a strong peristaltic movement. This is the principal factor causing the weak currents in the fluid filling the body cavity, which constitute the only circulation that the creature possesses.

The muscles.—Although the body of these parasites is quite distinctly segmented, there can be no movements of the segments one upon another, because there are no muscles to produce such movements. Here there has been a positive degeneration, and the system of body muscles which was present and operative in the copepodid larva at the time it attached itself to its final host entirely disappears in the adult.

The only muscles left are those connected with the head, the proboscis, the appendages, the vulvæ, and the anal papillæ. In the head there are two dorsal extensors which move the entire head from above downward, and thus hold it against the tissues of its host, and two ventral retractors which lift it up again. Similar extensors and retractors are connected with the proboscis, the antennæ, and the mouth parts.

Each pair of swimming legs retains the strong muscles which they originally possessed in the copepodid stage, including those connecting the basal joints with the inner walls of the body, those moving the respective joints of the rami, and those which operate the various swimming setæ.

Even the fifth legs retain the rudimentary muscles, which are all that they ever possessed. The muscles connected with the vulvæ are similar to those found in other copepod families, especially the Lernæopodidæ, and are the ones controlling the passage of the eggs out into the external sacks. The muscles which move the anal laminæ radiate from the bases of the laminæ to the surrounding walls of the abdomen. All these muscles are distinctly striated and are made up of bundles of fibrillæ.

The nervous system.—The copepodid larvæ possess a normal crustacean nervous system. (See fig. 62, pl. XIII.) How far is this system modified or changed in the adult? This question has not been answered by any of the investigators who have worked with the present genus, for they knew nothing of the larva, and the nerves of the adult are easily overlooked.

In the first place it is evident that the muscles we have just described must have some nerve center to control their movements. This is especially true of those in the head, which move the head itself, the antennæ, and the mouth parts. The need of a proper control of these muscles is even greater in the adult than in the larva, for they are all concerned in procuring food, so essentially necessary for the rapid and comparatively enormous growth from the larva into the adult, and for the formation and nourishment of the eggs after the creature has attained its maximum size. Accordingly, we find in the head some very respectable remnants of the supra-œsophageal and infra-œsophageal ganglia. (See fig. 7, pl. VII.) While the outer portions of these ganglia are frayed and indistinct, those portions nearest the œsophagus are well preserved, their nuclei are distinct, and there are still commisures connecting them around the œsophagus. A good optic nerve can be detected leading from the supraganglion to the eye and others to the antennæ and mandibles, while the infraganglion supplies the remaining mouth parts. A distinct ventral cord can not be detected, either in longitudinal or cross section, but both the reproductive and digestive organs must be connected with a nerve center in order to perform their functions aright. In general, therefore, we may say that the nervous system has not developed in accordance with the rest of the body.

The œsophageal ganglia and their commisures have increased in size from the copepodid stage, but the nervous elements in the adult are not as clearly defined or relatively as well developed as they were in the larva. The peripheral portions of the ganglia are broken and jagged, and the large ventral trunk into which the infraganglion was prolonged is so much reduced in size that it can not be followed into the free thorax with any degree of certainty.

The reproductive organs.—Claus and Hartmann both gave a very brief account of the reproductive organs, but as they drew their information from an examination of entire adults, so that their observation of the structure of these organs was made from the outside through the body wall, their description was both scanty and inaccurate in many particulars.

Claus[a] said: "The sex organs correspond in position and form with those of the Lernæopodidæ. Drawn back out of the cephalothorax, they fill the widened posterior portion of the body, and are made up of two symmetrically placed ovaries with attached oviducts and the same number of tubular cement glands."

Hartmann[b] said: "The sex organs are made up of two simple sacklike ovaries which occupy the last quarter of the posterior body. The wall of the same was very contractile, but I could not make out the structure." In the Lernæopodidæ, as shown by the author,[c] the ovaries are short, spherical masses of cells situated between the stomach and the dorsal body wall, partly in the first (cephalothorax) and partly in the second thorax segment, and the oviducts are given off from their posterior ends. Here, on the contrary, the ovaries are elongated and spindle-shaped, flattened dorsoventrally, and situated as Hartmann said "in the last quarter of the posterior body," namely, in the fifth thorax segment. They lie between the intestine and the dorsal body wall; posteriorly they taper to a sharp point, which is suspended from the dorsal wall by two short bands of striated muscle; anteriorly they are narrowed into the oviducts which turn down ventrally around the outside of the intestine, and in young females proceed straight back along the ventral surface to the vulvæ. (See fig. 10, pl. VII.)

In older females loops are formed in the oviducts coincident with the development of the eggs, until in a fully ripe female each oviduct turns backward along the dorsal surface of the intestine as far as the base of the abdomen, then forward nearly to the anterior end of the fourth segment, then curves around to the side of the intestine and runs backward to the vulva, just behind the pregenital prominence. (See fig. 11, 12, 14, pl. VII, VIII.)

On examining sections of the ovary under a higher power, the pointed posterior end is seen to be filled with a mass of genital protoplasm containing numerous scattered nuclei, but without definite cell structure.

Proceeding forward the protoplasm gradually breaks up into rounded masses, each containing many nuclei. (See fig. 15, pl. VIII.) A little farther forward these masses are divided transversely into separate cells, discoidal in shape and packed like rows of coins, each with its own nucleus, which is now much enlarged and provided with a nucleolus.

At the anterior end of the ovary where these egg filaments pass into the oviducts the individual cells are separated from one another, and each oocyte thus set free absorbs food or yolk material, swells into a sphere, and becomes eventually a mature egg. (See fig. 16, pl. VIII.)

[a] Schrift. Gesellsch. Beförd. ges. Naturw. Marburg, vol. 9, supplement, p. 10, 1886.
[b] Arch. Anat. Pnysiol., p. 749, 1870.
[c] Proc. U. S. Nat. Mus, vol. 39, p. 219, 1910.

This formation of the egg differs from that of the Lernæopodidæ in that the egg filaments are much larger, and while in the Lernæopods the terminal oocyte alone develops with the rest of the filament still attached to it, here the whole filament breaks up and its integral oocytes develop simultaneously. But the resultant egg is practically the same in the two families. A thin and structureless vitelline membrane is distinctly visible around the newly formed egg. Inside of it the entire substance of the egg is made up of yolk globules evenly distributed throughout a matrix of finely granular protoplasm.

These globules are spherical or ellipsoidal in shape and differ but little in size; they are loosely packed together without being flattened, and without leaving the vacuoles seen in Lernæopod eggs, although these appear later. (See fig. 20, pl. VIII.) The egg nucleus is a little ellipsoidal, comparatively large, and contains a single large spherical nucleolus, without any chromatin granules. This nucleus is surrounded by a well-defined membrane and may be situated indiscriminately anywhere within the egg, as were the nuclei of the oocytes in the egg filaments.

The eggs pass down the oviducts in a single or sometimes a double row, with practically no flattening at all, or when there is any, it is fully as often lateral as longitudinal. This is very different from what is found in the other Lernæids, where the eggs are packed so tightly in a single row inside the oviduct that they are flattened lengthwise into thin disks or wafers. And they pass out through the vulvæ and assume the same shape and arrangement in the external sacks. Here, on the contrary, they pass loosely into the external sacks, where they are arranged in many rows, without any definite order and without being at all flattened.

There is no separate cement gland, but the posterior portion of the oviduct acts in that capacity. From the vulva to about the center of the fifth segment the oviduct is slightly narrowed and its walls are greatly thickened. Elsewhere structureless except for the muscle fibers they contain, the walls here become definitely glandular and secrete the cement substance. (See fig. 17, pl. VIII.) At the point where this change in structure occurs there is a constriction in the oviduct and also an S-shaped curve in its direction. The eggs striking this constriction are fertilized and then pass through the glandular portion in single file, being covered with a layer of the cement substance during their passage. There is no semen receptacle connected with the oviduct, at least none is revealed either in gross examination or in sections, and hence it is impossible to prove just where the eggs are fertilized. Nor should we expect to find any, for the spermatophores are fastened by the male directly to the vulvæ, and their contents are discharged into the oviducts. It is therefore only a question of how far up the oviducts they go, and it would seem most reasonable to suppose that they reach the portion just above the glandular walls.

The sperm would not likely be mingled with the cement substance in the glandular portion of the oviduct, and if the eggs were fertilized very much above this portion they would not be fully matured.

The cement substance forms a thick outer membrane around the egg, separated a little from the vitelline membrane and stiffening into a tough covering. The egg sack itself is formed of the same material, and inside of it there are no secondary walls separating the individual eggs, as in the other Lernæidæ. The two membranes covering the egg are separated a little, and this together with the loose arrangement of the eggs in the sack secures enough free space around each egg to supply the requisite oxygen for the developing embryo.

EMBRYONIC DEVELOPMENT.

Segmentation.—Because the eggs are not regularly arranged in the external sacks there is a corresponding irregularity in the position of the embryos. In consequence of lack of material it has not been possible to follow the various cleavage stages as fully as in the Lernæopodidæ.[a] But the few stages that have been obtained corresponded exactly with those found in the Lernæopods, and there is thus a strong probability that the other stages also correspond. At all events it is safe to say that cleavage in this genus resembles that in *Achtheres*, *Clavella*, and *Brachiella* far more than it does in *Lernæocera* (*Lernæa*) as given by Pedaschenko (1898).

Blastula.—The blastula shown in figure 20 is practically identical with that of *Achtheres*,[b] the only difference being an increased thickness of the blastoderm disk.

The yolk here shows that all of the cytoplasmic material has migrated to the surface and entered into the blastoderm. Now, also, there are good-sized vacuoles in the yolk, possibly as a result of this withdrawal of material. There is no evidence in any of the sections of the formation of a blastodermic cuticle similar to that secreted by the *Achtheres* embryo. Further material may reveal the presence of such a cuticle, but its absence seems fully as much in accordance with the subsequent development of the present genus. For we do not have here a shifting back into embryonic life within the egg of the early stages of development, such as occurs in *Achtheres*.

In that genus all of the nauplius and metanauplius stages are passed within the egg, and the larva hatches either in the last metanauplius stage and molts within an hour into the first copepodid stage or hatches directly into the latter stage. Here, on the contrary, the larva hatches into an ordinary nauplius and none of the early stages are passed inside the egg.

THE NEWLY HATCHED LARVA.

Nordmann, Brühl, and Hartmann have given us figures of a newly hatched larva (fig. 22, pl. IX), but Brühl's figure was simply a copy of Nordmann's, and Brühl himself had never seen a larva. Of the other two figures, Nordmann's is by far the better and is accompanied by an excellent description. Hartmann showed a series of eggs taken from the egg sack in various stages of development and also a "free larva." But he gave no description, and the larva which he designated as "free" had four pairs of appendages instead of the three shown on another larva just emerging from the egg membranes. The former, therefore, probably represented a larva that had had at least one molt, and hence was not newly hatched.

Nordmann stated that he actually witnessed the emergence of the larva, inclosed in its two membranes, from the egg sack, the bursting of the outer membrane, and the swelling and rupture of the inner membrane.

Since his figures of the corresponding larvæ of the genus *Achtheres* were wonderfully correct, we can accept these of *Lernæocera* on the same basis. According to his account the larva was a nauplius with the usual three pairs of appendages. The body was oval or ellipsoidal, with its lateral margins tolerably parallel, and about 0.25 mm. long.

It was covered on both the dorsal and ventral surfaces by a delicate shield or carapace, of a greenish color in that particular species (*esocina*), well arched dorsally,

[a] Proc. U. S. Nat. Mus., vol. 39, p. 196.

[b] Proc. U. S. Nat. Mus., vol. 39, pl. 29, fig. 8.

flattened ventrally, and marked with dark-colored longitudinal stripes. The eye was bright red in color.

A female *L. variabilis* was obtained from a bluegill, and on examining her egg strings the eggs were seen to be ellipsoidal instead of spherical, but showed no pigment, as is the case with most copepod eggs when ready to hatch. On the strength of the

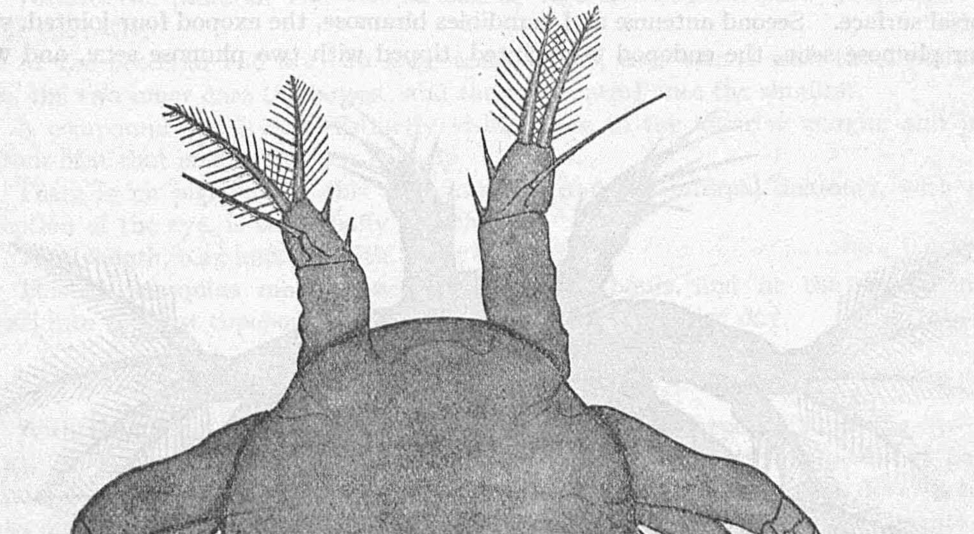


FIG. 1.—The newly hatched nauplius of *L. variabilis.*

difference in shape, however, this female was placed at night in a suitable aquarium, and the next morning all the eggs were hatched.

Some were examined and the others kept, and they molted during the second night into metanauplii and during the third day into the first copepodid stage, similar in all respects to the one obtained from the gills of the gar. With the stages thus happily obtained we can supplement Nordmann's account and present a complete life history, with every stage figured and described.

