LERNAEOPODA SCYLLICOLA N. SP., A PARASITIC COPEPOD OF *SCYLLIUM CANICULA*.

By W. HAROLD LEIGH-SHARPE, B.Sc. (Lond.).

Part II.

(With 11 Text-figures.)

(The figures are all drawn from specimens mounted in Farrant's medium.)

Part I of this paper, which dealt exclusively with the females, appeared in *Parasitology*, viii. 262. After examining some dozens of dogfish each month for the previous three years I, at length, on April 2nd 1918 obtained from two separate dogfish caught during the preceding week at Plymouth, three females of *Lernaeopoda scyllicola* which were accompanied by males.

Males, which are rarely collected in the family Lernaeopodidae, are unknown hitherto in some species, and for the genus *Lernaeopoda* have been described only very inadequately as to the appendages in *L. bidiscalis* by Kane (1892), and superficially in two other species, viz. *L. elongata* and *L. galei*. A detailed description of this species therefore supplies a pressing want.

Sexual dimorphism attains striking proportions in this family, the males showing a marked dissimilarity in size, structure of the body, and its appendages, as also in the methods of prehension and locomotion. For, as has been said, though the free-swimming period of the male larva is no longer than that of the female, and the two often fasten themselves side by side upon the same host fish, whereas the attachment in the case of the female is permanent throughout life, it is but temporary in the male. When each partner has arrived at sexual maturity, the male, which is fixed only by the frontal filament, describes, with the point of attachment as centre, an arc until, on coming in contact with the body of the female, he abandons the filament and fastens himself to the female by the second maxillae and maxillipedes, remaining there for the remainder of his life. Not being permanently attached he is able to crawl about over the female's body, but such motion is slow and laborious, and probably performed only when necessary. He does not increase his size at each successive moult like the female, but remains dwarfed showing less degeneration, and more distinct segmentation in the trunk region.

A curious similarity in position is exhibited by each of the attached males. Each was located on the *left* side of the female, immediately behind the cephalothorax. I have previously remarked and figured that the female

shows faint indications of segmentation at the anterior end of the trunk. The first somite by means of a lateral protuberance forms a point of attachment for the male, and will be referred to as the "shoulder," the male's second maxillae being anterior to the protuberance, the maxillipedes posterior to it (Fig. 1).

Although it is generally agreed that a single pair of spermatophores contain sufficient spermatozoa to fertilize all the eggs a female can lay during

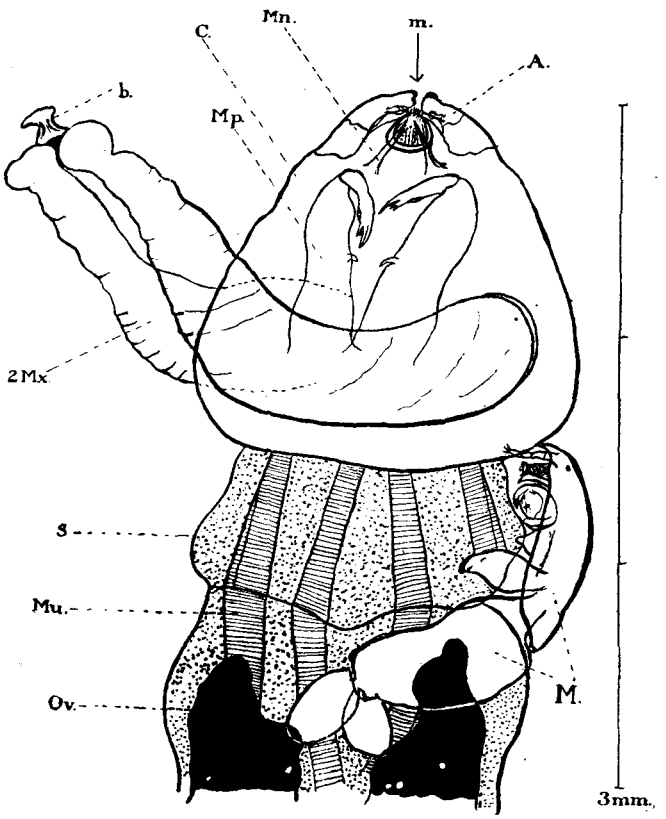

Fig. 1. *Lernaeopoda scyllicola*, the anterior two-thirds of a sexually mature, but not fully-grown female, in ventral aspect, with an attached male (*M*) *in situ*. *b.* bulla; *A.* antennae; *m.* mouth; *Mn.* mandibles; *2Mx.* second maxillae; *Mp.* maxillipedes; *Ov.* ovary; *S.* shoulder; *Mu.* muscles. (The appendages of the female are only roughly indicated; for details see Part I. Fig. 5.)

