# THE DEVELOPMENTAL STAGES OF *LERNAEO-CERA BRANCHIALIS* (LINN.)

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### (Text-figs. 1–6)

## CONTENTS

## INTRODUCTION

The remarkable life history of *Lernaeocera branchialis* was first described in detail by Claus (1868 b), who also recognized the close relationship of the old family Lernaeidae, highly modified though it is, to the Caligidae (1868 a); more recently this close similarity has been emphasized by Gurney (1934). Though the genus *Lernaeocera* is so common on gadoid fishes, the larval forms from pleuronectids are not frequently recorded; indeed, none has yet been found in the western hemisphere. Andrew Scott (1901) obtained abundant material from flounders from the Piel Hatcheries, but his descriptions are not in very great detail, and he leaves some doubt as to the number of stages passed through during metamorphosis.

Wilson's (1917) account is largely based on that of Scott, from whom he borrows his figures. He gives an original description, however, of a nauplius and a metanauplius of a species which he identifies with *L. branchialis*, which he obtained from a gadoid at Woods Hole. In the opinion of Schuurmans Stekhoven (1936 a) there are so many points of discrepancy between his description and that of the European forms, that (in 1937) he renamed the

American form *L. wilsoni* (Wilson, 1917). Stekhoven gives adequate descriptions and figures of many species of the genus (1935, 1936*a*, 1936*b*, 1937), but he concerns himself only with adult (mature) females; though he refers (1935) to the finding of larval forms on *Pleuronectes flesus* off the Belgian coast and again at Helder (1936*b*) he does not describe them.

During the examinations of flounders from inshore waters near Plymouth, referred to in a previous paper (Sproston & Hartley, 1941*a*), about a hundred developmental forms of this parasite were collected, and the study of them has served to elucidate many points which were not clear from Claus's account and at the same time has raised new problems. It has been possible during the present studies to correct some details in the existing descriptions of *Lernaeocera* larvae, and an attempt has been made to follow the exact way in which the peculiar suspensory 'filament' of the chalimus stages arises. A comparison of the length data of the various stages has shown a somewhat unusual type of growth curve.

These investigations have been carried out during the tenure of the University of London Post-Graduate Research Studentship at the Marine Biological Laboratory, Plymouth. My thanks are due to the Director and staff of the Laboratory for their encouragement and practical help, and to Dr R. Gurney, who has read the manuscript and given his helpful advice.

## The Nauplius

In a previous paper I have mentioned that it was possible to keep the mature female *Lernaeocera* alive for periods up to 9 days in circulating sea water in the laboratory, provided that no injury was done to the parasite during the dissection from the vascular tissues of the host. When the eggs were ripe and the nauplii began to emerge the parasite was transferred to a plunger jar, and some of the nauplii were taken for immediate examination and their moulting into the copepodid form was observed microscopically. Hatching was also observed, but only one form of nauplius was found and no nauplius was ever seen to moult into a second nauplius stage. The enormously long uniseriate egg-strings hatch very slowly, so that some days may elapse before all the nauplii have been liberated—unlike *Chondracanthus lophii*, whose almost equally long multiseriate egg-strings fragment and hatch within a few hours. Hatching eggs have been found throughout the year, and as concluded elsewhere, breeding is continuous in this as in some other parasitic copepods (Sproston & Hartley, 1941*a*). Unfortunately, owing to war-time fishing conditions, it was not possible to obtain flounders for infection experiments, but the identity of the copepods reared in the laboratory with those found from time to time on the gill-tips of flounders left no doubt that the forms described from the latter habitat were *Lernaeocera branchialis* (Linn., 1767) Blainville, 1822.

It may be mentioned that whereas the nauplii soon after hatching swam

freely in the circulating sea water and even tended to prefer the surface levels, when about to moult they sank to the bottom. The resulting copepodids, though actively swimming, also tended to keep near the bottom of the container: they would often cease swimming and crawl, largely by a 'hand-over-hand' movement of their chelate second antennae, which during the more active swimming were kept folded back along the under side of the cephalothorax, and so were invisible from above. This observation may be correlated with the behaviour of the intermediate host, the flounder, and it is interesting in that it supports an analogous observation by Gurney (1930). He found that the nauplii of *Nicothoë astaci* and *Chondracanthus lophii*, after a brief period of activity at all levels in the aquarium, sank to the bottom where they remained until moulting. It may not be insignificant that all three species are about to seek hosts which live on the bottom.

Claus did not describe or figure the nauplius stage of *Lernaeocera*, and though Van Beneden (1861, figs. 7, 8) gave two figures, neither these nor his descriptions are sufficiently detailed to be of much value. Wilson (1917) described two nauplius stages: a more or less rhomboidal nauplius 0·45 mm. long and with a maximum width of 0·40 mm. (pl. 12, fig. 107), and a metanauplius 0·55 mm. long, with a maximum width of 0·25 mm. which occurs near the anterior end (pl. 10, fig. 88). The metanauplius differs in shape from the nauplius, and has two pairs of limb rudiments in the form of bud-like protrusions on either side of a small median process at the hind end of the tapering body. No such form was found in the present material.

Andrew Scott (1901, pl. 4, fig. 2) shows 'a newly hatched nauplius' which is broadly club-shaped and in many ways resembles Wilson's metanauplius, especially in the slight indication of two segments near the narrow truncated hind end; the length is given as 0·45 mm., which agrees with Wilson's rhomboidal nauplius in size.

Fig. 1 represents a typical nauplius from the present material from Plymouth, and though there was rather a wide range of size, 0·345–0·405 mm. (see Fig. 6*A*) —the mean of ten random samples being 0·371 mm. long with a maximum width of 0·2–0·25 mm.—it was markedly smaller than either Scott's or Wilson's material. The general colour is slightly yellowish due to the contained fat globules. Irregular chromatophores occur laterally at about the middle two-thirds of the animal; they are of a dark puce colour, and a still darker pigmentation surrounds the eye. The nerve mass, chiefly below this, is bilobed and stains deeply with haematoxylin. Neither my speci-
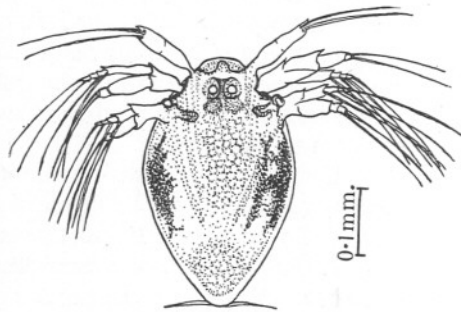


Fig. 1. Nauplius (stage I) of *Lernaeocera branchialis*—dorsal aspect.

mens nor Scott's show limb rudiments near the hind end and I saw no free nauplius showing segmentation, though I have fixed specimens in the process of moulting into copepodids in which such faint segmentation is seen under the skin at the hind end. It seems that in my material the metanauplius stage has been suppressed and is passed through very rapidly just before the emergence of the copepodid. This takes place some 24 hr. after hatching from the egg at laboratory temperatures.