The nauplius.—General form elliptical, one-half longer than wide, not narrowed posteriorly, with nearly parallel sides. First antennæ uniramose, two-jointed, basal joint twice the length of the terminal and unarmed, terminal joint tipped with two long, plumose setæ, two short spines on the inner margin, and a long nonplumose seta on the dorsal surface. Second antennæ and mandibles biramose, the exopod four-jointed, with four plumose setæ, the endopod two-jointed, tipped with two plumose setæ, and with

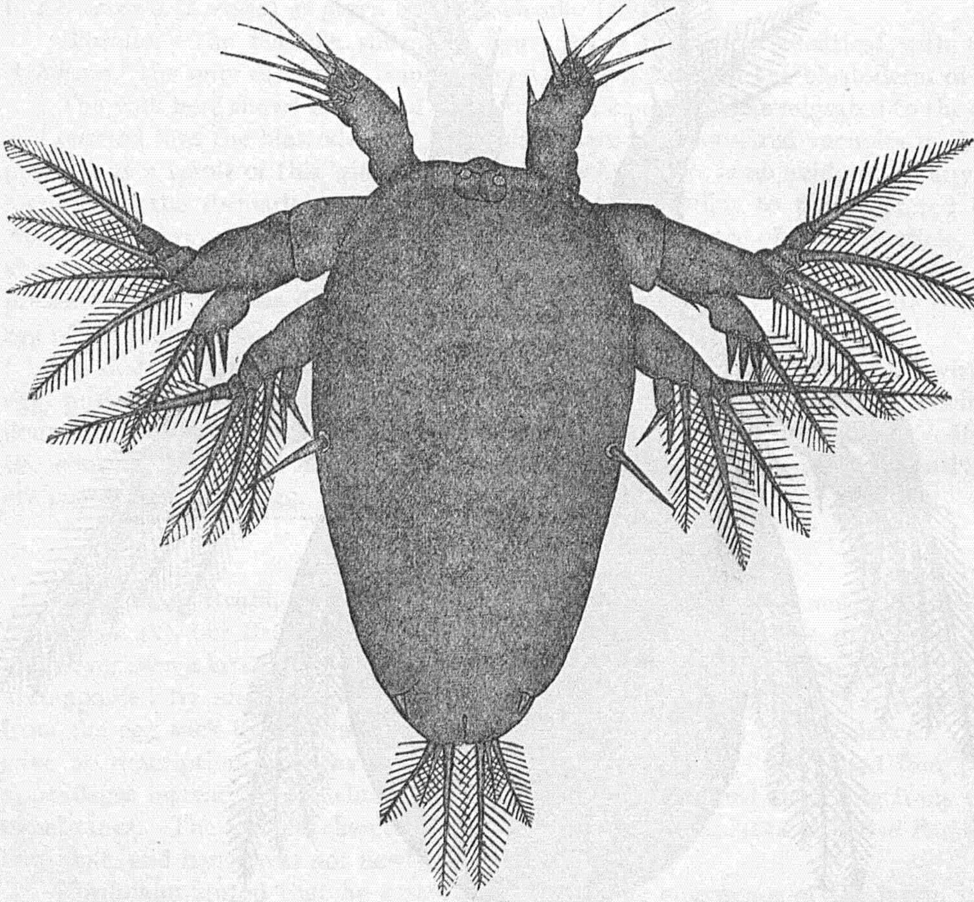


FIG. 2.—The metanauplius of *L. variabilis*.

a short spine on the inner margin of each joint. The balancers are straight spines, comparatively short and slender, and placed rather close together on either side of the midline. There is no pigment of any sort in this nauplius, no eye is visible, nor is the body transparent enough to show any of the internal anatomy. In these respects it differs from the one described by Nordmann, but is like it in all essentials.

The metanauplius.—The nauplii molted once and at the second molt passed into a metanauplius stage.

Body elongate, obovate, twice as long as wide, strongly narrowed posteriorly, with evenly rounded margins. First antennæ uniramose and two-jointed, the terminal joint without plumose setæ, but armed with 8 or 10 long spines. Second antennæ and mandibles as in the nauplius, except that the endopod of the second antennæ is now tipped with a single plumose seta, and three large spines on the posterior margin.

Behind the mandibles on the dorsal surface of the body there is a single large spine on either side close to the lateral margin.

Toward the posterior end the swimming legs can be seen partly differentiated inside the body.

At the posterior end are two large anal laminæ, each armed with three plumose setæ, the two inner ones the largest, and the two central ones the smallest.

A compound eye is now distinctly visible close to the anterior margin, and just in front of it that margin projects slightly.

There is no pigment on this metanauplius, and the internal anatomy, with the exception of the eye, is still wholly invisible.

Total length, 0.25 mm. Width, 0.125 mm.

This metanauplius molted once within a few hours, and at the second molt passed into the first copepodid stage some time during the third day.

THE FIRST COPEPODID LARVA.

With the molt from the metanauplius into the first copepodid stage (fig. 31–35, pl. x), the larva ceases its free-swimming life and enters upon its first period of parasitism. It seeks out a temporary host, upon whose gills it can continue its development up to sexual maturity and fastens itself to the outside surface of the gill filaments by means of its second antennæ and maxillipeds. While this attachment is strong enough to hold the larva securely in place even when the gill is rinsed off under a faucet, it can still be easily loosened at the pleasure of the larva. Indeed, these copepodid larvæ are much the most lively parasites of all the copepods infesting fish. It is practically impossible to catch one of them alive without injuring it, for upon being touched they let go of the filament, dart about swiftly in the water, and then seize the gill in another place. But they can often be deceived by cutting off the entire filament and removing it while they still cling to it. Having obtained one in this way from the gills of the short-nosed gar, *Lepisosteus platostomus*, we may examine its structure. It is the larva of *Lernæa variabilis*. (See fig. 31.)

The cephalothorax is elliptical in shape, its longitudinal and transverse diameters being in the proportion of 4 to 3. It is somewhat enlarged through the bases of the first antennæ and the anterior and posterior margins are nearly straight. It is followed by three free thorax segments, which diminish regularly in width, but are of about the same length. Finally, there is a rectangular segment, longer and narrower than the last free thorax segment, which represents the fused abdominal segments. It bears two large anal laminæ at its posterior corners, each armed with a very long and jointed inner seta and four much shorter outer ones, which diminish in size regularly outward.

The first and second antennæ are the same size and each is two-jointed, the terminal joint a little smaller than the basal and heavily armed with setæ. In addition to the setæ the second pair have a strong prehensile claw at the inner distal corner, and they share with the maxillipeds the task of holding the larva in place upon its host.

The mandibles, maxillæ, and maxillipeds are the same in all particulars as those of the adult. Each swimming leg of the two pairs is made up of a short and wide basal joint and two one-jointed rami, well armed with plumose setæ and spines. The first pair of legs is some distance in front of the posterior margin of the cephalothorax and close to the bases of the maxillipeds.

On the lateral margins of the second free joint near the posterior end are the rudiments of a third pair of swimming legs in the shape of small papillæ, each armed with two setæ.

Total length, including anal setæ, 0.53 mm. Carapace, 0.16 mm. long, 0.12 mm. wide.

Color a uniform yellowish white, digestive tube black, eye a reddish purple.

When one of these larvæ molts the old skin cracks open along the back of the thorax and the larva crawls out through the hole thus made, just as a dragonfly or cicada crawls out of its nymph case, and two minutes after emerging it is able to swim about as before.

Some molts occur without any change in the appendages or body segmentation and with only a slight increase in the size of the larva.

THE SECOND COPEPODID LARVA.

In the second copepodid stage (fig. 21, pl. IX) obtained from the gills of the short-nosed gar a new thorax segment has been formed just in front of the genital segment, but the abdominal segments are still entirely fused.

The first antennæ have become four-jointed, while the second pair still remain two-jointed. There are now three pairs of legs instead of two; the first two pairs have two-jointed rami, while in the third pair the rami have but a single joint. The new fourth segment carries at its posterior corners the rudiments of a fourth pair of legs, each consisting of a large rounded papilla and two terminal setæ.

The second (first free) thorax segment has increased until it is fully as wide as the cephalothorax, the third and fourth segments are about the same width, which is two-thirds that of the second segment, and the abdomen has not increased at all.

THE THIRD COPEPODID LARVA.

The third stage (fig. 23–30, pl. IX) was obtained from the gills of the sauger, *Stizostedion canadense*, and is evidently a different species from the one found upon the gar. But it serves just as well to illustrate the changes which mark this stage. Another new segment has been added to the free thorax, the second (first free) thorax segment still remains as wide as the cephalothorax, while the other segments, including the genital segment, diminish regularly in width behind it, though they are all about the same length. The antennæ are four-jointed and two-jointed, as before, but the second pair has increased considerably in length.

There are now four pairs of biramose legs, with the rami two-jointed, and a fifth pair which is rudimentary, each leg made up of two papillæ side by side and tipped with short spines. There is also on either side of the genital segment at the posterior corner a tiny papilla tipped with two small spines, the rudiment of a sixth leg.

The abdomen has lengthened considerably and now has two joints, the basal joint about half the length of the terminal one. There are also many differences in the anal laminæ and their setæ, but these are probably specific differences rather than changes due to advanced development.

THE FOURTH COPEPODID LARVA.

A large number of both sexes of this stage (fig. 53–61, pl. XII) were obtained from the gills of the short-nosed gar, thus completing the larval development, since during this period both kinds of larvæ become sexually mature and mating takes place.

The female larva.—This larva has greatly elongated and is now 1.25 to 1.50 mm. in length, including the anal setæ. The cephalothorax is somewhat oval in shape, being narrowed anteriorly, and its longitudinal and transverse diameters are in the proportion of 8 to 5. No new thorax segment has been added, but the genital segment has greatly increased in size, and there are now three abdominal segments instead of two.

The first antennæ remain four-jointed; the second pair have become longer, and the prehensile claw at their tips has increased greatly in size. Of the mouth parts the mandibles and first maxillæ can be made out much more easily than in the adult. The first four pairs of swimming legs have three-jointed rami, and each fifth leg now has a single distinct one-jointed ramus tipped with long setæ.

At the posterior corners of the genital segment is a single large seta on either side, marking the sixth legs. The fifth segment is fused with the genital segment, the separation being indicated by deep lateral notches behind the bases of the fifth legs.

In a little older larva there is a marked elongation of the thorax, the segments separating from one another so as to leave wide lateral notches. (See fig. 54, pl. XII.)

Female larvæ of another species in the fourth copepodid stage were obtained from the gills of the bullhead, *Ameiurus nebulosus*, from Drury Slew, July 23, 1915. In these the carapace and the free thorax segments were relatively shorter and wider (fig. 41–49, pl. XI); the fifth segment was distinctly separated from the genital segment, the latter being the wider of the two and nearly twice as wide as long; and the anal laminæ and setæ were also longer and narrower.

The fifth legs had a wider basal joint, armed with a stout spine on the outer margin, while the ramus was armed with three spines, two at the tip and one on the outer margin; no rudiments of the sixth legs were visible in dorsal view. In the maxillipeds the terminal joint was relatively shorter and narrower, and the basal joint was much less inflated through the center. It is impossible to locate this species with certainty, but it is at least highly improbable that it is a larval form of *tortua*, the adult female of which is sometimes found upon this same bullhead. It is also worthy of note that its host, the bullhead, is a fish which stays on or close to the bottom, while the short-nosed gar, the host of the *variabilis* larva stays close to the surface of the water.

The male larva.—This larva is similar to the female in most particulars, but shows some sex differences. The body in general is shorter and relatively wider, especially the cephalothorax, whose longitudinal and transverse diameters are in the proportion of 7 to 6. The free thorax segments are also wider and shorter than in the female (See fig. 36, 53, pl. X, XII.)

The only differences in the appendages are in an increase in the size and curvature of the prehensile claws on the second antennæ and the terminal claws on the maxillipeds, longer and stouter rami on the swimming legs, and in the size of the sixth legs.

Male larvæ of another species, probably *cruciata*, were obtained from the gills of the sauger. (See fig. 36, pl. X.) On these the cephalothorax is relatively longer and narrower, but the anterior margin is wider and projects some distance over the bases of the antennæ. The second (first free) thorax segment is as wide as the carapace, but the third, fourth, and fifth segments diminish very rapidly, the fifth being only one-third the width of the second. The genital segment is wider than the fifth segment, while the abdomen segments are considerably narrower.

The maxillipeds have a rather slender basal joint, with an enlargement on the inner margin just above the spine and close to the base of the terminal joint.

Total length of female, 1.25 to 1.50 mm.; of male, 1 to 1.15 mm. Carapace of female 0.32 mm. long, 0.20 mm. wide; of male 0.28 mm. long, 0.24 mm. wide. Anal laminæ and setæ 0.20 to 0.30 mm. long.

Color of both sexes like that of yellowish cartilage, the digestive tract black, the tripartite eye a bluish-purple.

THE INTERNAL STRUCTURE OF THE FOURTH COPEPODID LARVA.

Circulation.—The most conspicuous part of the internal mechanism (fig. 62–67, pl. XIII) of the living larva is the digestive tube, which runs straight through the center of the body. Its contents are jet black in color and reach back into the genital segment, the portion of the intestine behind that, together with the rectum, being transparent and colorless.

Every little while a small portion of this black material, which is the partly digested blood from the gills of the host, is separated from the rest, rolled up into a rounded mass, and passed back into the rectum, from which it is soon ejected.

The only circulation in the larva is produced by these movements of the digestive canal. The anterior end of the stomach is fastened to the dorsal wall of the head by three muscles, whose contraction draws the entire digestive tube forward. It is then drawn back again by muscles connected with the rectum and the posterior end of the intestine.

In addition to these forward and backward movements there is also a peristaltic wave of contraction, which starts at the anterior end of the stomach at the same time that the latter is drawn forward. This wave travels backward and reaches the rectum at about the time the forward movement of the whole digestive canal ceases. Accordingly when the backward movement of the canal begins the peristaltic contraction is reversed and passes forward again. The combination of these two kinds of movements produces corresponding impulses in the contents of the body cavity around the digestive tube. But this is evidently more of a pulsation than a circulation, the body fluid simply moving back and forth longitudinally and transversely, without crossing from one side to the other and with very little real mixing of the various portions. It may be noted here that this same backward and forward movement of the digestive tube persists in the mature female and constitutes her only method of respiration.