her lifetime, yet the male may remain clinging to her shoulder for a short period after mating (which takes place upon reaching maturity immediately after the moult at the close of the second copepod stage), since all my specimens of females were provided with well developed, normal egg-strings. It is unlikely, however that the male lives very long after fastening the first pair of spermatophores in place in the spermathecae of the female, judging from rarity of males in this and other species.

I may here record that the dogfish consigned to me from Plymouth during the year 1917, bore remarkably few examples of *Lernaeopoda scyllicola* ♀. In no case were more than two present, and about half the total number was devoid of them. As far as the present year has gone (April, 1918), the number of parasites present appears to show a slight increase. Dividing the number of male dogfish examined into the total number of parasites taken yields the following "periodicity table" of females:

1914 (the latter six months)	**4**
1915	**4** (maximum 6)
1916	**3**
1917	**1**
1918 (the first three months)	**2**

Only two individuals of *L. scyllicola* ♀ were observed on *female* dogfish during the whole of the foregoing period, and those during 1915. Besides the usual locations within the extra-cloacal aperture, and on the grooves of the claspers, I have recently found *L. scyllicola* ♀ in other, probably fortuitous, situations. In April 1918 I took a specimen outside the extra-cloacal aperture posterior to and between the fusion of the pelvic fins and the body, and one specimen (sexually immature) from the extreme tip of the right clasper. Although specimens from the clasper grooves are not uncommon, it is an extraordinary coincidence that hitherto I have only taken them from the dogfish's *right* clasper, and never from the left. I have heard it authoritatively stated by mariners and sea-faring men that sharks and other Elasmobranch fishes at the natatory "roll," or when they turn over to seize their prey, invariably depress the right side of the body, and I have observed the same phenomenon in the rolling of porpoises. Possibly in the rolling dogfish the left clasper is elevated, and the Copepod larvae sucked against the right clasper. I believe that the cloaca of the female dogfish would not be opened at the natatory roll, the pelvic fins having a different conformation posteriorly from those of the male, which may account for the rarity of *L. scyllicola* upon female dogfish.

From recent observations I conclude that the length of the "arms" (2nd maxillae) is so liable to variation, in the genus *Lernaeopoda* at any rate, that no reliance can be placed upon it as a specific character. The "arms" of female specimens taken on the clasper grooves are invariably much shorter than of those attached within the extra-cloacal space, while the one attached to the tip of the clasper had "arms" barely longer than the cephalothorax. Conversely the more anteriorly are the parasites located, the longer do their "arms" become, those situated practically within the cloaca and around the urino-genital papilla possessing the longest "arms" of all. It is obvious that these admit of, and possibly require, more movement about a fixed centre (the bulla), while such radial movement would be disadvantageous to an individual affixed to a clasper, as it would be liable to accidents causing detachment. The other, shorter-armed genera of the Lernaeopodidae are found upon the gills of various fish, where there is little freedom for movement, so that, in fine, the length of the "arms" has a biological rather than a specific significance.

DESCRIPTION OF THE MALE.

Body. The outline of the animal is best seen from Figs. 2, 3 and 4. The animals are of a yellowish white colour, though, as a rule, paler than the female. Length 2 mm. or about one third the length of the female which, though sexually mature, has not yet attained her full growth. The body is