The usual three pairs of appendages are found in the nauplius, though the labrum could not be made out, and a pair of stiff setae, 'balancers', occur at the hind end, usually held at right angles to the body axis, though they have some degree of freedom posteriorly. Pedaschenko (1898, pl. 5, fig. 169) figures them with small articular bosses, but I am unable to confirm this (he also shows small basal joints on the first antennae).

The *first antennae* arise from the sides of a somewhat flattened frontal region by a narrow isthmus, and there is a faint indication of segmentation into two equal joints: they are not so distinct as Scott shows them, and in Wilson's figure of the nauplius the antennae are unjointed and bear two small spines on the posterior subterminal region which I have not seen. In all my specimens there is a short sharp spine on the anterior angle of the tip which also has two long setae. Between these appendages there is a small median papilla under the skin, slightly ventral, which stains darkly with haematoxylin; in nauplii about to moult it is distinctly but minutely papillose. I suspect this of being the precursor of the 'rostral gland' which secretes the peculiar attachment apparatus of the later (chalimus) stages.

The *second antennae* arise somewhat ventrally in a shallow depression on the anterior lateral margins; the basal joints narrow abruptly at their insertion, and there is a short anterior spine on the broad distal end of this joint which gives rise to a four-jointed exopodite and a three-jointed endopodite. The exopodite is more slender and the first joint is about one and a half times longer than the other three together, each of which bears a long seta—four in all. The endopodite is much stouter, and the first two joints are about equal; the first bears a short anterior spine, and the end joint is short and stout with two long setae.

The rami of the second and third appendages have a considerable degree of freedom: Fig. 1 is a camera lucida drawing showing the position of the rami of the second appendage on the right side interchanged; this appendage has a marked tendency to be displaced ventralwards, and the endopodite on the left side is seen in perspective.

The third pair of appendages is similar to the second and the rami bear four and two setae respectively. The proportions of the segments differ slightly, the first joint of the exopodite being shorter and about equal to the remaining three, and the endopodite has a long basal joint and two short ones following it. At the base of the third appendage is what appears to be an excretory gland: a pear-shaped granular mass which stains deeply with haematoxylin and has a non-staining lumen which seems to open on to the basal segment of

this limb on its anterior side. In some specimens some indication of a similar aperture could be made out on the base of the second antenna, but no underlying gland was visible.

In his account of the developmental stages of *Thersitina gasterostei*, Gurney (1913, p. 422) states that the maxillary gland was present in the third nauplius (the antennary gland was present in the second nauplius), but even in the later nauplius stages of this copepod he was unable to make out the second maxilla. Owing to the telescoping of the early stages of *Lernaeocera*—a single copepodid following a single nauplius stage—it may be that the antennary gland, which is the normal excretory gland of the copepod nauplius, has only a transitory existence and that it is soon replaced by the maxillary gland of the later stages, this being present even in the nauplius in which there is no second maxilla as yet developed on which it can open. This would mean that at this stage external development is lagging behind internal development. The gland is apparently functional, since it has a clearly defined lumen, and it discharges through a specially formed aperture on the base of the third appendage (the mandible), which in this sense has the functional significance of a second maxilla. Unfortunately, it was not possible to make out the further development of this gland[1] in the copepodid stage, and its aperture has not yet been seen in any of the later stages of this species. When more material becomes available it will be possible to settle this question by serial sections and dissection.

## THE FREE-SWIMMING COPEPODID

Large numbers of free-swimming copepodids (Fig. 2*a*) were obtained from nauplii moulting in plunger jars in the laboratory, and others exactly similar were taken from time to time throughout the year on the gill-tips of the flounders caught near the mouths of the estuaries at Plymouth. This stage shows a remarkable variation in size, the length varying from 0·385 to 0·633 mm. with an average of 0·484 mm.; but only three individuals were longer than 0·55 mm., and these will be referred to later when the rate of growth is considered. In spite of the difference in size there was no difference in form of these copepodids, so that whether there is a moult or not in the copepodid stage, it is not thought that more than one stage form can be represented.

The cephalothorax is about five-eighths of the body length and has a strong equatorial line of segmentation behind the second maxillae, and other intermediate folds are present which hint at segmental boundaries. The cephalothorax in all the developmental forms shows a clear ventral infolding along the lateral margins, particularly in the anterior half, as shown in the figures. The mouth-parts in the early stages are not easy to see and they have been omitted from many of the figures. The first antennae are indistinctly five-articled and

[1] Colonel R. B. S. Sewell, with whom I discussed this matter, made the interesting suggestion that it is more likely to represent the primitive segmental organ of the mandibular somite which has become the functional excretory organ in this type.

are abundantly beset with fine setae, the terminal joint bearing four stronger setae; the second joint is the longest, though this is not obvious, especially in the later stages when the first antenna has a tendency to be bent ventrally and laterally along the fold of the cephalothorax, so that in many of the figures it is seen in perspective. These appendages arise immediately in front of the strong chitinized bars which run forward from the anterior lateral angles of the cephalothorax, bifurcate in front, and support the wide basal joints of the chelate second antennae. The second antennae therefore arise only slightly ventrally to the anterior margin of the cephalothorax; they are the main pre-hensile organs and have a remarkable degree of freedom—rather more than 180°—for at this stage the rectangular rostrum has not yet developed to re-strict some slight movement dorsally. Their independent movement in the vertical plane has already been referred to when they crawl over a solid sub-stratum. On finding a gill-tip of a flounder the chelae take a firm hold and this is seldom relinquished, so that it becomes the anchorage of the animal until the adult free-swimming stage (VII) is reached. Owing to the violent currents in the gill chamber the copepod is twisted and twirled on its support; some-times it is washed off, but though it swims for a time it will soon take a fresh hold. Such currents were imitated for the purpose of observation by removing the gills of flounders to watch-glasses of sea water under the microscope and a one-way current provided by a pipette. The specimen, of which Fig. 2a is a camera lucida drawing, was fixed in situ and shows the left chela turned through 180° on its own axis, a compensatory movement just before the animal lost its hold. The gill filaments were grasped by the now well-formed second maxillae, so that the mouth-parts were kept in close contact with the tissues on which they browse, in spite of currents.

Two pairs of well-formed biramous swimming legs are present, the first on the last thoracic segment fused in the cephalothorax and the second on the first free thoracic segment. The second free segment is of characteristic shape and bears two long stout spines on its posterior lateral corners which represent the third pair of legs; the third free segment is also characteristic in shape and represents the pregenital and genital segments; the fourth is the abdomen and bears two relatively large caudal laminae each with five long setae. The expo-dite and endopodite of the first pair of legs are two-jointed and the first joint is produced into a fine spine; the distal joint of the exopodite in both limbs bears an outer spine and five long setae, but the endopodite in both bears five long setae only. In the second pair of legs the rami are as yet only one-jointed, but the short spine between the joints of the adult limb is already formed.