The digestive canal.—The mouth is comparatively large and opens into a long and narrow œsophagus (*oe*, fig. 62, pl. XIII) which extends back of the center of the cephalothorax, the sphincter muscle at the opening into the stomach being exceptionally large. The walls of the stomach are thick and the digestive cells (*dc*) project so far as to nearly close the lumen. In this larva there is no distinction between stomach and intestine or between intestine and rectum; it is all one tube tapering gradually backward. The walls of the œsophagus are composed of an inner layer of pavement epithelium and a very thin outer muscular layer. The latter is much thickened over the stomach and intestine, where it produces the peristaltic movements just described. In place of the pavement epithelium both stomach and intestine are lined with a glandular epithelium made up of digestive cells of varying lengths, all of which are filled with a digestive fluid containing small black granules, which are so numerous as to cause the black color of the entire canal.

The nervous system.—The supra-œsophageal ganglion is comparatively small and subtriangular in horizontal outline. (See fig. 64, pl. XIII.) From the dorsal surface of the blunt posterior angle a nerve extends backward to the reproductive organs and the digestive canal, and from the rounded anterior side other nerves go to the antennæ.

The infraganglion is by far the largest that has thus far been found in any larval or adult copepod, the nearest approach to it being the one in the adult Ergasilid. It is so wide where it joins the œsophagus as to cover nearly the whole length of the latter and it extends backward into the genital segment. It tapers rapidly at first, shows a large swelling opposite the bases of the maxillipeds, and then tapers very gradually through the first five and into the sixth thorax segment. No swellings are found in it opposite the bases of the successive pairs of swimming legs, although good-sized nerves are given off to these. It is pierced close to the œsophagus by stout muscles which run from the anterior end of the stomach to the ventral wall of the head. Both ganglia contain a thick outer layer of cells, while the interior is made up of fibers, and the two are distinctly differentiated throughout the entire length of the ganglion.

These copepodid larvæ thus possess relatively the largest and best developed nervous system amongst the parasitic copepods, which is retained by the male throughout the rest of his life. But in the subsequent exaggerated elongation of the thorax of the female after she has attached herself to her final host, this nervous system is pulled out as if it were ductile into longer and narrower parts, and the two ganglia are greatly reduced in size. The outer cellular layer almost entirely disappears, and the infraganglion can not be traced beyond the second thorax segment. It looks as if during the great increase in size of the female no more nerve material could be obtained, and so the nervous system of the 1-mm. copepodid larva had to be made over to supply the 10-mm. or 15-mm. female.

The reproductive organs.—The ovaries and testes are paired and are situated in the posterior part of the cephalothorax and the first one or two free segments. They are close to the dorsal body wall above the stomach, and from their anterior end the oviduct or sperm duct, as the sex may be, leads back above the stomach and intestine to the genital segment.

In the male each testis is spindle-shaped and flattened dorsoventrally; the posterior end is usually more pointed than the anterior and is attached to the dorsal body wall; from the anterior end the sperm ducts run back to the genital segment, where it is greatly enlarged and forms an ellipsoidal pouch in which the spermatophores are prepared. (See fig. 63, pl. XIII.)

The walls of the ducts are very thick and glandular, secreting the cement substance which forms the outer covering or wall of the spermatophores. These latter are cylindrical and oblong with rounded ends and occupy the whole side of the genital segment. (See fig. 63, pl. XIII.)

In a horizontal section (fig. 64, pl. XIII) one testis is seen to be behind the other, the anterior one occupying the cephalothorax and first free segment, the posterior one the first and second free segments, both of them between the stomach and intestine and the dorsal body wall. Each testis is swollen until it fills nearly the whole width of the body, and in it can be seen the whole spermatogenesis—the large, nucleated sperm mother cells (*sm*) filling the posterior half of the testis, followed by a zone of sperm daughter cells (*sa*), and these transforming into the sperms (*se*) in the anterior end of the testis and filling the lumen of the sperm duct. In a cross section through the third thorax segment (fig. 67, pl. XIII) the posterior testis is seen to be saddled upon the dorsal surface of the intestine, while the sperm ducts appear on either side opposite the center of the testis. Beneath the intestine and close to the ventral surface is the broad thick trunk of the infra-œsophageal ganglion.

In the female the ovaries are also spindle-shaped and flattened dorsoventrally. The posterior end is attached to the dorsal body wall, and from the anterior end the oviduct leads back to the vulvæ in the genital segment. The posterior portion of the oviduct has not yet become glandular but is like the anterior portion, and the whole duct is without convolutions. The spermatophores of the male are attached to the vulvæ and their contents are discharged into the oviducts. The sperms probably remain here during the subsequent growth of the female's body and the ripening of the eggs, and when the latter pass down the oviduct they are fertilized just before reaching the glandular portion where the cement substance forms the egg membranes.

There is no frontal gland in these larvæ, the space in the anterior portion of the head being occupied by the powerful muscles which operate the mouth parts.

ADDITIONAL DATA.

Fifty gars whose gills were infested with the copepodid larvæ of *Lernæa variabilis* were obtained from Patterson Lake, near Fairport, Iowa, August 15, 1915, and were placed in cages in one of the fish ponds.

Three or four of these were examined twice a week in order to determine if possible how long the larvæ remained and what became of the two sexes after fertilization. The author could only carry the examination up to September 1, but W. B. Gorham, one of the regular station staff, very kindly continued it through the month of September and up to October 4, sending the specimens found upon the gills to the author for examination. H. W. Clark also collected samples of plankton, which were sent similarly for examination. In this way it has been determined that:

1. These larvæ appear first about the latter part of June and may be found upon the gills of the short-nosed gar until the middle of October.

2. Each copepodid stage occupies from 10 to 14 days and apparently is accompanied by several molts.

3. Fertilization occurs during the fourth copepodid stage, as was proven by finding the two sexes fastened together upon the gills and by witnessing the union once or twice while handling the larvæ in watch glasses.

4. After fertilization the female apparently seeks out her final host at once, since nothing more is seen of her either on the gills or in the free-swimming plankton. The male, on the contrary, remains upon the gills of the temporary host, and specimens were found every time the gills were examined.

5. During the several copepodid stages and for some time subsequently the two sexes are found in about equal numbers. Then the proportion of females diminishes steadily and by the last of September only an occasional female is left, while the males are apparently undiminished.

6. Careful and repeated search of the plankton does not reveal any of these larvæ, and hence we can only conclude that the male does not become a free-swimmer for a second time, but remains upon the gills of the first host until his death.

SYSTEMATIC.

The genus *Lernæa* differs from the other Lernæan genera in the following particulars:

1. The body is formed by a lengthening of all the thoracic segments instead of only the fifth and sixth. This separates the swimming legs and leaves them distributed throughout the length of the body instead of being bunched closely together behind the head; moreover there are five pairs of legs instead of four or only three.

2. The first antennæ are on the anterior margin and the second antennæ are on the ventral surface of the head, instead of being dorsal, and while the second pair are uncinate they are not chelate. There are two pairs of maxillæ and a pair of well-developed maxillipeds, instead of a single pair of maxillæ.

3. The egg strings are relatively short and club-shaped or spindle-shaped instead of being long and filiform. The eggs are large and spherical and multiseriate instead of being flattened into thin disks arranged in a single series like a row of coins.

4. In the ovary egg filaments are formed, consisting of oocytes packed tightly together in a single row; these separate from one another at the entrance into the oviduct and each oocyte absorbs food and yolk and becomes an egg. In the oviducts the eggs remain spherical and are arranged loosely in one or two rows. In the other Lernæidæ there are no egg filaments, but the eggs are formed singly and are tightly packed together in a single row exactly like those in the external cases.

5. The copepodid larvæ have no frontal filament but attach themselves to their first or temporary host by means of the second antennæ and the maxillipeds. Hence there is no loss nor even any diminution of the power of locomotion during the copepodid stages. In the other Lernæidæ there is a large frontal filament, and while the larva is attached by it to its temporary host the swimming legs and some of the mouth parts degenerate and become immovable, but are restored to their former condition during the second free-swimming period.

It would seem at first as if these differences were enough to separate this genus from the other Lernæids and to make of it a distinct family, as was advocated by Brühl. But as we examine and compare more closely we find similar differences among the other genera, which naturally lead up to the ones here mentioned.

In other words, these are differences in degree rather than in kind, and hence would not warrant separation as a distinct family. Thus in *Peniculus* there is an elongation of all the thorax segments, with a consequent separation of the swimming legs, and what we find here is only the same thing carried a little further. Again, most of the Lernæan genera have four pairs of swimming legs, but there are some that have three pairs and others that have only two, so that there is no fixed and constant number, and the presence of five pairs only makes the series so much the more complete.

The copepodid larvæ of such genera as are known possess the same antennæ and mouth parts as those of the present genus. It is only in the subsequent metamorphosis of the female that some of them are lost, and it is evident that such a loss by one sex only could hardly constitute a family distinction. The differences in the external egg strings and in the internal ovary and oviducts are very real differences, but even in this particular the other genera are not alike. In some the egg tubes are coiled into a tight spiral, in others they are gathered into a loose mass, while in most of the genera they are straight, filiform, and much longer than the entire body. The lack of a frontal filament is duplicated among the Caligidæ, where the larvæ of the Caliginæ, the Pandarinæ, and the Cecropinæ possess such a filament, while it is lacking in the larvæ of the Euryphorinæ.

The life history ought to count for more than anything else when considering relationships, and in all its essential features the life history of the present genus corresponds with that of the other Lernæans.

The likenesses, therefore, are as numerous and of greater importance than the differences and warrant the retention of this genus *Lernæa* in the family of the Lernæidæ.

Genus LERNÆA Linnæus.

External generic characters of female.—Head a rounded knob projecting from the anterior margin of the cephalothorax and placed nearly at right angles to the body axis, with a deeply buried, three-parted eye near the center of the dorsal surface. One or two pairs of horns, simple or forked, on the lateral margins of the cephalothorax; sometimes an unpaired horn on the center of the dorsal margin; horns conical and soft; neck soft, slender, and cylindrical, twisted but not flexed, enlarging gradually into the body, which is also cylindrical; a pregenital prominence on the ventral surface in front of the vulvæ; on the dorsal surface a bluntly rounded abdomen, which terminates in a minute papilla on either side of the anus; egg strings elongate-conical or ovoid, eggs large and multiseriate. Two pairs of antennæ, second pair uncinate; a very short conical proboscis; mandibles claw-shaped and without teeth; two pairs of maxillæ; four pairs of biramose swimming legs attached to transverse chitin bars, indicating segmentation; a fifth pair of one-jointed stumps just in front of the vulvæ.

Internal generic characters of female.—Œsophagus short, nearly straight, and diagonal to the body axis; anterior stomach with lateral lobes extending into the bases of the horns and more or less convoluted; posterior stomach passing insensibly into the intestine, which is straight, the same diameter for its entire length, and is abruptly contracted at the base of the abdomen into a short rectum, which is suspended from the abdomen walls by muscle strands; ovaries paired, close to the dorsal surface and near the posterior end of the body; matured oviducts with two long posterior and two shorter anterior loops; eggs remaining spherical and never flattened anteroposteriorly; no separate cement glands, the thickened glandular walls of the posterior oviducts serving that purpose; no distinguishable semen receptacles.

External generic characters of male.—Not developed beyond the fourth copepodid stage, which must hence be regarded as the adult stage; cephalothorax made up of the head and first thorax segment fused; second, third, and fourth thorax segments free; fifth and genital segments more or less fused; abdomen made up of three segments of about the same size; anal laminæ large, each terminated with a very long and stout plumose seta, jointed near its base, and two or three small spines. Appendages similar to those of the female, except that the prehensile claws on the second antennæ and maxillipeds are larger, the rami of the swimming legs are longer and stouter, and there are the rudiments of a sixth pair at the posterior corners of the genital segment.

Internal generic characters of male.—Œsophagus long and nearly parallel with the body axis; stomach passing insensibly into the intestine and that into the rectum, the entire tube lined with digestive cells filled with black granules; supra-œsophageal ganglion comparatively small, infraganglion very large and stout and extending back into the genital segment; testes paired but not side by side, in the head and anterior thorax above the stomach and intestine, spindle-shaped, with the sperm ducts leading from the anterior end back to the large spermatophore receptacles in the genital segment.

Type of the genus, *Lernæa cyprinacea*, Linnæus, first species.

(Lernæa, Λέρνη, a lake and town near Argos where Hercules slew the hydra.)

KEY TO THE SPECIES.

1. Two cephalothoracic horns, a lateral pair .... 2.
1. Three cephalothoracic horns, two paired and lateral, one unpaired and dorsal .... 3.
1. Four cephalothoracic horns, a dorsal and a ventral pair .... 5.
   2. Horns directed laterally at right angles to body axis; posterior body not much wider than neck; pregenital prominence inconspicuous (8.40 mm.)[a] ..*diceracephala* (Cunnington), 1914, p. 194.
   2. Horns diagonal to body axis, directed posterolaterally; posterior body suddenly enlarged to four times the diameter of neck; pregenital prominence large (8 mm.).
   anomala, new species, p. 194.

[a] These figures in parentheses represent the average length of each species.