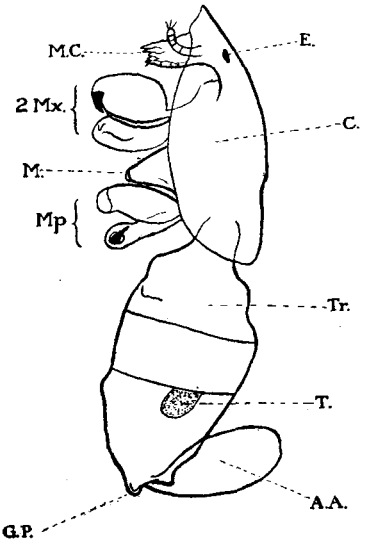

Fig. 2

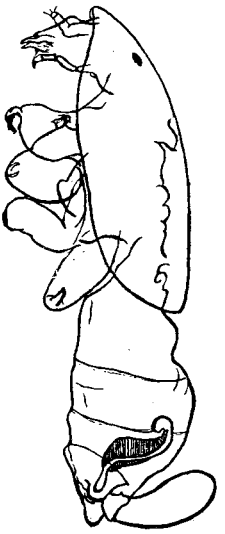

Fig. 3

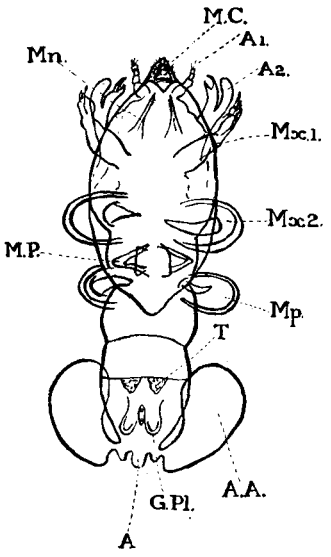

Fig. 4

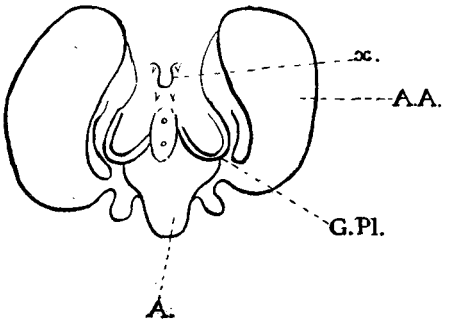

Fig. 5

Fig. 2. *Lernaeopoda scyllicola* ♂, viewed from the left side. *C.* cephalothorax; *Tr.* trunk; *T.* testis; *M.C.* mouth cone; *2Mx.* second maxillae; *Mp.* maxillipedes; *M.* mediative processes; *A.A.* abdominal appendages. *G.P.* genital process; *E.* eye. (Diagrammatic.)

Fig. 3. *Lernaeopoda scyllicola* ♂, the same as Fig. 2, but in greater detail; the reproductive system is indicated.

Fig. 4. *Lernaeopoda scyllicola* ♂, in ventral aspect. *M.C.* mouth cone; *A*1. antennules; *A*2. antennae; *Mx*1. first maxillae; *Mx*2. second maxillae; *Mp.* maxillipedes; *M.P.* mediative processes; *T.* testes; *A.A.* abdominal appendages; *A.* abdomen; *G.Pl.* genital plates; *Mn.* mandibles. (The anterior appendages are slightly exaggerated.)

Fig. 5. *Lernaeopoda scyllicola.* The posterior end of Fig. 4 enlarged. *A.* abdomen; *A.A.* abdominal appendages; *G.Pl.* genital plates; *x.* genital process (see p. 25).

bent so that the *cephalothorax*, which is proportionately larger than in the female, is more or less inclined to the trunk, from which it is separated by a well-defined groove, covered by a distinct dorsal carapace and strongly flattened dorsi-ventrally. The carapace has a two pointed rostrum. The *trunk* is conical and inflated, and shows traces of segmentation. Three regions are readily distinguishable. There are large paired *anal laminae*, which are curved in such a way as to turn forwards dorsally. These are homologous with the *abdominal appendages* of the female and should be called such. A pair of peculiar processes, found also in other species of *Lernaeopoda* (and perhaps homologous with an unpaired rounded protuberance *between* the maxillipedes in *Brachiella* and *Clavella*) protrude from the body wall between the second maxillae and the maxillipedes. These Kane (1892) calls "Intermaxilliped processes," since he considers the second maxillae to be a first pair of maxillipedes, a view held likewise by other authors, but, as it has been established by Hansen (1893), Giesbrecht (1893), Claus (1895) and Wilson (1910), that the penultimate pair of appendages arises in early development *in front* of the suture which separates the head from the thorax, while the ultimate pair arises *behind* that suture, the former are to be regarded as a second pair of maxillae, and Kane's name is no longer appropriate.