### The First Chalimus Stage and the Suspensory Mechanism

At the time of moulting from the copepodid a chitinous secretion appears to come from the mid-frontal region and to be extruded as a laterally flattened thread between the now closely clinging second antennae into the surrounding

gill tissue. It penetrates the latter in two diverging filaments—apparently through the perforations made by the claws. The rest of the secretion falls dorsally and laterally forming the hood which is at first attached to the newly formed cephalothorax, enclosing in it the new second antennae and the distal joint of the old pair which remains attached to the gill, inside the hood, and embedded in the chitinous mass. Ventrally the secretion falls as a pear-shaped mass to the level of the chelae of the new antennae.
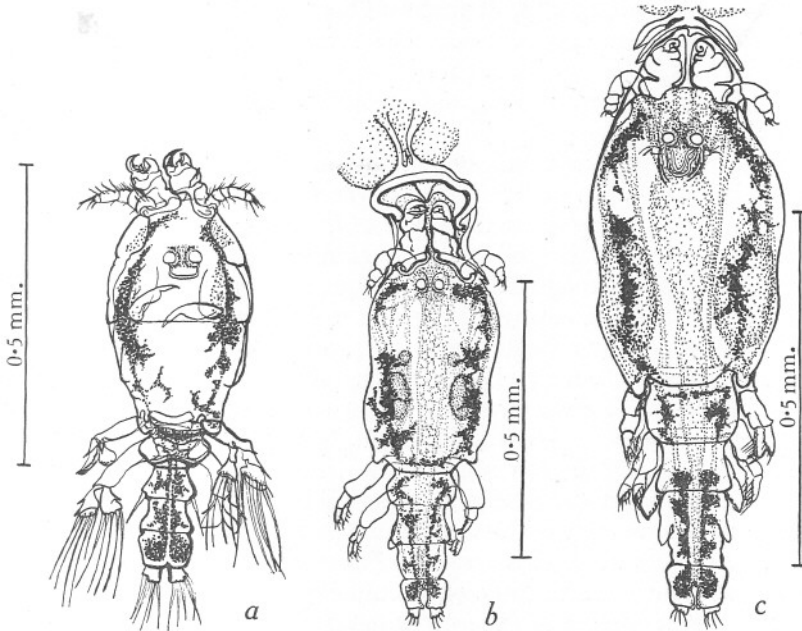


Fig. 2. *a*, Free-swimming copepodid (stage II)—ventral aspect of female. *b*, first chalimus (stage III)—dorsal aspect of male. *c*, second chalimus (stage IV)—dorsal aspect of male.

Soon after this moult has been completed, the movement of the chalimus causes the hood to crack along the transverse line joining it to the dorsal region of the head, and occasionally the dorsal triangular hood section breaks off, but usually the hoods remain attached by their apices to the common filament and the particular stage can be determined by counting these, as Claus has already shown (1868*a*). For example, the fourth chalimus (Fig. 3*b* below) has four hoods, that of the last moult being still attached to the carapace.

Fig. 2*b* shows the first chalimus stage with hood (which was formerly attached to the dorsal region of the copepodid during the moulting period) broken away, but the old chelae are hidden under the chitinous plate: the new hood has broken away except for its lateral edges. The two intrusions of chitin into the gill tissue are seen and in between them is a fine filament—the axial thread of the suspensory apparatus. The ventral pear-shaped masses are best seen in the lateral view of the fourth chalimus stage (Fig. 3*b*).

It seems, therefore, that it is justifiable to refer to the fixed stages of *Lernaeocera* and its allies as 'chalimus stages', since in all essentials they are so similar to the chalimus stages of the Caligidae. Gurney (1934) has given an admirable account of the developmental stages of *Caligus labracis* and *C. centrodonti* and the mode of attachment to their host, but in these as in other Caligidae the arrangement is much simpler, for the sole attachment is by a long filament, secreted once and for all by the first chalimus at the time of moulting from the copepodid. It suspends the animal well away from the host tissues and none of the appendages are involved as they are in *Lernaeocera*; the only addition at each succeeding moult is a small bulb cementing the new frontal region on to the last bulb, and the number of bulbs is an indication of the stage.

A curious intermediate condition is found in *Pennella varians* as illustrated by Wierzejski (1877, pls. 32, 33). These larvae were found on cephalopods and they are very similar, except in the shape of the forepart of the cephalothorax and the wider spread of the free thoracic region and limbs, to the parallel forms of *Lernaeocera*. The strong chelate second antennae begin by suspending the copepodid; but on its moulting they appear to lose hold of the tissues and the secretion alone suspends the first chalimus, leaving a small knob at the top of the conical chitinous funnel, which is much narrower than in *Lernaeocera* and does not include the second antennae but is well anterior and dorsal to them. A bulb of secretion is formed at each moult, but no succession of hoods is left as in *Lernaeocera*. Dedifferentiation of the chelae and other appendages and their loss of segmentation is seen in these chalimus stages as in the present material, but whereas this is at its maximum in the second and third chalimus stages in *Lernaeocera*, it begins earlier in *Pennella*—the first and second stages showing maximum dedifferentiation. Similarly, in *Sarcotretes scopeli*, which is probably a near relative of *Pennella*, Jungersen (1913) has shown four chalimus stages which all appear more retrograde than any stages of the other two genera; the second antennae are more ventrally placed in the copepodid and remain ventral and rather feeble until the free pelagic stage which follows the fourth chalimus. In this species there seems to be no question of the involvement of the anterior appendages in the suspension filament, and the arrangement is somewhere between that of *Pennella* and *Caligus*, differing from the latter in that the filament appears to arise from a broader base as in *Pennella* and so appears as a conical thread; but unlike either no clearly formed bulbs are seen, and certainly no succession of hoods as in *Lernaeocera*. Jungersen admits to using caustic potash (KOH) for the removal of these forms from the fins of *Scopelus glacialis*. This drastic treatment may have dissolved some of the more delicate secretion if this is not pure chitin, for he says: 'In all the present pupal stages I find the structure [of the filament] to be identical.'

To return to the structure of the first chalimus of *Lernaeocera* the most striking change is in the loss of the long-swimming setae on the two biramous legs, the change in shape of the free thoracic segments, and the appearance of

a stump in the place of the long spine representing the third leg. The anal laminae are relatively smaller and their setae are also short and poorly developed: only four of them could be made out in this and the following stages. The rami of the limbs have lost their fine structure, though those of the second leg are now two-jointed. No new segment has been added to the thorax.

### THE SECOND CHALIMUS: STAGE IV

There has been little change in general shape (Fig. 2c) since the last moult, but dedifferentiation has increased. The second antennae are swollen masses with their segmentation shown only by folds, and in the legs it is becoming more indistinct, that of the third leg being barely discernible, though this shows a notched inner margin with vestigial setae. There is an indication of the third free segment dividing into the pregenital and genital segments, and the former shows the rudimentary stump of the fourth pair of legs. In the specimen depicted the dorsal part of the hoods has been broken off, but the axial filament is well shown arising below the bases of the antennae and passing up between them. The mouth tube has not joined up and the mandibles, which are relatively long at this stage, are seen at the sides; in the next stage they are seen within the mouth tube which is in the process of being formed. The second maxillae and maxillipedes have been omitted from these figures to avoid confusion. All the chalimus stages are illustrated by males, though there is only a very slight difference in the shape of the hind body in the female and she is always larger (see Fig. 6 A).