3. Lateral horns simple, dorsal one bifid at apex; pregenital prominence inconspicuous; abdomen short (10 mm.)..*dolabrodes*, new species, p. 194.
3. Lateral and dorsal horns all dichotomously branched..4.
3. Lateral horns three or four pronged; dorsal horn stout and bifid at apex; pregenital prominence large; body club-shaped; abdomen long and wide (7.50 mm.)......*pectoralis* (Kellicott), 1882, p. 195.
4. Lateral horns once bifid, dorsal horn twice bifid; body spindle-shaped; pregenital prominence absent (8 mm.)..*lagenula* (Heller), 1865, p. 195.
4. All three horns twice bifid; body club-shaped; pregenital prominence divided, its two lobes and the abdomen the same size (10 mm.)................*catostomi* (Krøyer), 1863, p. 195.
4. Lateral horns twice bifid; dorsal horn simple or once bifid; body club-shaped; pregenital prominence simple and much smaller than abdomen (12 mm.)..*tortua* (Kellicott), 1882, p. 195.
5. Dorsal and ventral horns about the same size..6.
5. Ventral horns much smaller than the dorsal..9.
6. Pregenital prominence simple and much shorter than abdomen..........................7.
6. Pregenital prominence divided, its lobes nearly as long as the abdomen..................8.
7. Abdomen short and plump; pregenital prominence forming a distinct heel; ventral horns bifid (5.75 mm.)..*phoxinacea* (Krøyer), 1863, p. 195.
7. Abdomen short and plump; pregenital prominence not forming distinct heel; dorsal horns bifid (13.50 mm.)..*esocina* (Burmeister), 1835, p. 195.
7. Abdomen long and stout; pregenital prominence forming distinct heel; all the horns simple (14 mm.)...*haplocephala* (Cunnington), 1914, p. 195.
8. Pregenital prominence divided into three broadly rounded lobes; horns long, slender, and straight (13.50 mm.)..................................*pomotidis* (Krøyer), 1863, p. 196.
8. Pregenital prominence twice bifid, forming four narrow lobes; horns short, plump, and curved (10 mm.)...*cruciata* (Le Sueur), 1824, p. 196.
9. Pregenital prominence divided into distinct lobes; dorsal horns simple and undivided.......... 10.
9. Pregenital prominence simple or only slightly indented; dorsal horns distinctly forked......... 11.
10. Abdomen a short and broad triangle; dorsal horns cylindrical and standing out laterally at right angles to body axis (9 mm.)...........................*tenuis* (Wilson), 1916, p. 196.
10. Abdomen long and conical; dorsal horns flattened dorsoventrally and curved forward in front of head, parallel to body axis (11.50 mm.)..........*variabilis* (Wilson), 1916, p. 196.
11. Abdomen short and inclined to body axis; egg cases broadly elliptical; ventral horns mere knobs (14 mm.)..*barnimii* (Hartmann), 1870, p. 196.
11. Abdomen short and inclined to body axis; egg cases narrow and elongate; ventral horns half the length of dorsal (22.50 mm.)................................*cyprinacea* (Linnæus), 1758, p. 196.
11. Abdomen long and parallel with body axis; ventral horns very short and slender (10 mm) ....*temnocephala* (Cunnington), 1914, p. 196.

Remarks.—Dr. W. A. Cunnington recently (1914) issued a valuable little paper on "Parasitic Eucopepods from Tanganyika, Africa," in which he included a list of described species with synonyms and a key to all the known species (seven in number), including three new ones described in the paper. But he overlooked Hartmann's paper (1870) on *barnimii*, one of the best that has ever been published, and also Kellicott's two papers describing *tortua* and *pectoralis*. The key published by Cunnington is an excellent one and is made the basis of the one here presented. One or two facts in connection with it are worthy of comment. It is based entirely upon characters that can be seen with an ordinary hand lens, as such a key ought to be for convenience. Amongst these characters the horns, of course, take a prominent place, but too much specific value ought not to be placed upon either the number or the arrangement of the horns. Consequently all the other external characters, including the average length of the species, have been introduced into the key, and these should be given their full value.

Cunnington, in writing of his own key, said: "I am not responsible for the rather remarkable assertion that *L. catostomi* possesses three cephalic arms, which, of course, renders the head quite asymmetrical" (p. 823).

The author can not see how the possession of three horns is any more remarkable than the possession of two or four. And certainly a median, dorsal, unpaired horn no more destroys the symmetry of the head than does the nose or the mouth on a man's face compared with his two eyes or ears. Moreover, there are five species which have such a dorsal horn instead of one, as will be seen from the key.

An outline drawing of the head and horns of all the species except *pectoralis* [a] is here included for facility of comparison. (See pl. xv.)

The four with three horns (*pectoralis* is the fifth) are arranged with the dorsal horn uppermost; the others are arranged as seen from the dorsal surface, as they are usually represented in figures, except *anomala*, whose distortion compels a diagonal view from the anterior end.

Lernæa diceracephala (Cunnington), 1914.

Lernæocera diceracephala Cunnington, Proceedings Zoological Society of London, 1914, p. 824.

Found in Lake Tanganyika on the gill arches of a large *Clarias mossambicus*. Only one perfect specimen known.

Lernæa anomala, new species. (Pl. XIV, fig. 68–70, 73, 74.)

Host and record of specimens.—Two females, one badly mutilated, were taken by H. D. Lucas from the body of *Micropterus salmoides* caught in Black Creek, N. C. The better specimen has been given Catalogue no. 47756, U. S. National Museum, and becomes the type of the species.

Specific characters of female.—General body form quite bizarre. In consequence of a flexure just behind the second swimming legs the cephalothorax is turned ventrally at right angles to the body axis, making the head parallel with that axis. A single pair of forked horns are attached to the dorsal surface of the first and second thorax joints. They are slightly flattened dorsoventrally, but very plump, and extend backward with their tips projecting slightly behind the angle of the flexure; these tips are swollen into subspherical knobs. The neck behind the head gradually increases in diameter back to the third swimming legs; just beyond these it is rather abruptly contracted to one-third its former size for a short distance. This constricted portion probably represents the region in contact with the skin of the host, all the anterior portion being buried in the tissues of the fish while the posterior part hung free in the water. Behind the constriction the neck again widens, but not as much as before, back to the fourth swimming legs, where it is again slightly constricted. Immediately behind these legs the genital segment begins and is widened abruptly to three and a half times the diameter of the fourth segment, forming a spherical swelling, which then narrows to twice the diameter and extends backward as an abdomen of uniform thickness, as long as the fourth segment and bluntly rounded at the tip, where it ends in two minute anal laminæ, each tipped with a short nonplumose seta. On the ventral surface, behind the spherical swelling and in front of the vulvæ, is the pregenital prominence in the form of a sphere of the same diameter as the abdomen and projecting its entire length. In the angle between this sphere and the abdomen posteriorly are the vulvæ with the remains of a pair of emptied egg sacks attached to them.

Head ovoid, the base of the oval posterior and raised considerably above the dorsal surface; first antennæ four-jointed and moderately armed with setæ; second antennæ two-jointed, the terminal joint uncinate; second maxillæ of the usual pattern ending in two claws; maxillipeds with a swollen basal joint, armed on the inner edge with a short spine, and a much narrowed terminal joint bearing five long curved claws.

Total length, 8 mm. Cephalothorax in front of flexure, 1 mm. Neck from the flexure to the genital segment, 4.65 mm. Genital segment and abdomen, 2.80 mm. Diameter of neck at third legs, 0.50 mm. Diameter of genital segment, 1.20 mm.

Color (preserved material), a brownish gray, genital segment and abdomen, darker than the head and neck.

(*anomalus*, unusual, exceptional, alluding to the general form.)

Remarks.—There can be no doubt that this represents a new species, since it has not a single feature in common with other species and yet possesses every generic detail. Its unlikeness to other species is so pronounced that it may be a monstrosity, but even as such it is worthy of description and record.

Lernæa dolabrodes, new species. (Pl. XIV, fig. 71, 72, 75–78.)

Host and record of specimens.—Five females with egg strings were taken from *Lepomis pallidus* in Lake Pepin, Wis., by A. F. Shira, director of the U. S. Fisheries biological station, Fairport, Iowa, and were generously turned over to the author. The most perfect of these has been selected as a type female and has been given catalogue no. 47757, U. S. National Museum. The others become paratypes with catalogue no. 47758, U. S. National Museum.

[a] No figures of this species have ever been published.

Specific characters of female.—Cephalothorax in line with the neck axis and sending out at right angles on either side a long tapering and unbranched horn and dorsally a single very short horn, slightly bifid at the tip. Neck of uniform width as far as the third pair of legs, then increasing gradually in diameter and passing insensibly into the trunk, which is widest at the posterior end, with a short bilobed prominence over the base of each egg string. Between these on the ventral surface is the pregenital prominence, which is about half the length of the abdomen and the same width. On the dorsal surface is the abdomen, tapered considerably but bluntly rounded and tipped with the two tiny anal laminæ, each carrying a short terminal seta. Egg strings half the diameter of the genital segment and two-fifths the entire body length, cylindrical, and about the same diameter throughout; eggs not arranged in rows, about 200 in each string.

Head small, nearly circular in outline, and projecting only a little; first antennæ four-jointed, basal joint the shortest and stoutest, second joint the longest; first three joints with a heavy fringe of setæ along their anterior margins, third joint giving off at the distal end a very large and long seta, fourth joint short and narrow with a terminal tuft of setæ. Second antennæ two-jointed, basal joint about half the length of the terminal, the latter tipped with a stout claw and a tuft of large setæ. Maxillæ projecting well beyond the tip of the mouth tube, their terminal claws large and sharply-pointed. Maxillipeds tipped with five rather short and slender claws, basal joint with a prominent knob at the inner distal corner and a smaller knob, tipped with a spine, on the inner margin. The swimming legs are of the usual pattern, the most essential difference being in their respective locations as seen in the table on page 176.

Total length, 10 mm. Transverse length of two arms and head, 6 mm. Diameter of neck, 0.33 mm. Greatest diameter of trunk, 1 mm. Length of egg strings, 4 mm.

Color (preserved material), a uniform grayish-white.

(*dolabrodes, dolabra*, a pickax and εἶδος, similarity.)

This species is easily recognized by its pickax form and by the short dorsal horn. These observations can then be supplemented by the position of the swimming legs and other details.

Lernæa pectoralis (Kellicott), 1882.

Lernæocera pectoralis, Kellicott, Proceedings American Society, Microscopists, vol. 4, p. 77.

Host and record of specimens.—Found in the axilla of the redfin shiner, *Notropis cornutus*, from the Shiawasee River, Mich.

Lernæa lagenula (Heller), 1865.

Lernæocera Lagenula, Heller, Reise der Fregatta Novara, p. 246; pl. 24, fig. 9.

Host and record of specimens.—Found upon an undetermined fish from Brazil.

Lernæa catostomi (Krφyer), 1863.

Lernæocera catostomi, Krφyer, Bidrag til Kundskab om Snyltekrebsene, p. 321; pl. 18, fig. 4, a–e.

Host and record of specimens.—Taken by Krφyer from the large-scaled sucker, *Moxostoma macrolepidotum*, caught in the Mississippi River near St. Louis, Mo.

Lernæa tortua (Kellicott), 1881.

Lernæocera tortua, Kellicott, Proceedings American Society, Microscopists, vol. 2, p. 41, 1 unnumbered pl.

Host and record of specimens.—Found in tumors upon the external surface of the bullhead, *Ameiurus nebulosus*, in Grindstone Creek near Lake Ontario. Subsequently found upon the hog sucker, *Catostomus nigricans*.

Lernæa phoxinacea (Krφyer), 1863.

Lernæocera phoxinacea, Krφyer, Bidrag til Kundskab om Snyltekrebsene, p. 325; pl. 18, fig. 3, a–d.

Host and record of specimens.—A single specimen was taken from the European minnow, *Phoxinus marsilii*, obtained from the Vienna Museum.

Lernæa esocina (Burmeister), 1835.

Lernæocera esocina, Burmeister, Acta Acad. Caes. Leop. Carol. Nat. Cur., vol. 17, p. 312. Nordmann, Mikrographische Beiträge, 1832, part 2, p. 123; pl. 6, figs. 1 to 6.

Host and record of specimens.—Found upon various species of European perch, carp, roach, pike, stickleback, burbot, etc.

Lernæa haplocephala (Cunnington), 1914.

Lernæocera haplocephala, Cunnington, Proceedings Zoological Society of London, 1914, p. 826; pl. 1, fig. 4–7.

Host and record of specimens.—Taken from different species of the ganoid genus *Polypterus* in Lake Tanganyika and the White Nile.

Lernæa pomotidis (Krøyer), 1863.

Lernæocera pomotidis, Krøyer, Bidrag til Kundskab om Snyltekrebsene, p. 323; pl. 15, fig. 5, a-h.

Host and record of specimens.—Found originally by Kroyer upon the bluegill, *Lepomis pallidus*, near New Orleans, La. Subsequently found on the same host at other places in the Mississippi River, and the copepodid larvæ upon the bullhead, *Ameiurus nebulosus*.

Lernæa cruciata (Le Sueur), 1824.

Lernæocera cruciata, Le Sueur, Jour. Acad. Nat. Sci. Philadelphia, vol. 3, p. 286; pl. 11, fig. 4.

Host and record of specimens.—Found originally upon the rock bass. *Ambloplites rupestris*, in Lake Erie. Subsequently found upon the sunfish, *Eupomotis gibbosus*, upon the largemouth black bass, *Micropterus salmoides*, upon the large-scaled sucker, *Moxostoma macrolepidotum*, and the copepodid larvæ upon the sauger, *Stizostedion canadense*.

Lernæa tenuis (Wilson), 1916.

Lernæocera tenuis, Wilson, Bulletin, U. S. Bureau of Fisheries, vol. XXXIV, p. 366.

Host and record of specimens.—Found upon the sheepshead, *Aplodinotus grunniens*, at Fairport, Iowa.

Lernæa variabilis (Wilson), 1916.

Lernæocera variabilis, Wilson, Bulletin, U. S. Bureau of Fisheries, vol. XXXIV, p. 365.

Host and record of specimens.—Found upon the bluegill, *Lepomis pallidus*, in the Mississippi River near Fairport, Iowa, and the copepodid larvæ upon the gills of the short-nosed gar, *Lepisosteus platostomus*.

Lernæa barnimii (Hartmann), 1870.

Lernæocera barnimii, Hartmann, Archiv fur Anatomie und Physiologie, 1870, p. 726; pl. 17, 18.

Host and record of specimens.—Found upon *Labeo nitoticus*, a fish of the River Nile.

Lernæa cyprinacea Linnæus, 1758.