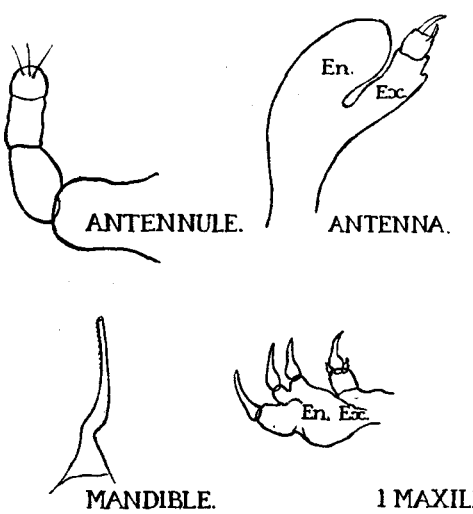

Fig. 6. *Lernaeopoda scyllicola.* The antennule, the antenna, the mandible and the first maxilla. *En.* endopodite; *Ex.* exopodite.

These *mediative* or middle-acting processes, though not prehensile, overlap the female, and may subserve the function of location, fitting, as their pointed ends do, over the protuberance that constitutes the female's shoulder. They shrink very considerably on mounting, and appear glandular rather than muscular.

There is no large postero-ventral spine on the abdomen, but instead a rounded protuberance and two pairs of small spines (Fig. 10).

The Appendages, all paired, are: 1st antennae (antennules), 2nd antennae, mandibles, 1st maxillae, 2nd maxillae, and one pair of maxillipedes, the same members as are represented in the female.

The 1*st Antenna* or *Antennule* (Fig. 6) is four-jointed. The basal joint is the largest, but has no spiral turn as it has in the female. The other joints diminish regularly in size, and the terminal joint is tipped with (two or usually) three sensitive setae.

The *2nd Antenna* (Fig. 6) consists of a basal joint bearing a large unjointed endopodite with a round or blunted end, and a small exopodite whose diameter is half that of the endopodite, and which is distinctly two jointed, the terminal joint being a claw which forms a true chela in conjunction with a spine projecting from the penultimate joint.

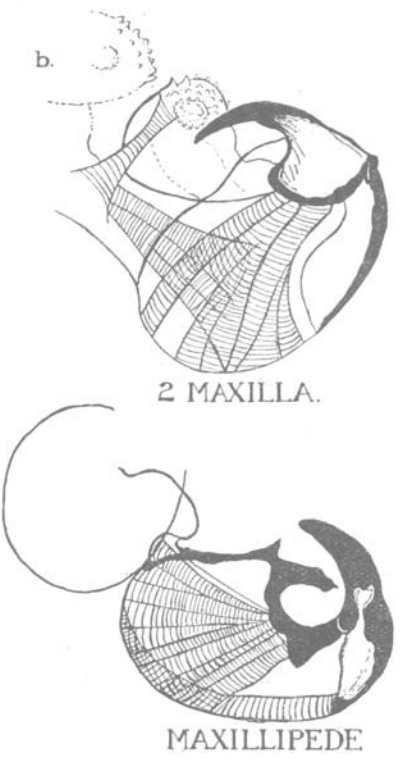

Fig. 7. *Lernaeopoda scyllicola.* The second maxilla and the maxillipede *b.* the pad of spines on the basal joint of the fellow maxilla seen in perspective.

The *Mandibles* (Fig. 6) precisely resemble those of the female. The teeth appear to be vestigial.

The 1*st Maxilla* (Fig. 6) consists of an unsegmented endopodite, and an exopodite or palp which is two-jointed and tipped with a large mammillated claw and two small subsidiary claws. The endopodite is tripartite at the distal end, the outer ramus being terminal, and the other two on the inner margin. Each ramus ends in a long mammillated claw.

The 2*nd Maxilla* (Fig. 7) is stout, two-jointed, with a large spinous process on the basal joint for the apposition of the terminal claw.

The *Maxillipedes* (Fig. 7) closely resemble the 2nd maxillae. They are two-jointed, and again the terminal claw is curved and fits against a process on the basal joint which is not spiniferous. They are not appreciably larger than the 2nd maxillae, as in most species. They arise close to the bases of these maxillae and are swollen and fleshy, terminating in an auricular disc. The two discs approximate at the inner edge, and thence conjointly give rise to a saucer-like *tenaculum*.