### THE THIRD CHALIMUS: STAGE V

The general shape of this stage (Fig. 3a) is similar to the last, but some of the appendages are beginning to redifferentiate, though the second antennae appear to be more regressive than in the preceding stage and their segmentation is only indicated by notches; the distal ends of the tips of this appendage belonging to previous moults are seen below each hood—the suspensory apparatus is shown in optical section, the dorsal parts being omitted for clarity. The free segments of the thorax are less clearly marked; but there is an indication of the presence of five, and this is confirmed in the next stage (Fig. 3b) in which the genital segment of the adult is clearly shown to be composed of two segments. (This has already been formulated for the Caligidae by Gurney (1934).) Fig. 3a shows the emergence of the fourth pair of legs, which are clearly two-jointed at this stage though the small distal blade-like joint has no setae.

### THE FOURTH CHALIMUS: STAGE VI

There is again little change in shape (Fig. 3b), but the segmentation of all parts is better defined than in the previous chalimus stage; the limbs, though not functional, are beginning to resume their characteristic form and the setae

are slightly stronger, as are also those on the caudal laminae and first antennae. The second antennae have again recognizably chelate ends. The mouth tube is nearly closed and the first maxillae can be seen at its sides, though its bipartite structure is not apparent at this stage. The second maxillae are both shown,
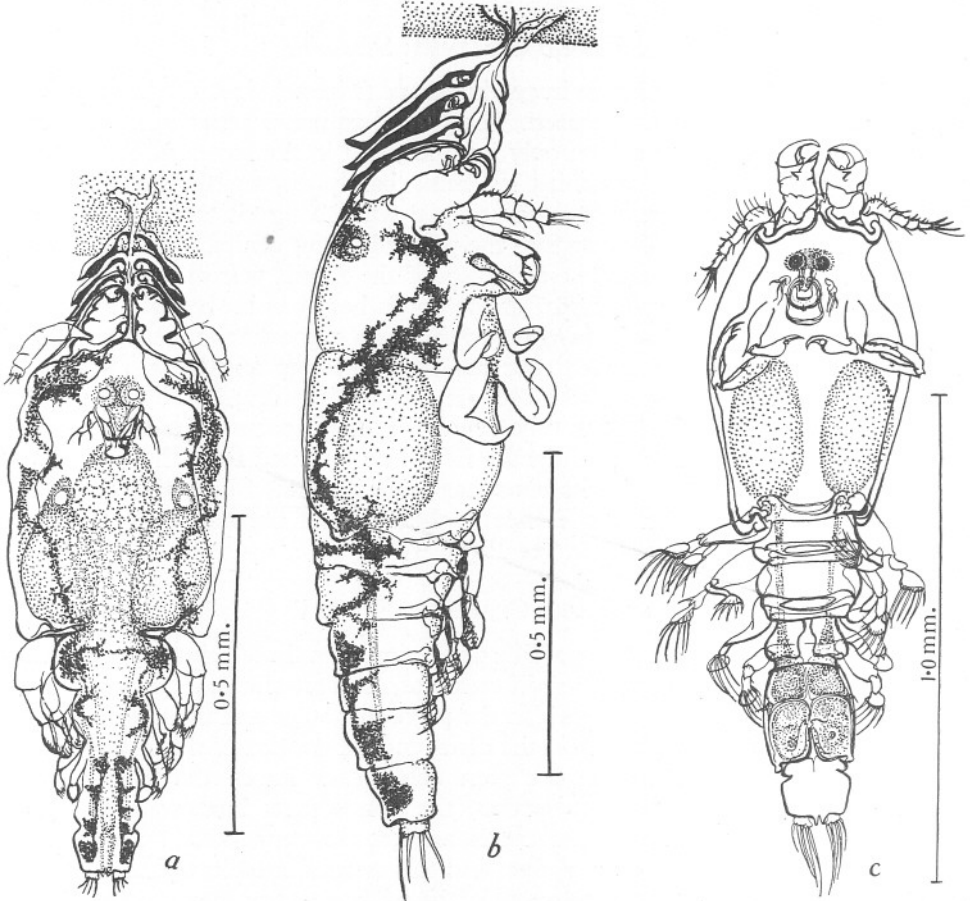


Fig. 3. *a*, Chalimus (stage V)—ventral aspect of male. *b*, fourth chalimus (stage VI)—male from the right side. *c*, adult free-swimming male (stage VII)—ventral aspect, the pigmentation has been omitted.

the distal joints reflexed on the middle ones; they are still rather swollen and lack the characteristic shape of the adult (and copepodid stage). The maxillipedes are relatively even more swollen and are quite unlike the long slender limbs they become at the next moult; indeed, they resemble the adult second maxillae in general outline. They bear no spines or claws.

## THE ADULT MALE: STAGE VII

There has been a marked change in shape (Fig. 3c) at this moult, and the body form of the copepodid has returned: the setae on the swimming legs are not quite so long, but in fine structure they resemble those of the early stage very closely. The two additional pairs of legs are uniramous and clearly three-jointed; they bear four long setae and a shorter one. Each ramus of the first two pairs of legs bears five long setae and a shorter spine on the outer side, and as foreshadowed in the copepodid each ramus is two-jointed.

The *genital segment* is particularly interesting in the male, for, as mentioned above, its two component segments were indicated quite clearly in the last chalimus stage: they have now coalesced into a barrel-shaped segment containing the spermatophore sacs which open near the median line in two spout-like tubes whose function is not quite clear. It is difficult to make out whether these are the internal openings (? communications with the vas deferens), for they are probably not the external openings for the discharge of the large spermatophores, which Scott holds are beneath the posterior corners of the genital segment. The heavy pigmentation in this region makes it difficult to see the relationships of these structures clearly. The characteristic disposition of the chromatophores has been shown in all the preceding figures, but since the intense dark pigmentation is so heavy in the male, it has been omitted from this figure. That the genital segment does represent two segments is shown in this species almost as well as in the male of *Caligus diaphanus* as figured by Gurney (1934, fig. 17); it is a double segment bearing the vestiges of legs 5 and 6. In the male of *Lernaeocera* the vestige of leg 5 is not easy to see in all specimens, but in some a small spine can be seen arising from a minute boss beneath the cuticle, though sometimes the spine does not reach the surface. Leg 6 is represented by the small indented knob on the ventral side of the posterior corners of the genital segment, but I have not been able to see a seta on this in any of my specimens. Immediately below the genital segment is a short segment preceding the terminal trapezoidal abdominal segment to which it evidently belongs. The anus is terminal and there are two small triangular processes immediately ventral to it; the setae on the anal laminae are four in number, the two innermost are the longest and the two outer, and slightly dorsal, are much finer and shorter.

The first antennae are five-partite as in the copepodid stage and the second joint is longer than the rest, all being richly supplied with short setae; the terminal joint bears four stronger setae and a small curved one. The second antennae are very similar to those in the copepodid, though their relative size is slightly greater and they are very strongly chitinized; they are three-jointed and the terminal joint bears a strong short outwardly directed spine at about the middle of its width on the ventral side.