Lernæa cyprinacea, Linnæus, Systema Naturæ, 10th ed., p. 655, pl. 2, fig. 1. Burmeister, Beschreibung einiger Schmarotzerkrebse, 1833, p. 309; pl. 24, A, figs. 1-3.

Host and record of specimens.—Found upon the European carp and pike.

Lernæa temnocephala (Cunnington), 1914.

Lernæocera temnocephala, Cunnington, Proceedings, Zoological Society of London, 1914, p. 827; pl. 1, fig. 8, 9.

Host and record of specimens.—Found upon *Barbus bynni* caught in the River Nile.

EXPLANATION OF PLATES.

PLATE VI.

Anatomy.

FIG. 1. Median longitudinal section of head and anterior thorax of *L. cruciata: c*, cephalon; *œ*, œsophagus; *s*, stomach. FIG. 2. Eye of *L. variabilis*. FIG. 3. Dorsal view of head, and anterior thorax of *L. variabilis*. FIG. 4. Head and neck of *L. tortua* from Black Creek, N. C., showing three complete revolutions. FIG. 5. Cephalon and mouth parts of *L. cruciata: an′* and *an″*, first and second antennæ; *c*, cephalon; *lb*, labium; *mx′* and *mx″*, first and second maxillæ; *mxp*, maxillipeds; *r*, rostrum. FIG. 6. Anal lamina of *L. cruciata*.

PLATE VII.

Internal morphology.

FIG. 7. Median longitudinal section of head of *L. cruciata: ig*, infraganglion; *m*, muscles; *oe*, œsophagus; *s*, stomach; *sg*, supraganglion. FIG. 8. Section of skin: *hy*, hypodermis; *il*, inner layer; *ol*, outer layer; *pc*, pore canal. FIG. 9. Head and anterior thorax of *L. variabilis*, showing *e*, the eye, and *s*, the convolutions of the stomach. FIG. 10. Young female of *L. variabilis*, ventral view, showing l^4 and l^5, fourth and fifth swimming legs; *ov* and *od*, ovary and oviduct; *rc*, rectum. FIG. 11. Fully grown female of same species, side view, lettering as before, and *cg*, cement gland. Fig. 12. Median longitudinal section of posterior body of *L. cruciata*, lettering as in fig. 11. FIG. 13. Section through pregenital prominence of *L. cruciata*, showing inner layer divided into separate cells, lettering as in fig. 8.

PLATE VIII.

Internal morphology.

FIG. 14. Reproductive organs of adult female of *L. cruciata*, lettering as in fig. 11. Fig. 15. Posterior end of ovary enlarged, showing genital protoplasm (*gp*) and egg filaments (*ef*). FIG. 16. Anterior end of same ovary, showing much enlarged egg filaments (*ef*) and the mature eggs (*e*) resulting from them. FIG. 17. Section of cement gland of *L. variabilis*, showing an egg (*e*) just ready to enter the glandular portion of the oviduct, and gland cells (*gc*). FIG. 18. Transverse section of the glandular portion of another specimen. FIG. 19. Transverse section through the body of *L. cruciata*, posterior to the ovaries: *cg*, cement gland; *od*, oviduct containing eggs; *i*, intestine. FIG. 20. Section of a fully formed blastula, showing superficial cleavage.

PLATE IX.

The nauplius and second and third copepodid larvæ.

FIG. 21. Second copepodid larva from gills of *Lepisosteus platostomus*. FIG. 22. Newly hatched nauplius, after Nordmann. FIG. 23. Third copepodid larva from gills of *Stizostedion canadense*. FIG. 24. Mouth parts, ventral view, lettering as in fig. 5. FIG. 25–29. First, second, third, fourth, and fifth swimming legs. FIG. 30. Maxilliped.

PLATE X.

Copepodid larvæ.

FIG. 31. First copepodid larva from gills of *Lepisosteus platostomus*. FIG. 32. First antenna. FIG. 33. Second antenna. FIG. 34, 35. First and second swimming legs. FIG. 36, 37. Male and female fourth copepodid larvæ from gills of *Stizostedion canadense*. FIG. 38. Ventral view of maxillæ. FIG. 39. Dorsal view of maxilla. FIG. 40. Maxilliped.

PLATE XI.

Copepodid larvæ.

FIG. 41. Female fourth copepodid larva from gills of *Ameiurus nebulosus*. FIG. 42. First antenna. FIG. 43. Second antenna. FIG. 44. Maxilliped. FIG. 45–49. First, second, third, fourth, and fifth swimming legs. FIG. 50. Mandible of fourth copepodid larva from gills of *Lepisosteus platostomus*. FIG. 51. First (upper) and second (lower) maxillæ. FIG. 52. Maxilliped.

PLATE XII.

Copepodid larvæ.

FIG. 53, 54. Male and female fourth copepodid larvæ taken together from gills of *Lepisosteus platostomus*. FIG. 55. Second antenna. FIG. 56. Dorsal view of mouth parts separated from mouth tube. FIG. 57–61. First, second, third, fourth, and fifth swimming legs.

PLATE XIII.

Internal anatomy of fourth copepodid larvæ.

FIG. 62. Median longitudinal vertical section. FIG. 63. Vertical section of posterior body a little to one side to show spermatophore receptacle. FIG. 64. Horizontal longitudinal section. FIG. 65. Longitudinal diagonal section, showing eye. FIG. 66. Section of sperm duct, enlarged. FIG. 67. Transverse section of body through the testes. Lettering; *dc*, digestive cells; *e*, eye; *i*, intestine; *ig*, infraganglion; *m*, muscles; *oe*, œsophagus; *sa*, sperm daughter cells; *sd*, sperm duct; *se*, sperms; *sg*, supraganglion; *sm*, sperm mother cells; *sp*, spermatophore; *sr*, spermatophore receptacle; *s*, stomach; *r*, rectum; *t*, testis.

PLATE XIV.

Lernæocera anomala and L. dolabrodes, new species.

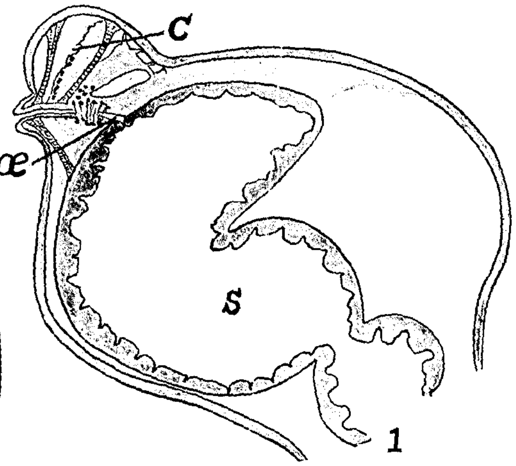
FIG. 68. *L. anomala*, side view. FIG. 69. Ventral view of same. FIG. 70. Cephalon, antennæ, and mouth parts. FIG. 71. First antenna of *L. dolabrodes*. FIG. 72. Second antenna. FIG. 73. First swimming legs of *L. anomala*. Fig. 74. Second antenna of same. FIG. 75. *L. dolabrodes*. FIG. 76. Mouth parts. FIG. 77, 78. First and second swimming legs.

PLATE XV.

Head outlines of the different species.

FIG. 79. *dolabrodes*. FIG. 80. *tortua*. FIG. 81. *lagenula*. FIG. 82. *catostomi*. FIG. 83. *anomala*. FIG. 84. *cruciata*. FIG. 85. *esocina*. FIG. 86. *cyprinacea*. FIG. 87. *temnocephala*. FIG. 88. *phoxinacæ*. FIG. 89. *tenuis*. FIG. 90. *diceracephala*. FIG. 91. *variabilis*. FIG. 92. *haplocephala*. FIG. 93. *pomotidis*. FIG. 94. *barnimii*.

PLATE VI.



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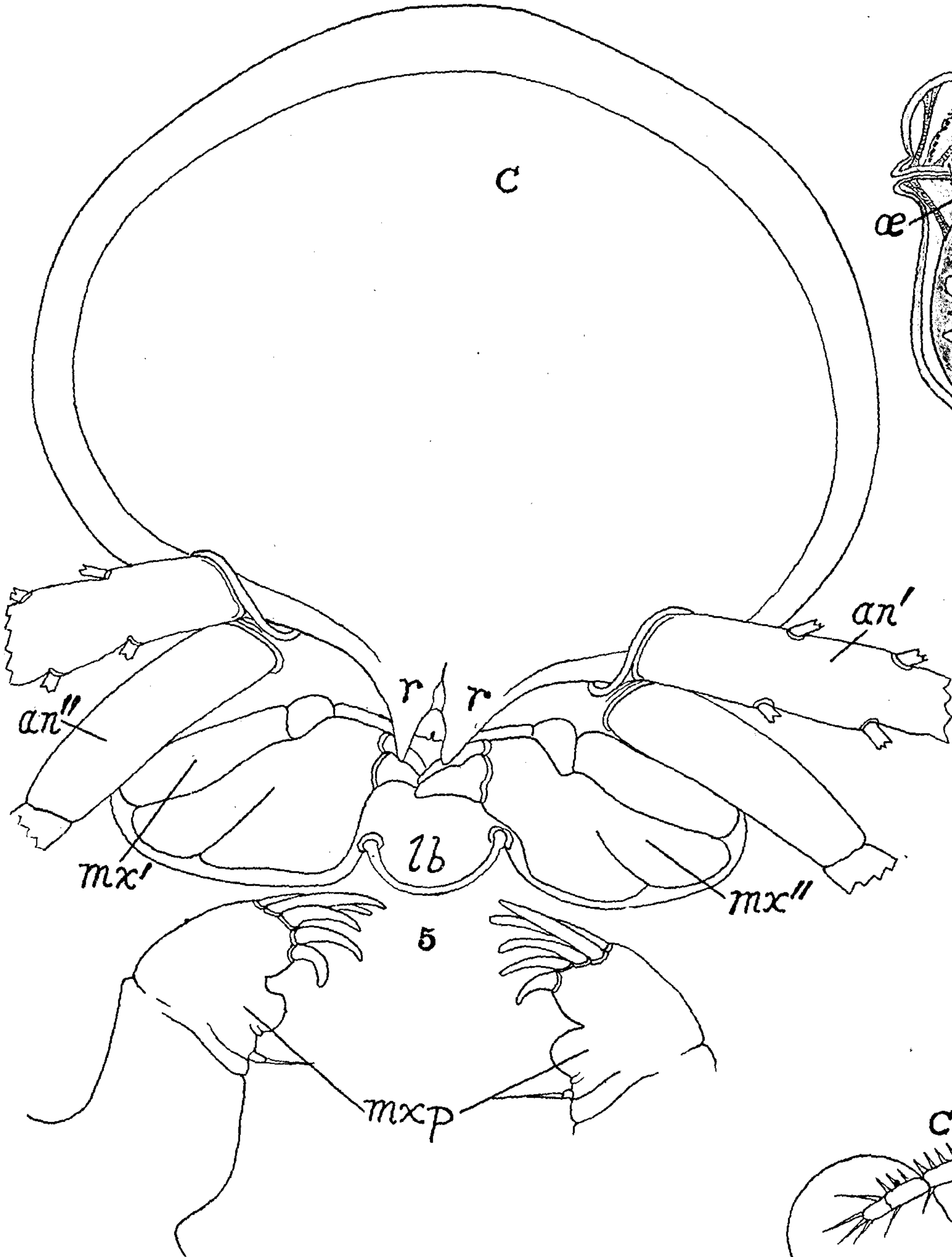

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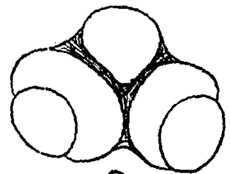

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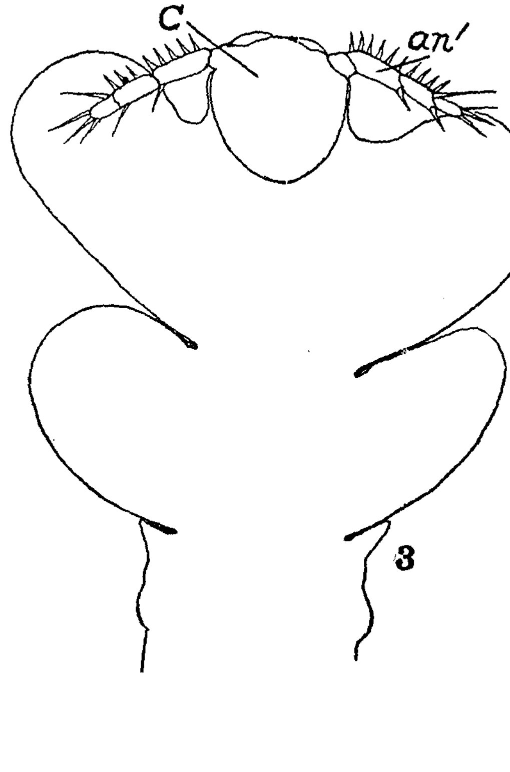

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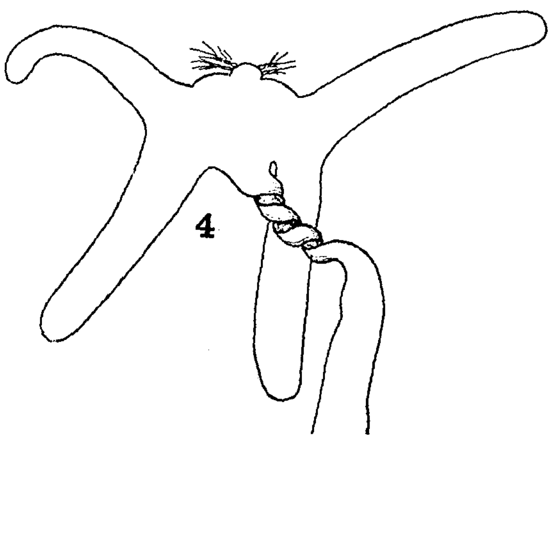

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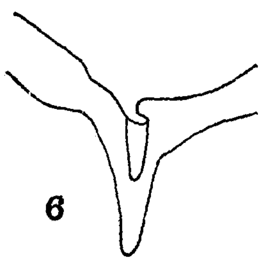