The musculature of the appendages is seen from Fig. 8, and calls for no comment. It is much more powerfully developed than in the female.

The unpaired median nauplius **eye** is retained in these males. Kane also found it in *L. bidiscalis*; but none of the male Lernaeopods described by Wilson (1915) are figured as possessing such an organ. A very noticeable optic nerve connects it with the supra-oesophageal ganglion. The eye appears pink.

The Mouth parts. The mouth forms a suctorial proboscis situated at the summit of a cone which is bent at right angles to the cephalothorax, so as to be directed downwards. There is an upper and a lower lip each of which is bordered by setae of characteristic shape. In appearance it exactly resembles that of the female *q.v.*

The Alimentary canal, like that of many parasites, is degenerate and has no visible contents. A moderately long oesophagus leads into a dilated stomach which tapers off to form an intestine which apparently ends blindly (Fig. 11). Wilson (1915) is emphatic that no male member of the entire family possesses an anus.

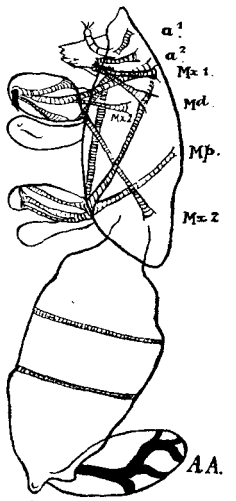

Fig. 8. *Lernaeopoda scyllicola*, showing the musculature of the appendages. a^1. antennular muscles; a^2. antennal muscles; *Mx*1. and *Mx*2. muscles of the first and second maxillae respectively; *Mp.* maxillipedal muscles; *A.A.* chitinous ridges of the abdominal appendages; *Md.* mandible.

No special glands are present apart from those cells lining the canal, so that digestion is probably intra-cellular. Both stomach and intestine are thick-walled, and the inner layer of the latter is stated by Wilson to contain many modified cells which secrete a digestive enzyme, and thus it takes the place of a digestive gland.

The males are merely epiphytic (epizoic) upon the females; certainly not parasitic. It has been suggested either: (1) that the males do not feed at all; hence perhaps the brief duration of their adult life, and the absence of functional teeth on the mandibles, and of an anus (though apparently Kane figures one in *L. bidiscalis*); or (2) that they are commensal, and participate in the meal of cellular tissue which the female has rasped off the unprotected soft portions of the extra-cloacal region of the host. An examination of the fluid extruded from the cloaca of the host under a high magnification revealed large numbers of characteristic spiral-headed spermatozoa of the dogfish, and enormous quantities of the eggs of the parasitic Nematode so well known to infest all parts of the dogfish's alimentary canal. I suggest that he feeds on either of these, either being especially nutrient; if on the former, it may be the failure of the supply of these out of the breeding season (or "temporary season") that leads to his early decease.

The Reproductive System of the male consists of a pair of testes situated in the posterior third of the trunk (Fig. 2). Each testis is a pear-shaped body, obliquely placed, with its pointed end facing dorsally and forwards. The spermatocytes are situated at its base, while spermatozoa in various stages of development appear in the more pointed region. From the pointed end a short curved duct leads in an anterior direction to a relatively large cavity, the *spermatophorogonium*, whose thick and glandular walls secrete the spermatophore. From the spermatophorogonium the *vas deferens* finally descends, parallel at first with the previous duct in a posterior direction, but soon it turns ventrally and passes across the side of, or immediately below the testis, enlarging finally to form the genital aperture of that side. Each genital aperture is bounded laterally by a *genital plate* having a double border,

and is separated from its partner by the *genital process* (*sensu stricto*), homologous with that of the female. Both Kane (1892), and Wilson (1915, Plate XXIX, fig. 22), in which I believe he follows Dana, call these genital plates spermatophores. I do not see how they can possibly be such. They do not appear to me to be solid bodies, nor to contain any contents, but merely spoon-shaped expansions with their concavities facing inwards, towards one another, and, as such, capable of grasping the spermatophores when partially extruded and ready for insertion in the female. Moreover as my females bear egg-strings I presume the eggs are fertilized, which predicates that the spermatophores have already been deposited (Fig. 9).