*The mouth-parts.* The mouth tube and its immediate appendages do not differ in the two sexes, and they are shown in Fig. 4a. It is difficult to state

with certainty the exact morphological entities composing the mouth tube, for though it is usually stated that it is formed by the fusion of the upper and lower lips, such an explanation seems too facile. Gurney (1930, fig. 2) figures the mouth tube of the copepodid larva of *Nicothoë astaci* in side view: the lateral suture can be seen, through which the 'masticatory process' of the mandible has already entered the closed tube, while the basal joint of the protopodite remains outside, slightly lateral and anterior to the base of the first maxilla. This lateral suture can be seen in the fourth chalimus stage of *Lernaeocera* (Fig. 3 b). In Gurney's fig. 4, of the mouth-parts of the adult female *Nicothoë*, a U-shaped chitinous thickening can be seen projecting posteriorly from the dorsal edge of the tube; a similar heavily chitinized rectangular bar is present in *Lernaeocera* (Fig. 4 a), which seems to be identical with what was identified as the upper lip in the earlier stages (Figs. 2 a, 2 c and 3 a). In the adult it can be traced forwards and inwards, where it bifurcates, the anterior branch passing directly outwards, apparently joining the base of the first maxilla, and the other passing backwards dorsal to the mouth tube and within it forming the lateral borders of the mouth itself, continuing as a flattened concave rim round the lower edge of the mouth aperture to join its counterpart on the other side. The upper border is not similarly fortified, but seems to be flexibly opposable on to the former by virtue of the oblique sheets of muscle fibres in the walls of the mouth, which are attached distally round the orifice. This inner chitinous structure I take to be part, at least, of the lower lip (labium), though it is relatively smaller than this structure in the earlier stages (shown in Fig. 2 c).

That the labrum and labium are separate entities from the mouth-tube proper, is indicated by Wierzejski (1877) in his figure of these structures side by side in the third chalimus stage of *Pennella varians*. He shows (pl. 33, fig. 16) the tube itself as complete and, apparently separate from it, the labrum and bipartite labium within it. The mandibles are also enclosed in the tube at this stage as they are (for the first time) in *Lernaeocera*. In the mouth tube of the adult *Pennella varians* (pl. 33, fig. 17) the lips are not indicated, nor are they included in any of Brian's figures of the developmental stages of *P. sagitta* (1929). That the mouth tube is more likely to be composed of more than one modified sternite and therefore involves more than the 'paragnaths'—the labrum and labium—is suggested by its enormous development in the mature adult *Lernaeocera* (the figures of which, reproduced in Stekhoven's paper (1936 a), so nearly agree with my own that they will not be repeated here). Stekhoven's figs. 3 c and 4 on pl. 2 show the first maxillae carried more than half-way up the oral cone in *L. branchialis*, as do also those of Brian (1929, pl. 5, fig. 9) for *Pennella sagitta*.

If the mouth tube were formed largely from anterior and posterior moieties, its plane of symmetry would be transverse, whereas it is clearly vertical throughout in the adult (Fig. 4 a). Three pairs of strongly chitinized half-hoops support the structure, which is composed of a thinner membrane with apparent lacunae (or even thinner areas of chitin) along the posterior axis; at

least this is so in the adult stages on the flounder (stage VII), for in the mature female, after the final moult on the gadoid host, the mouth tube appears more evenly and far more heavily chitinized. The distal rim of the tube is a narrow membrane edged with minute prickle-like processes. In Wierzejski's figures, referred to above, the three pairs of chitinous bands are seen in an earlier stage of their development in *P. varians* as small projecting lobes within the tube, but not yet applied to its walls. Their late development in this species and their arrangement strengthens my suspicion that part of the mouth tube, at least,
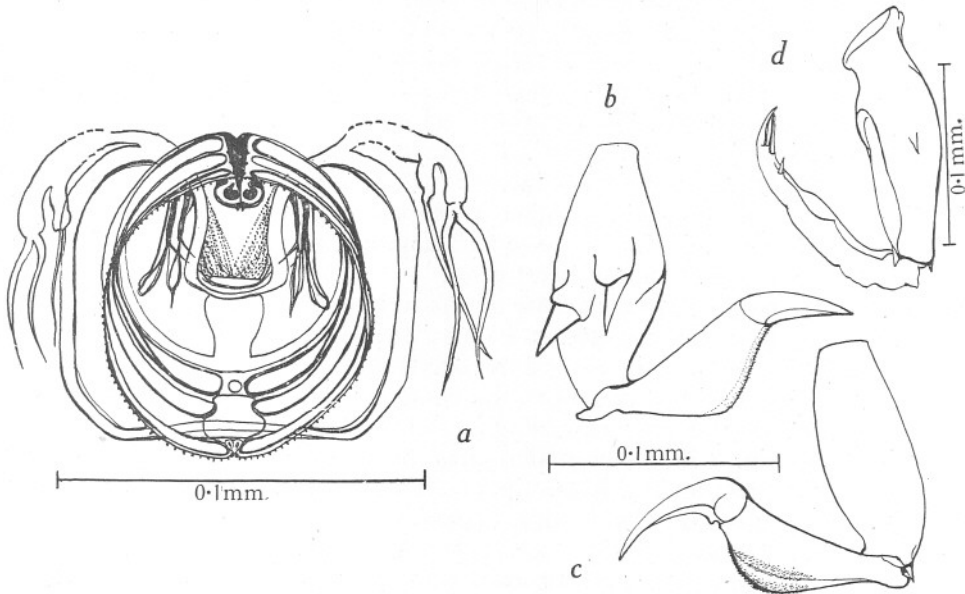


Fig. 4. *a*, Mouth tube in situ, showing first maxillae outside and the bipartite mandibles inside: a composite drawing from stage VII specimens. *b*, right second maxilla of female. *c*, left second maxilla of male. *d*, left maxilliped of male; all from the ventral aspect (stage VII).

represents the highly modified body of the mandibles. 'The masticatory process' of the mandible, which alone is said to be developed in parasitic copepods, is in *Lernaeocera* fairly well developed, but it is very different from that of the Caligidae (and Lernaeopodidae), in which it is a single lancet with an inner dentigerous margin. In the third chalimus stage of *Lernaeocera* (Fig. 3 *a*) the mandibles arise from the same origin as the incipient mouth tube, and comprise a stout basal joint with two fine lancet-like setae at its tip. In the adult the basal joint is only seen with difficulty at the bottom of the anterior part of the mouth tube, but the bipartite distal portions are more easily seen as they reach about half-way up the tube. Both rami are slightly concave and about half-way up give off a long sharp spine directed inwards, above which they are sheath-like; the inner ramus ends in a sharp point formed by the rolled-in

edges of the sheath. The outer ramus is an open sheath, and its thickened edges sometimes appear to project as two terminal spines owing to the tip being bent back. I am inclined to think that it was this appearance which led Leigh-Sharpe (1930, p. 336, fig. 5 *Mn*) to depict the mandible of *Lernaea barbicola* (mature female) as a bluntly rounded limb with two short spines: for at certain foci I have obtained almost exactly this view of the outer ramus in *Lernaeocera*. There has been much conflicting description of the mandibles of this group of copepods: Wilson (1917, p. 81), in stating the subfamily characters of Lernaeo-cerinae (female), says 'the mandibles are unknown', and regarding those of the male, 'antennae and mouth-parts as in the female'. Whereas in dealing with the external morphology of the entire family (p. 24): 'The mandibles are simple curved claws or spines, one-jointed and entirely devoid of teeth'; and in describing *L. branchialis* ('copepodid male') he states 'mandibles in the form of a long and slender spine'. This must have been copied from some previous author, for he does not include males in his material. Even Claus (1868 b) figures the mandibles, rather indistinctly, as a pair of double broad spines attached to the sides of the mouth tube and within it (which is in no serious disagreement with my own figure).