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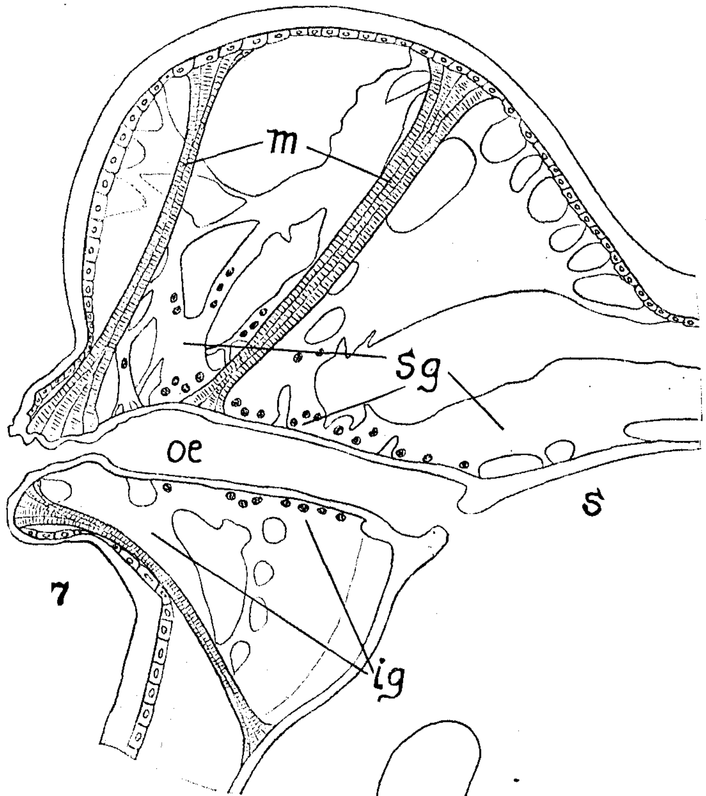

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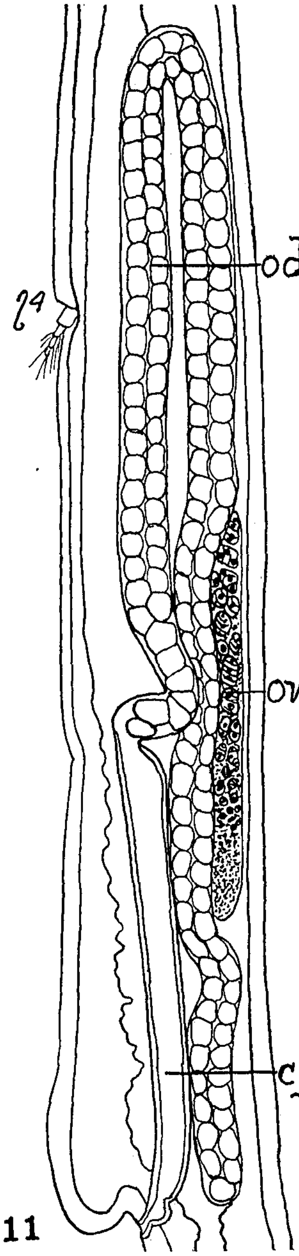

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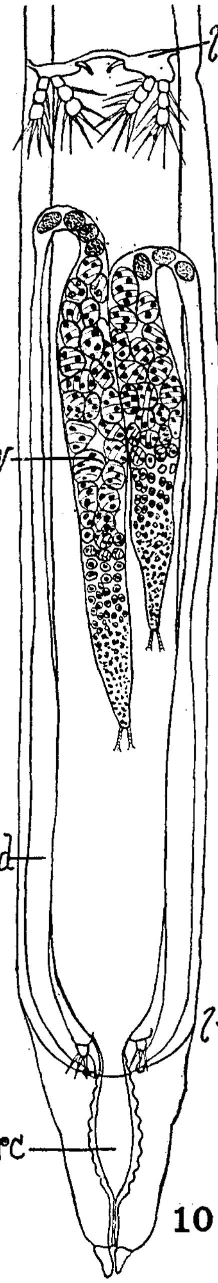

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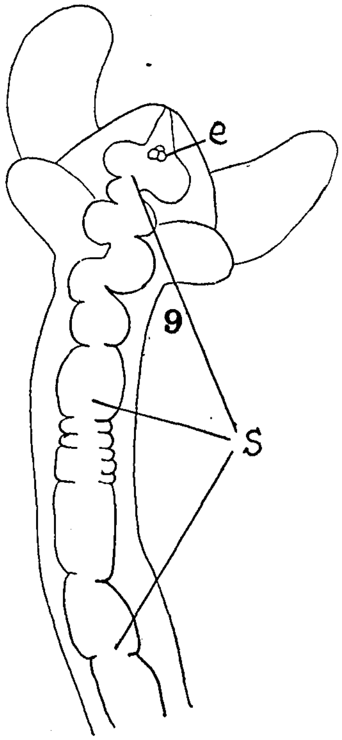

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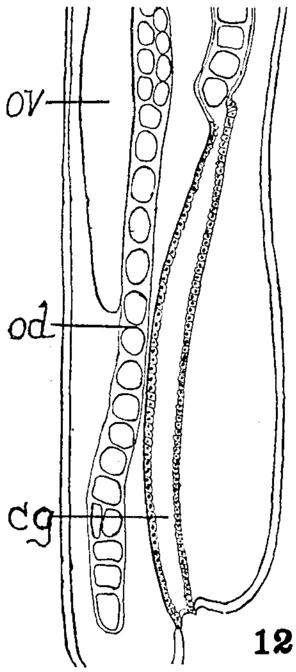

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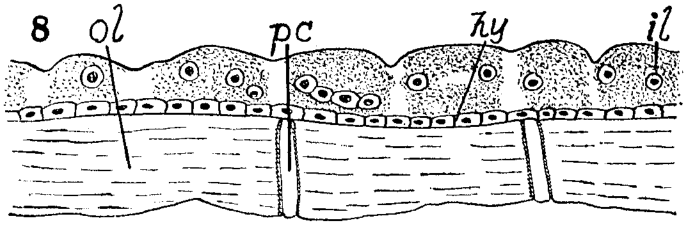

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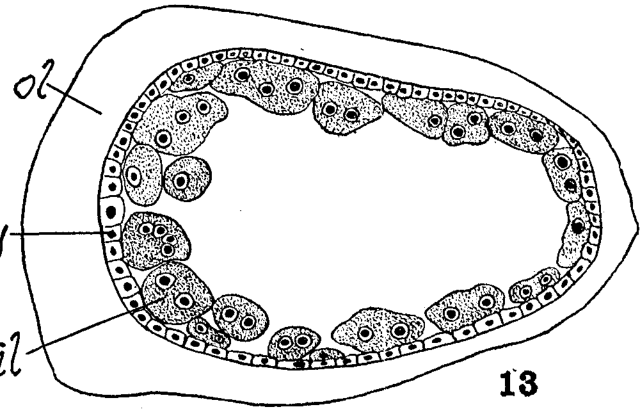

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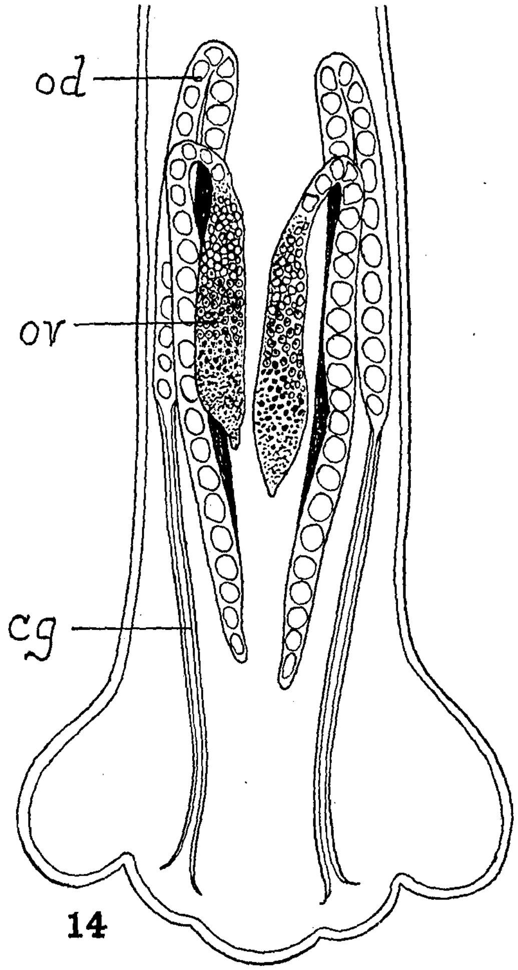

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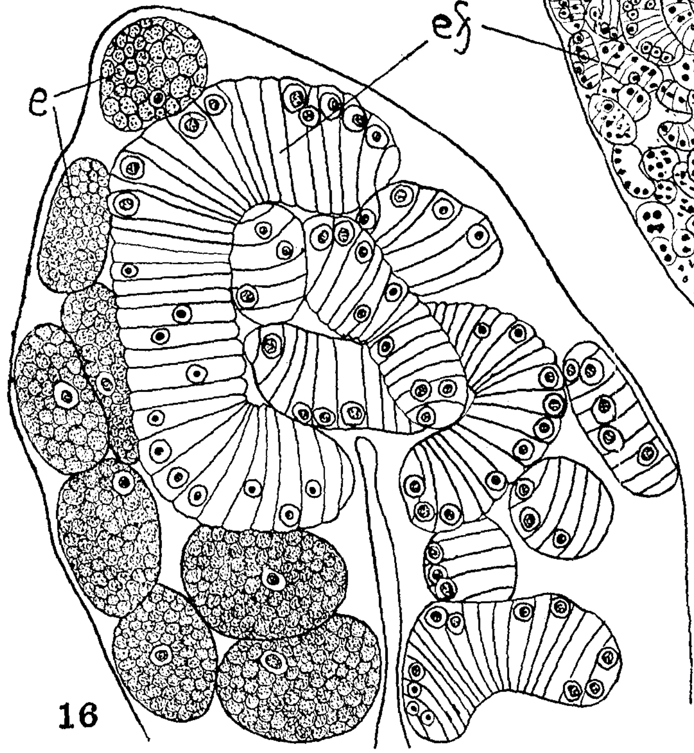

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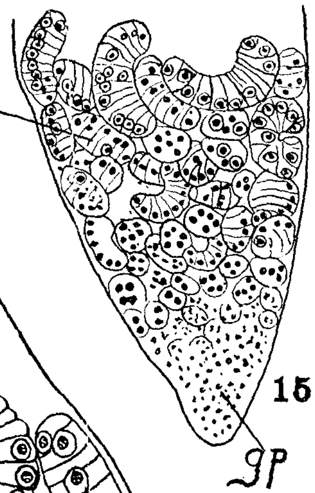

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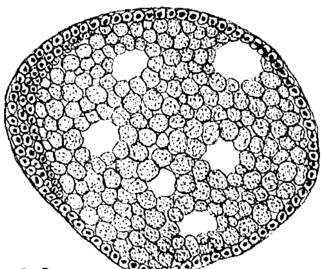

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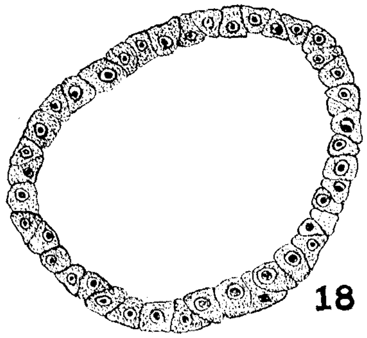

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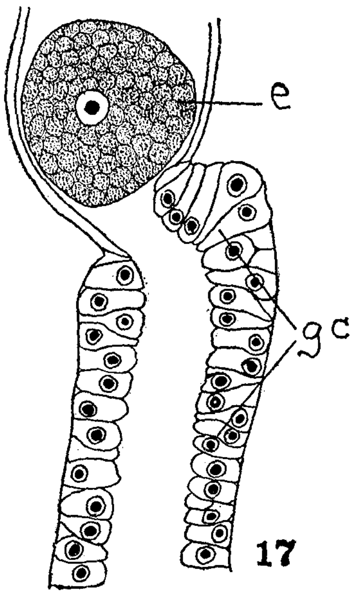

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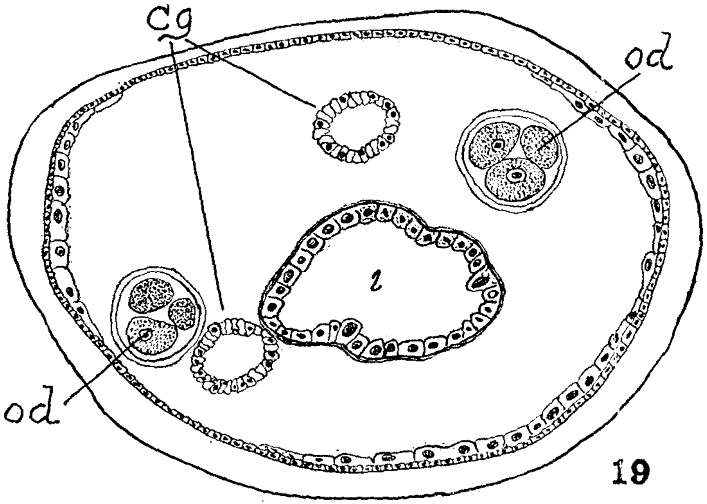