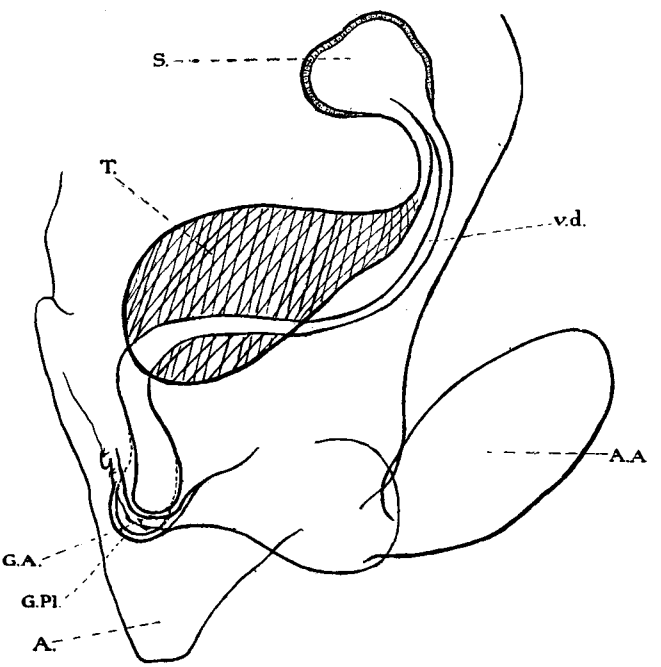

Fig. 9. *Lernaeopoda scyllicola*. ♂ Reproductive system. *T.* testis; *S.* spermatophorogonium; *v.d.* vas deferens; *A.* abdomen; *A.A.* abdominal appendages; *G.A.* genital aperture at the side of the genital process; *G.Pl.* genital plates.

The *genital process* (Fig. 10) bears anteriorly a small rounded projection having a pair of small spines before and a pair behind it, and, posteriorly between the genital plates, two small apertures, one in front of the other, whose significance I have not at present determined.

The Nervous System (Fig. 11) consists of a *supra-oesophageal ganglion* and an *infra-oesophageal ganglion* connected with one another by paired oesophageal commissures which run round either side of the oesophagus.

The supra-oesophageal ganglion, dorsal to the oesophagus, is very noticeable in a preserved specimen not specially stained or treated, situated close behind the eye, which is half the size of the ganglion. The latter is pigmented with a

pinkish-yellow colour. From its anterior end it gives off a readily discernible optic nerve to the eye. From the optic nerve, which is no doubt a compound trunk, branches pass to the antennules, antennae, and possibly to the upper lip.

The *infra-oesophageal ganglion* is large, double the size of the other ganglion, and irregularly shaped. The lower lip and the mandibles are probably innervated from this ganglion, but I have not traced the branches. From the anterior end of the ganglion a pair of nerves arises to supply the 1st maxillae;

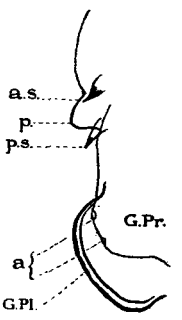

Fig. 10

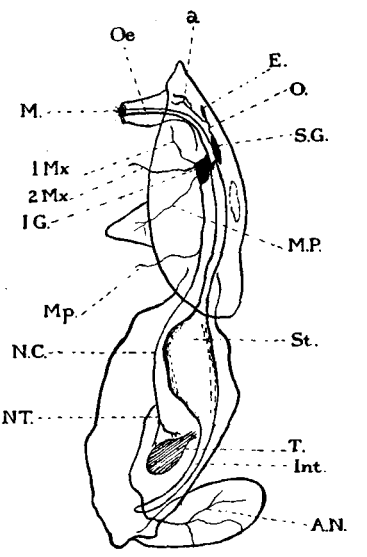

Fig. 11

Fig. 10. *Lernaeopoda scyllicola*, an enlarged view of the genital process (*G.Pr.*) in lateral aspect. *a.s.* anterior spines; *p.* protuberance; *p.s.* posterior spines; *a.* apertures; *G.Pl.* genital plate.