A. Scott (1901, p. 37) seems to have mistaken the first maxillae for mandibles, for he says they are not enclosed in the mouth tube, though he goes on to say that they are situated at the base of the lateral surfaces of the conical tube of the mouth and consist of two parts, the basal joint being cylindrical and the second joint flattened and terminating in a broad blade, which is serrated on the inner margin. I have seen nothing like this in any of my specimens, nor do Scott's figures support this description. From his figures it appears as one of the broad setae of the first maxilla. Stekhoven neither describes nor figures them; he admits that they are exceedingly difficult to see.

The *first maxilla* (Fig. 4a) is in two parts, an inner short joint gradually tapering into a long seta, and an outer joint also tapering off, this time into two long setae. In the chalimus stages the outer joint is relatively larger and stouter (Fig. 3a).

The *second maxilla* is clearly three-jointed, and it is particularly interesting in that it is different in the two sexes: that of the female (Fig. 4b) bears two very stout spines on the ventral side of the first joint, this also showing a faint transverse fold so that it may in reality be composed of two or three joints. No spines or indication of subdivision into more joints are found in the male appendage (Fig. 4c), though a small spine is present on the outer corner of its distal end. The penultimate joint in both sexes is somewhat triangular, and on the outer edge there is a shallow groove, the distal half of which is thickly beset with minute spines—these are rather more extensive in the male than in the female. The end joint is clawed, and in the male it is rather more curved. In the adult (stage VII) of both sexes these last two joints appear to be immovably articulated, and sometimes the suture is difficult to see; this is also true for the copepodid (Fig. 2a), but in the intervening chalimus stages

the joints lose their characteristic shape and they are flexed on one another (Fig. 3*b*).

The second maxillae, like the first, seem to be remarkably uniform in related genera: the above description agrees almost exactly with the figures of Wierzejski (1877, pls. 32, 33) of *Pennella varians*, where the two spines are shown on the proximal joint of the second maxilla of the female alone. The appendages of Brian's specimens of *P. filosa* (1912, pp. 16–18, pls. 3, 6) and of *P. sagitta* (1929, loc. cit.) are also in agreement in all but minute details.[1]

The *maxillipedes* are only present in the males, and I have not been able to make them out before the fourth chalimus stage; those of the adult male are shown in Fig. 4*d*. They are comparatively long and thin and superficially two-jointed. The proximal joint is the more robust, and like that of the second maxillae may be, in reality, composed of two or more joints, for there is a spine, directed slightly outwards, about the middle of its ventral face; there is also a short spine on its outer angle distally. On the inner face of this joint there is a long concavity and a corresponding one on the inner face of the distal joint which is about the same length. It is thought that this groove has a function in connexion with insemination, and the use of this pair of limbs during copulation is referred to below. There are a number of slight folds along the margin of the distal joint which may indicate its component segments, but they are indistinct. About a quarter of its length from the tip the concavity of the limb ceases, and at this point there is a small spine directed inwards; three longer spines occur at the end—two straight ones subterminally and a curved one terminally, all three being closely opposed.

## THE ADULT FEMALE: STAGE VII

Though her own gonads are not yet mature, the female at this stage (Fig. 5*a*) has attained, superficially, the same degree of structural development as the sexually mature male; it is the stage in which copulation takes place, and it is therefore justifiable to call her 'adult'. The ensuing metamorphosis involves superficial dedifferentiation, for the second time, and the final assumption of an entirely different form several times larger than the present one. The cephalothorax is slightly larger than that of the male and is oval, the maximum width being equatorial rather than anterior to the equator as in the male. The appendages are all similar to those of the male with the exceptions already mentioned, and in addition the swimming legs have slightly longer setae and their

[1] It therefore appears that Leigh-Sharpe's figure (1935, p. 108, fig. 1) labelled as the antennule of *Saucissona sauciatonis* is the second maxilla. It shows a three-jointed appendage ending in a blunt claw and having one blunt spine on the basal segment. Apart from the likeness of this figure to a second maxilla of *Lernaeocera* and its allies, its resemblance to the first antenna of any copepod known to me is remote. Leigh-Sharpe (1935) created a new genus for this species (represented by a single immature female) which he considers to be congeneric with *Lernaeocera lumpi* (T. Scott, 1901). Scott's species was described from a single mature female from the gills of *Cyclopterus lumpus*. The separation of the new genus rests on the absence of the familiar flexures in the body of the mature females.

basal joints are longer and more slender. The distribution of setae differs slightly from that in the male and copepodid stage and is as follows: leg 1, 7 + spine, 6 + spine; leg 2, 6 + spine, 6; leg 3, 6 + spine; leg 4, 5 (in legs 1 and 2 the exopod is cited first).

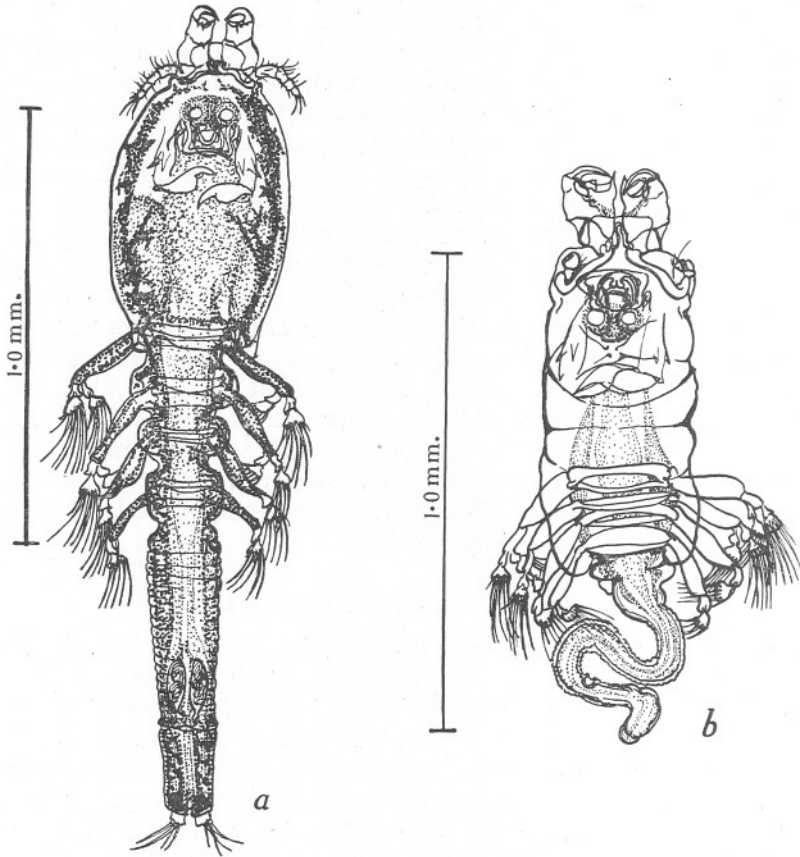The thoracic segments have lost the characteristic shape seen in the cope-