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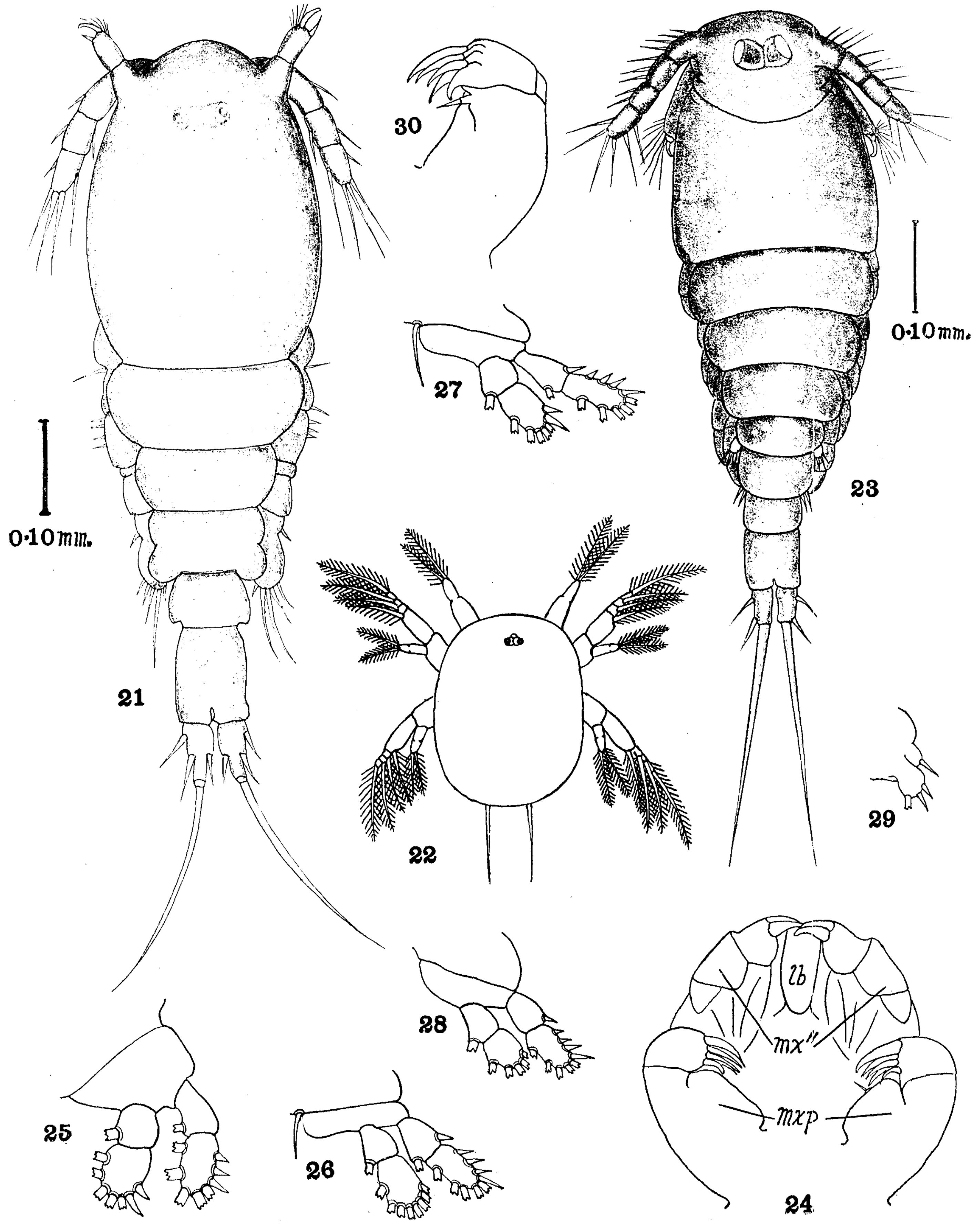
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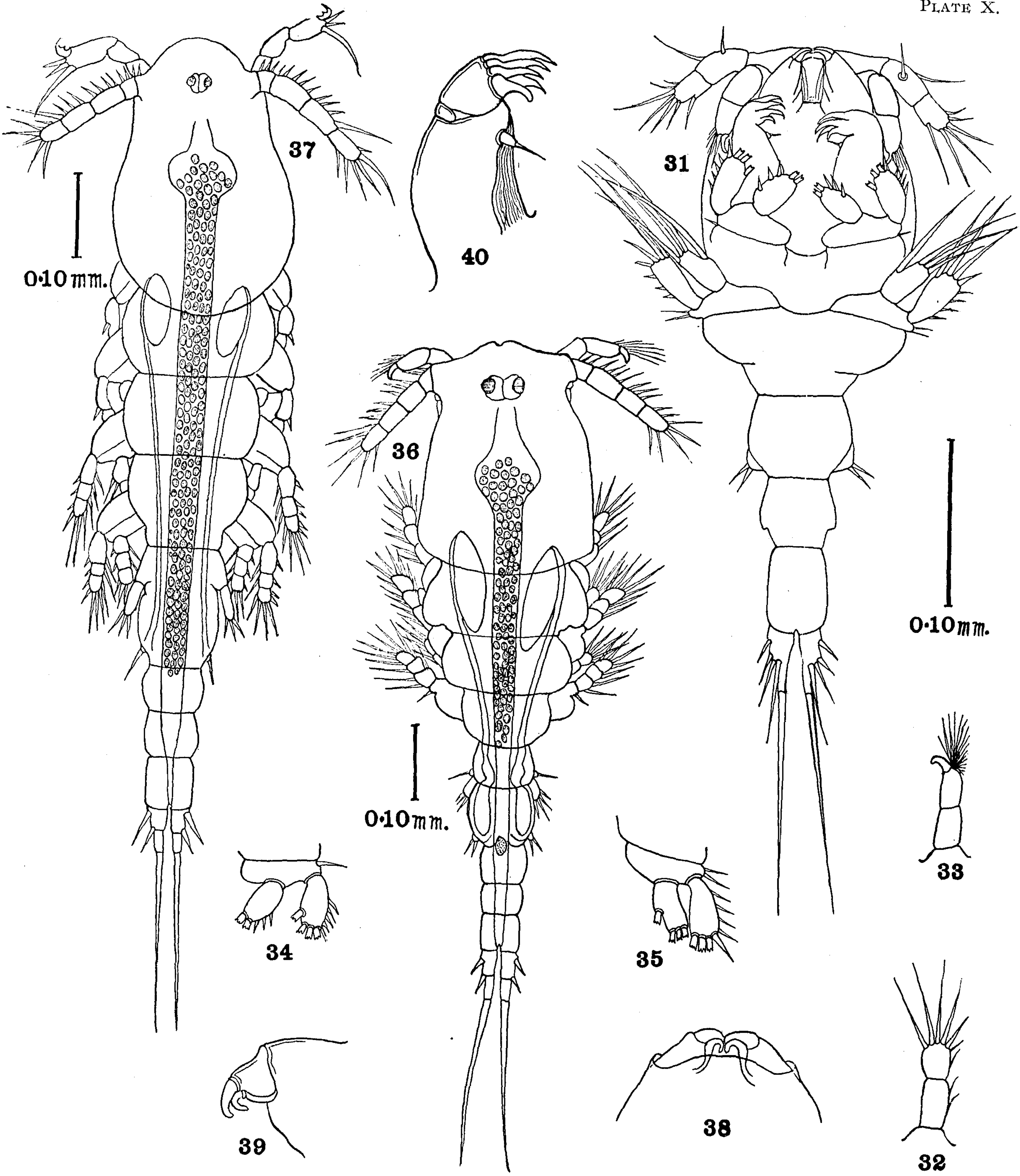
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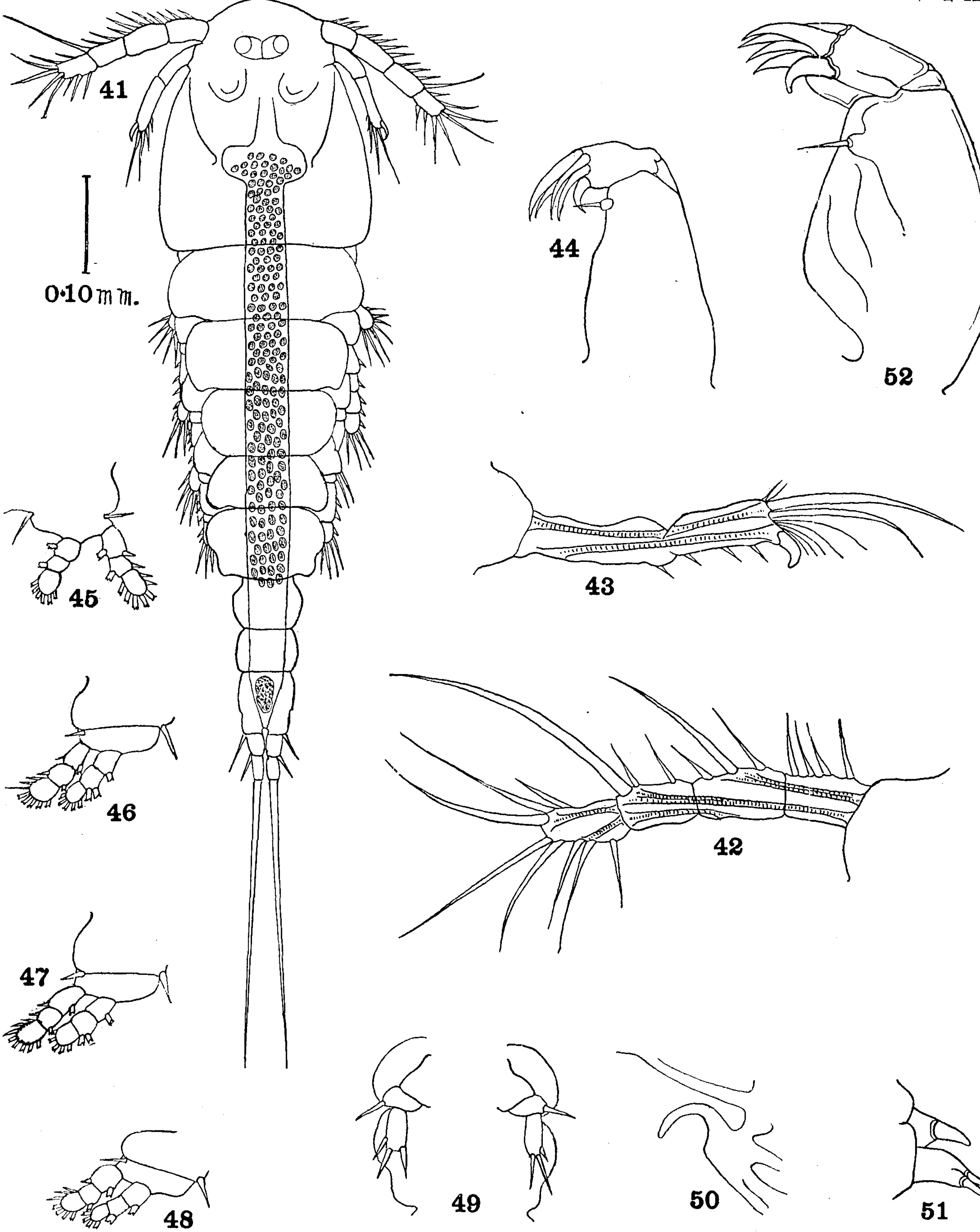
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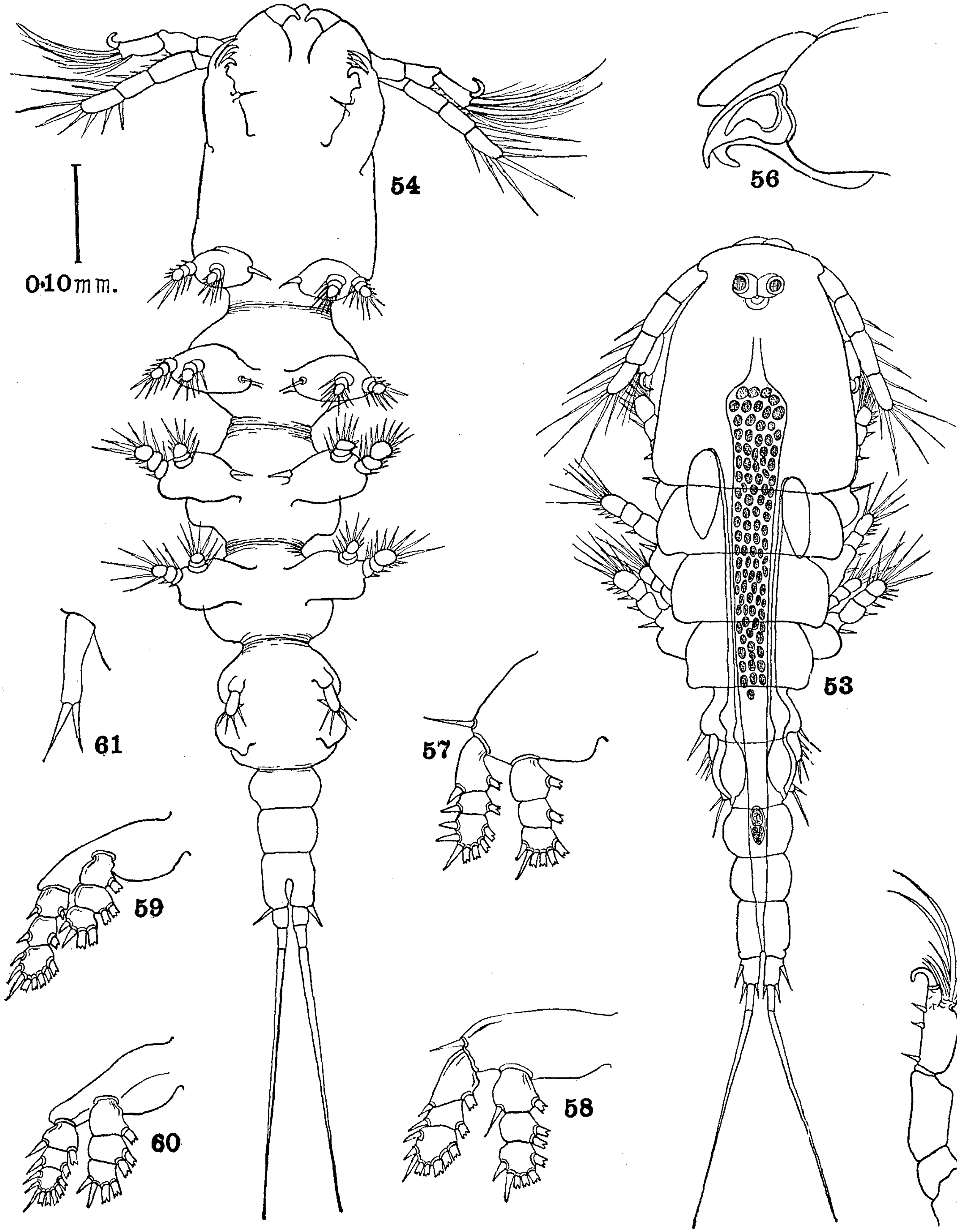
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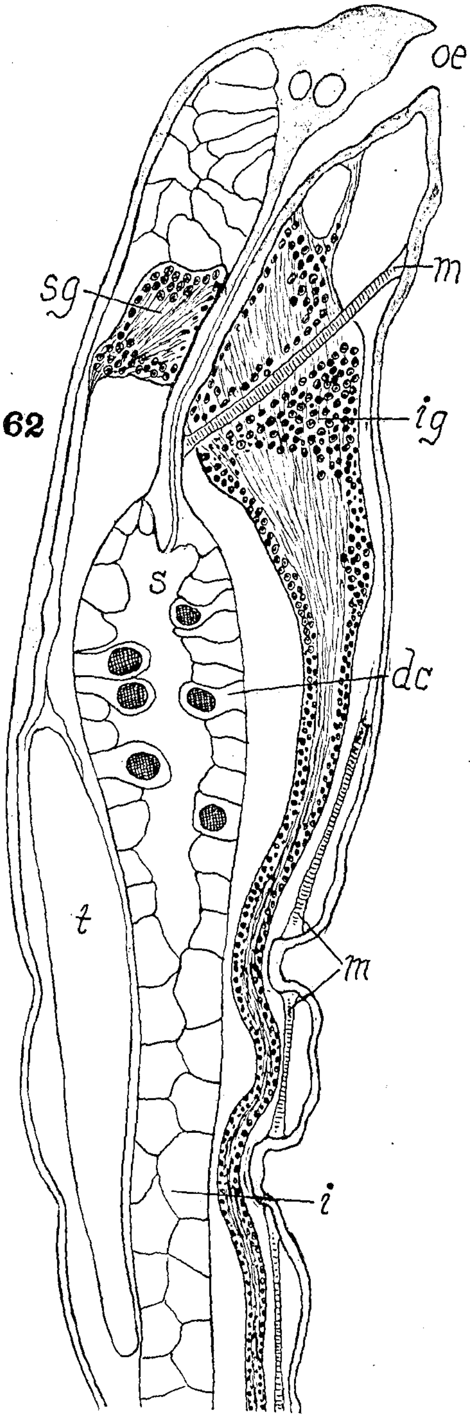
PLATE XIII.