Fig. 11. *Lernaeopoda scyllicola*, the alimentary canal and nervous system. *M.* mouth; *Oe.* oesophagus; *St.* stomach; *Int.* intestine; *T.* testis; *E.* eye; *S.G.* supra-oesophageal ganglion; *I.G.* infra-oesophageal ganglion, a commissure connecting it with the foregoing ganglion; *a.* antennular and antennal nerves; *O.* optic nerve; *1Mx.* nerve to first maxilla; *2Mx.* nerve to second maxilla; *M.P.* nerves to mediative process; *Mp.* nerve to maxillipede; *N.T.* nerves to testis; *A.N.* nerves to abdominal appendages; *N.C.* main nerve cord. (From a preparation treated with osmic acid 1 per cent.)

immediately behind these a pair to the 2nd maxillae. From the postero-ventral surface a pair arises which enters the mediative processes and branches freely within them. From the posterior end springs a main nerve cord which gives off branches to the maxillipedes; these branches (according to other authors) may, however, really arise directly from the ganglion and run coincidently for some distance with the main cord (cf. the origin of the lateral line branch of the 10th nerve in *Scyllium*). The main nerve cord gives off minute branches to the stomach, and a well-marked nerve which bifurcates to the testes. It is continued to the end of the body into the abdominal

appendages in which it ramifies freely, a point seemingly not hitherto made out by other investigators.

Posterior to the supra-oesophageal ganglion and apparently innervated by it, dorsal to the oesophagus, is a body which is probably one of a pair of excretory bodies mentioned by other investigators (the maxillipedal pair).

General note upon the females. From Fig. 1, and by comparing it with Fig. 1, Part I, various discrepancies in size may apparently be detected. The sexually mature females mentioned in this paper, it must be borne in mind, are not fully grown, and they show a much more striking likeness (*inter alia* as to dimensions) to *L. galei*; so much so that I hazard the conjecture that those authors who confounded the two species in former times based their conclusions on the examination of specimens that were not fully adult. Nevertheless the hook on the maxillipede,one of the more prominent characters on which I founded this species, is easily discernible on my young females though it is at present so small as to be more appropriately called a spine. It is obvious from Fig. 1 that the "arms" (2nd maxillae) must elongate considerably hereafter to become in time as long as the trunk, since they are at present not much longer than the cephalothorax. I have also a female so immature that as yet it shows no indications of ovaries; it is not accompanied by a male, and its arms are shorter still.

The Generic characters of the male are at present indeterminable owing to the comparatively few species that have been found. The following characters may be noted: Size larger in proportion to female than in other genera; cephalothorax slightly inclined to trunk, from which it is separated by a constriction; abdominal appendages exceptionally large, and turned forwards dorsally; mediative processes present and well developed; antennule four-jointed; antenna with a terminal claw and chelate; second maxilla with a large spinous process on the basal joint, forming a chela with the terminal claw; maxillipedes resembling the second maxillae.

Specific characters of the male. Cephalothorax strongly flattened dorsi-ventrally and covered dorsally with a distinct carapace which is prolonged forwards into a two-pointed rostrum. Cephalothorax not much inclined to trunk, which is of about equal length, cylindrical, inflated, and distinguishable into three regions as well as a minute posterior abdomen. Genital process with two pairs of minute spines and two apertures. Trunk without large postero-ventral spine. The abdominal appendages narrow into a slender neck where they join the abdomen, then swell into large bodies rounded at the extremities. Single median eye present. Maxillipedes not appreciably larger (if any) than the 2nd maxillae.

REFERENCES.

CLAUS (1895). Ueber die Maxillarfüsse der Copepoden. *Arb. Zool. Inst. Univ. Wien,* XI. 49.

DANA. *United States Exploring Expedition during the years* 1838–1842, vol. XIII. part II. Poecilopoda, p. 1309.

GIESBRECHT (1893). Mitteilungen über Copepoden. VI. Zur Morphologie der Maxillipeden. *Mittheil. Zool. Stat. Neapel,* XI. 83.

HANSEN (1893). Zur Morphologie der Gliedmassen und Mundteile bei Crustaceen und Insekten. *Zool. Anz.* XVI. 193.

KANE (1892). On a new species of *Lernaeopoda* (*bidiscalis*) from the west coast of Ireland and Polperro, Cornwall. *Proc. Roy. Irish Acad.* Ser. 3, II. 203.

WILSON (1910). The Development of *Achtheres ambloplitis* Kellicott. *Proc. U.S. Nat. Mus.* XXXIX. 263.

—— (1915). North American Copepods belonging to the Lernaeopodidae, with a revision of the entire family. *Ibid.* XLVII. 565.