Fig. 5. *a*, Adult female (stage VII)—dorsal aspect, showing spermatophores within the hind body which has not yet expanded to its full length for this stage. *b*, adult metamorphosing female from the gill region of the gadoid host (the first antennae have broken off)— ventral aspect.

podid and adult male, and they are rounded in outline except the pregenital which is slightly quadrangular. The genital segment is without the vestigial appendages of somites VI and VII which were found in the male: it is enormously elongated with a crenulated outline which indicates the region of imminent expansion. Copulation takes place immediately the male comes along, even though the female has barely finished moulting, and she be still

attached to the gill in her original position with the chitinous attachment apparatus adhering to the mid-subrostral region. As soon as copulation is over the genital segment elongates very rapidly until it is slightly longer than the rest of the body. By this time the female has let go her hold on the tissues of the flounder and has begun to swim actively; but she does not make much progress, for she is not a good swimmer and relies mainly on currents to waft her out of the gill cavity of the flounder and up to the water inhabited by her next host—a suitable gadoid. From time to time she will use her anteriorly projecting second antennae to rest on the gills of the flounder before quitting them for a pelagic life. The rostrum is rather large and rectangular in the adult and prevents any dorsal movement of the second antennae, which are held rigidly forwards.

During copulation the male first grasps the genital segment of the female, about a third of its length from the proximal end, by means of his chelate second antennae: so firm is his grip on the still soft cuticle of this region that a papilla is raised and some injury done, for when the male retires the papilla persists for a time but finally subsides when the cuticle is stretched in elongation. Specimens fixed at this time and stained show an area of penetration of the dye around the papilla, elsewhere the cuticle is impervious to all but the fiercest stains. Insemination is effected by the male applying himself parallel to the body of the female on her ventral side, which he does with the further aid of the maxillipedes. His body is then flexed vigorously back and forth several times, the spermatophores suddenly appear and are shed opposite to the vulva, where partly by pressure of his body and by the manipulation with the maxillipedes which have now released their hold (the flexed body tearing unmercifully on the cuticle of the female), the spermatophores are introduced into the vulva where they remain intact. I have not been able to see them discharge or migrate higher up the oviducts. The external opening of the vulva is a transverse elliptical fold, but just inside it are two small apertures leading to the oviducts.

The segmentation of the abdomen is not clear; it has several transverse striations and is, like the limbs and thorax, very heavily pigmented. The anlage of the ovaries can be seen indistinctly in the hinder region of the cephalothorax, and the descending oviducts can also be made out. Cement glands appear to be situated in the lateral fields of the genital segment, but details are obscured by pigmentation.

### THE ADULT FEMALE: STAGE VIII

I have been unable to find A. Scott's 'pennella stage'—the fertilized female with the long hypertrophied, though straight, genital segment—on the gills of gadoids (Fig. 5*b*). Though Scott found only a single specimen (on the gills of *Gadus merlangus*), Stekhoven has been fortunate in finding what he considers to be a complete series on the gills of the cod (Stekhoven & Punt, 1937). These authors do not figure the specimens showing the formation of the antlers, but

they agree with A. Scott (1901) that the latter are produced, and the body elongates (to about eight times the length of the cephalothorax) before flexure begins.

There is, however, some variation in this stage. Stekhoven found one specimen in 1936 of length 13 mm. and a cephalothorax to hind-body ratio of 1 : 8·0; the genital segment had a right-angled flexure and antlers were present. Whereas another found by him on 13 May 1937 had a length of 14 mm. and a ratio of 1 : 8·85, yet the body was straight and there were no antlers. I also found a specimen of total length 14 mm., on 14 November 1940 on *G. pollachius*, in which there was a right-angled flexure in the genital segment, and the second flexure had progressed some 30°; also, not only were antlers present but they had each dichotomized. All specimens found by me on *G. pollachius* and *G. merlangus*, with one exception, have had antlers; and in all the flexure of the body had already begun. There seems to be a moult immediately the impregnated female settles herself on the gadoid, and there may be another later, but the specimen in Fig. 5*b* is, I feel sure, the stage immediately following the pelagic female. I have found only one, on 29 April 1940, situated in the usual position in the anterior angle of the fourth gill-arch of *G. pollachius*. It was hanging on to the tissues surrounding the blood vessels at the base of the gill filaments by means of the second antennae. It was dissected away without damage (except for the loss of the distal segments of the second antennae), and I think it was probably dead, though there were no signs of decomposition. It was fixed immediately, without pressure, in Bouin Duboscq, and no apparent shrinkage occurred. I am inclined to think that moulting had just occurred, as the chitin was very soft and the gut appeared empty; it thus seems that the parasite had probably just arrived on the gadoid after its pelagic (starving) phase and had not yet had its first meal of gadoid blood. It is possible, of course, that this is the final moult and that growth by swelling, on imbibition of gadoid blood, was just about to take place; at all events, the most striking feature of this specimen is the typically flexed genital segment of Stekhoven's later stages, yet the antlers have not yet formed.

Though the cephalothorax is no longer than that of the larger females of stage VII, it is of a different shape, narrower and with parallel sides, and all the leg-bearing segments have become incorporated in it. There are transverse folds across the soft fore-body, and the four radiating folds beneath the nerve mass appear to be the beginning of the dorsal antler, though nothing is visible of the lateral antlers. The first antennae have broken off and their basal joints alone remain. The mouth tube was rather larger than previously and became bent forwards during the mounting of the specimen, and the upper lip is seen above it. The genital segment was very soft and its cuticle more finely crenulated than in stage VII; the opening of the oviduct through which the egg-strings will emerge later is clearly seen at its distal end. It is remarkable to find, at this early stage, that the four right-angled flexures of the mature female are completed. The existence of this specimen is a demonstration of the extreme

variability in the order of development of the maturing stages of the female of *Lernaeocera branchialis*. It may be mentioned that the anus appears to be closed in this specimen: the abdomen ends in two lateral flaps, but the lumen of the rectum does not persist to the extremity in mature specimens. The significance of this has been examined at length in a previous paper (Sproston & Hartley, 1941 b).

## THE RATE OF GROWTH

The measurements of over a hundred specimens are represented in graphical form in Fig. 6 A, B. Wherever possible the sexes have been distinguished, but doubtful individuals are shown unsexed. The arithmetic means of the total lengths are indicated for each sex, and the mean of all the specimens at each stage is also shown by a short horizontal line. It is curious that my measurements in all instances should be less than those of Claus (1868 *a*, *b*); but one reason for this is that in expressing the total length of the body I have omitted the projecting second antennae, and where present, the attachment apparatus and rostrum. The anterior limit of the body proper I have taken to be the transverse line across the front of the cephalothorax marked by the bifid ends of the chitinous bars supporting the second antennae. The posterior limit of the cephalothorax is taken at the distal edge of the hindermost coupler of the first pair of swimming legs (except in the specimen in Fig. 5 *b*). The hind end of the body is measured to the tips of the anal laminae, excluding their setae.