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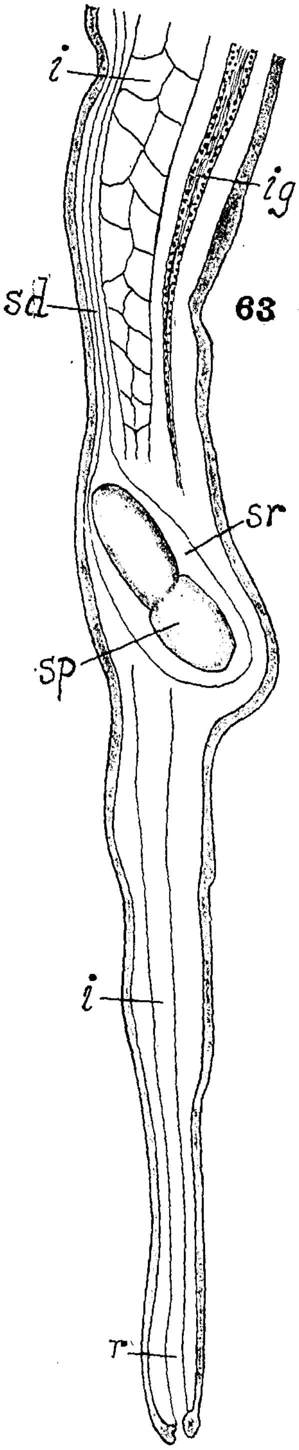

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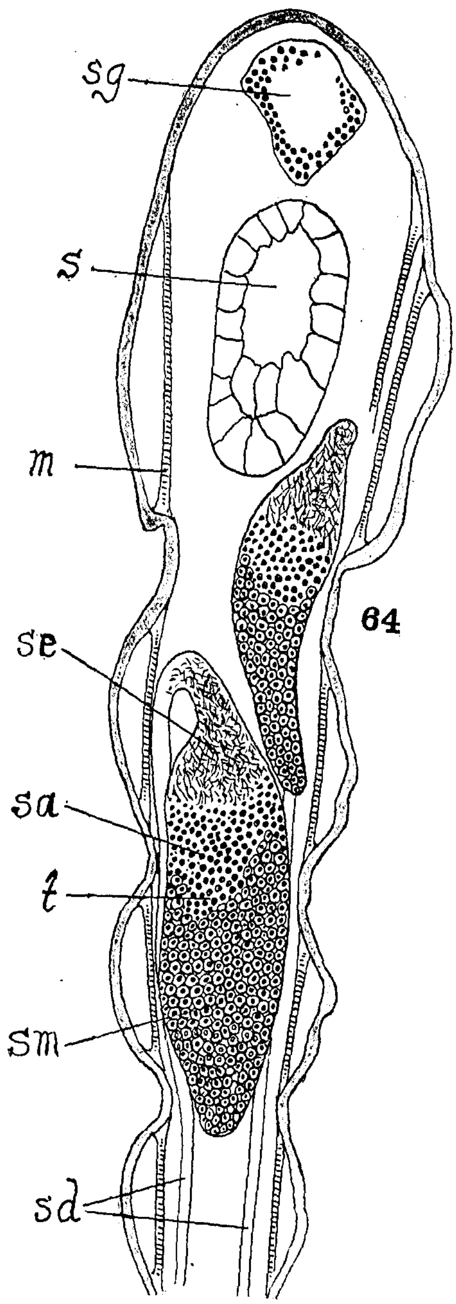

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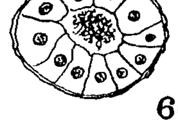

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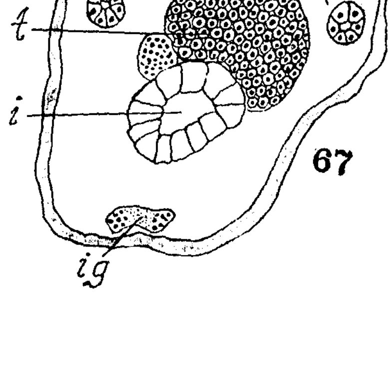

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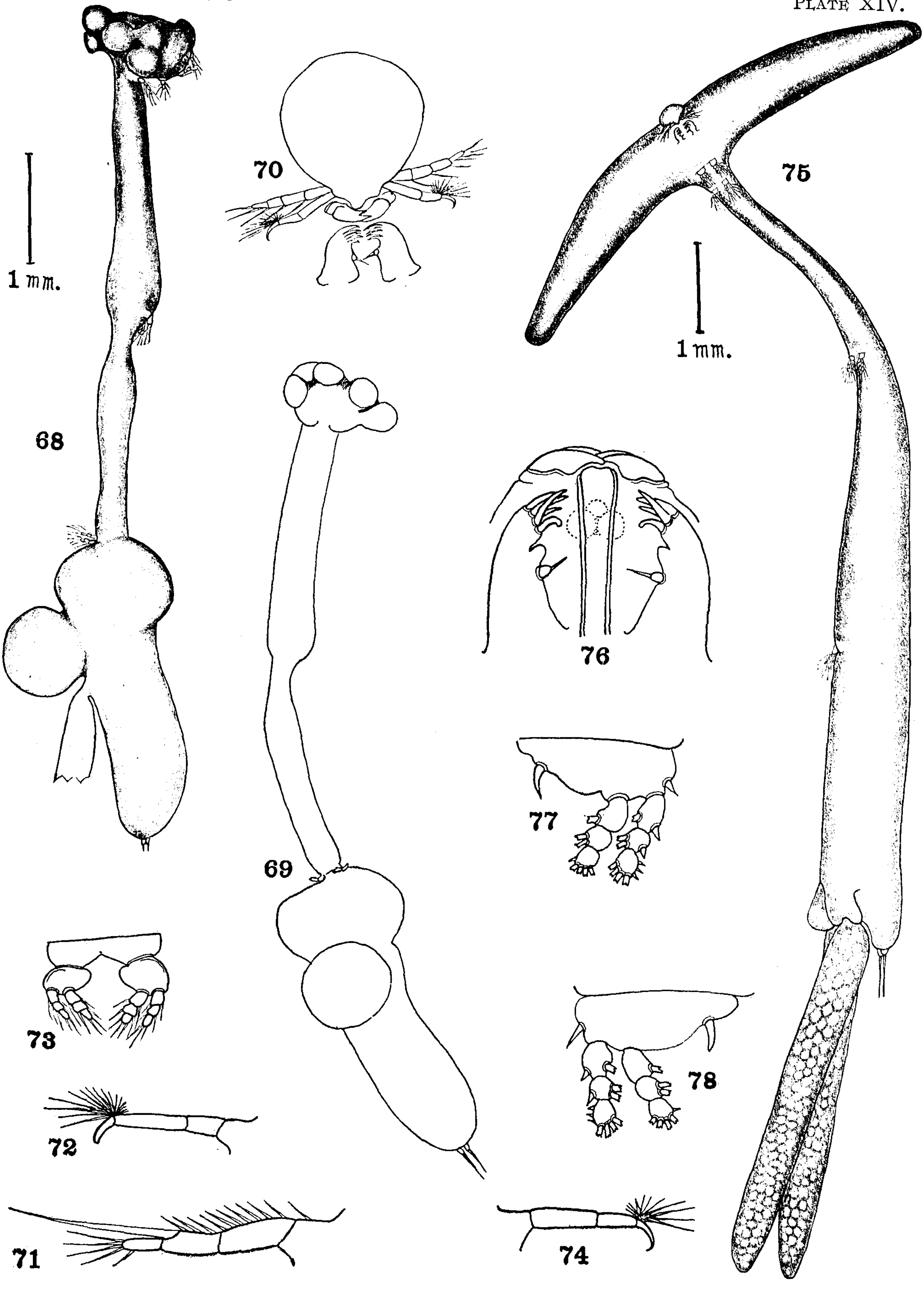
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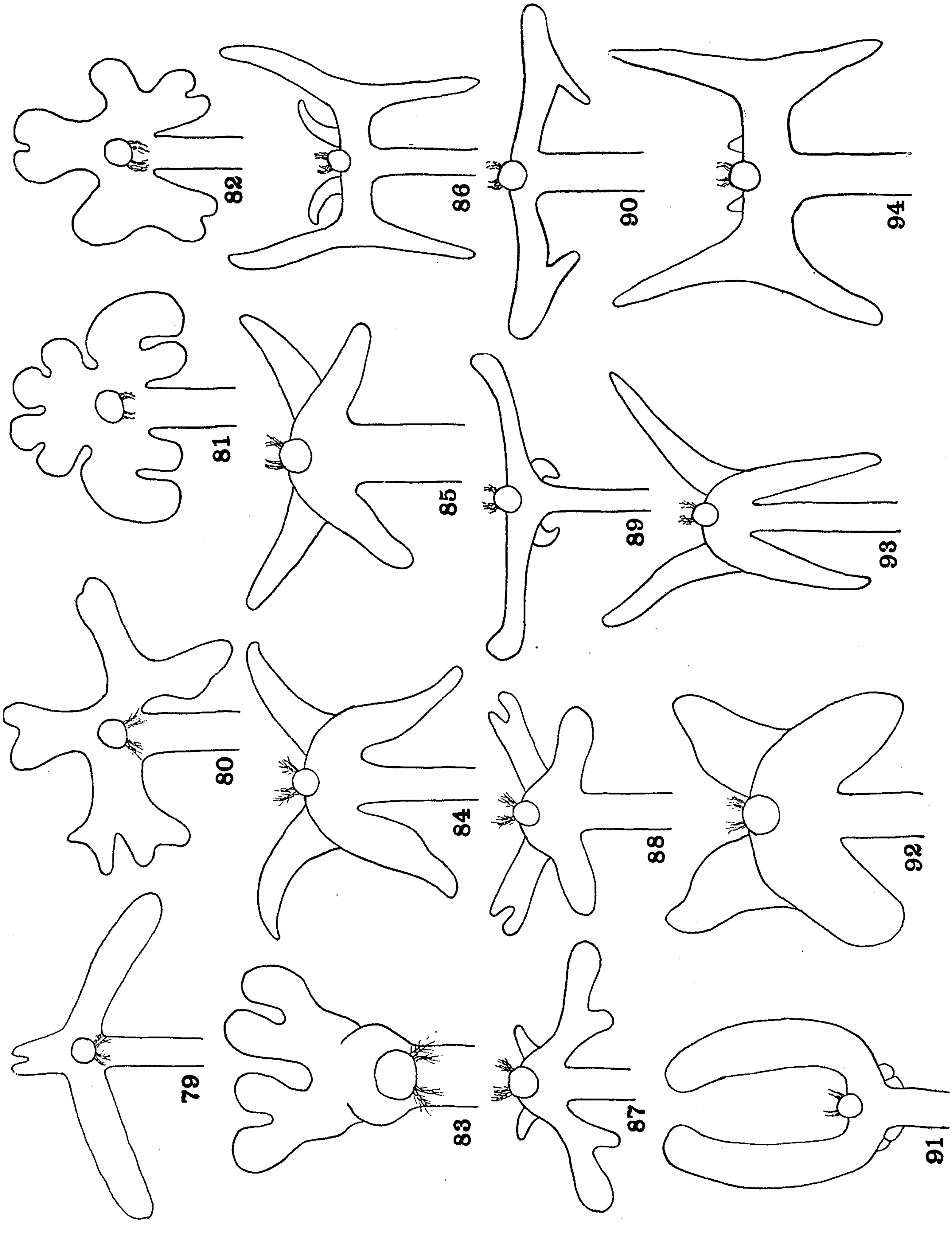
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