In order to test the applicability of Przibram's (1931) law to the growth of the larval stages of *Lernaeocera*, the length of the cephalothorax was chosen as the most convenient part of the body for measurement in all the stages II–VIII; but when it was compared with the total length of the body in all the specimens, the ratios were found to be highly variable. The high degree of scatter of the values for the cephalothorax can be seen in the graph (Fig. 6 B), and the standard deviations of these measurements are given in Table I for comparison

TABLE I. MEASUREMENTS OF THE DEVELOPMENTAL STAGES OF
*LERNAEOCERA BRANCHIALIS*

| Stage | Mean length of body mm. | | Standard deviation from the mean | | Mean length of cephalothorax mm. | | Standard deviation from the mean | |
|---|---|---|---|---|---|---|---|---|
| I | 0·371 | | 0·0145 | | — | | — | |
| II | 0·484 | | 0·0449 | | 0·297 | | 0·0465 | |
| III | 0·609 | | 0·0431 | | 0·353 | | 0·0386 | |
| IV | 0·732 | | 0·0529 | | 0·426 | | 0·0375 | |
| | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ |
| V | 0·797 | 0·920 | 0·0529 | 0·0183 | 0·461 | 0·498 | 0·1072 | 0·0302 |
| VI | 0·937 | 1·047 | 0·0559 | 0·0277 | 0·506 | 0·537 | 0·0410 | 0·0683 |
| VII | 1·255 | 1·700 | 0·1188 | — | 0·517 | 0·619 | 0·1176 | 0·0492 |
| | | (1·246–1·91) | | | | | | |

with those of the total body length. Owing to the unreliability of the measurements of the cephalothorax, and the fact that it does not show isogonic growth,
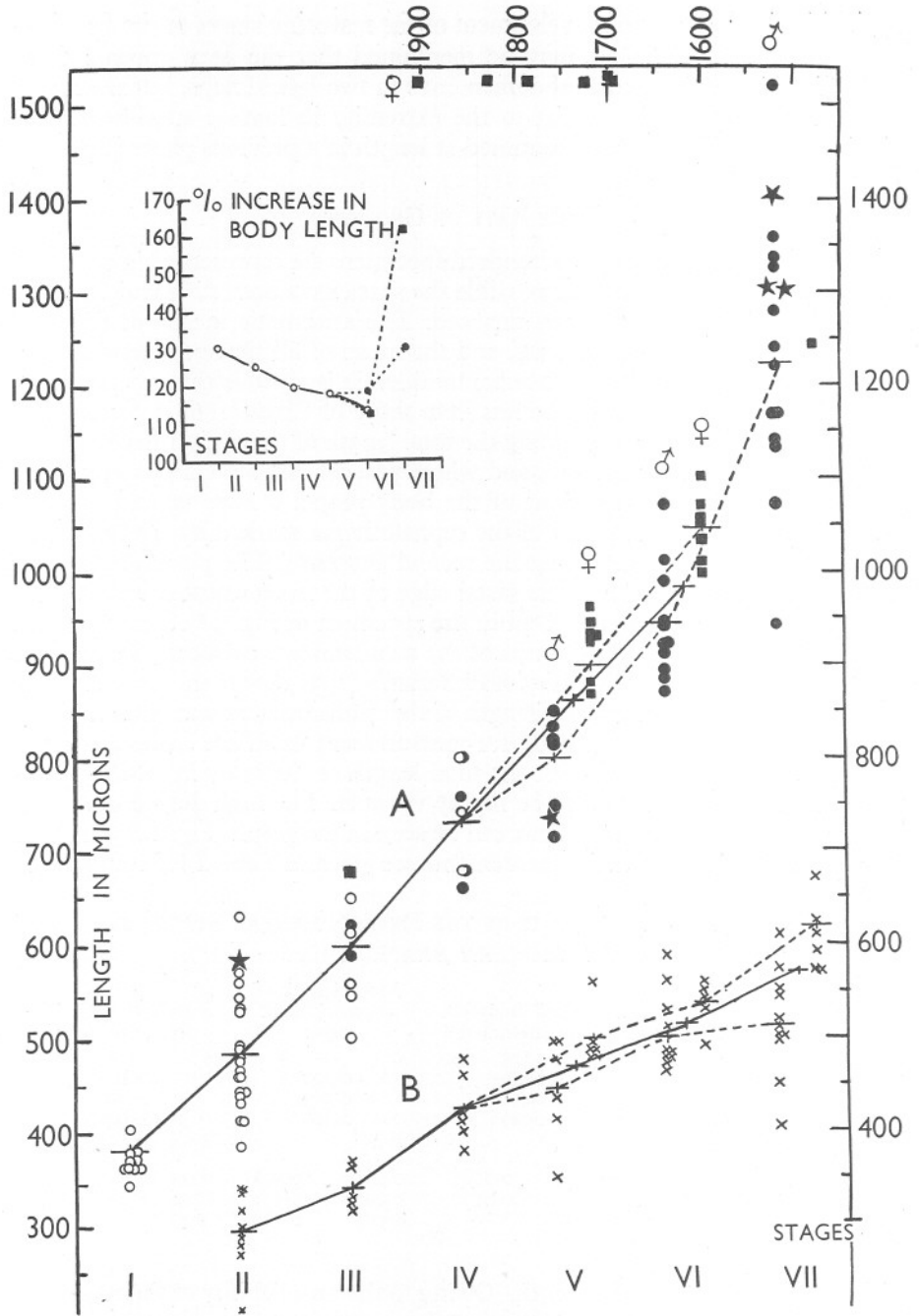
Fig. 6.

the values could not be used in the usual allometric expressions to examine relative growth. Neither could the length of those appendages common to all stages be used, since their measurement in the retrogressive chalimus stages is obviously unreliable.

When the means of the simple lengths of the body, stage by stage, are plotted the result is rather surprising, for instead of obtaining a logarithmic curve—as others have done with the higher Crustacea (Harrison (1940), for example for the caprellid *Pseudoprotella phasma*)—the result is a straight line. The growth approximates to a straight line even when the nauplius is included (stage I) and holds good up to the adult stage VII. There is some irregularity when the sexes are considered separately: the males grow more slowly up to the third chalimus stage, then the curves are parallel until the adult form is reached, and the growth is more rapid. The females grow more quickly than the unsexed earlier stages, and in the final stage on the flounder there is a sudden increase in length of the genital segment, which of course causes the growth curve to bend steeply upwards. In the smallest female shown (1·223 mm. long) the genital segment had only just begun to elongate, and the animal was still attached to the gill tissue by the chitinous apparatus, and though it had only recently moulted fertilization had taken place. However, it is very interesting to note that this specimen is very nearly the same length as the average adult male (see Table I, in which minimum and maximum length are given for stage VII females).

When rate of increase in length is expressed graphically (Fig. 6, inset), it is seen to decrease uniformly up to stages V–VI and then to show a marked increase in both sexes. It is interesting and rather remarkable that this decrease in rate of growth should be so uniform, especially as it is generally assumed that one or more stages are omitted in the early phases of the life history. For instance, there is a marked jump in development, from the structural point of view, between the nauplius and the copepodid with its two pairs of biramous legs and well-developed hind body.

Fresh problems are raised in comparing the rates of growth of presumably related and unrelated copepods. For simplicity, a growth factor has been

Fig. 6. Graphical representation of the growth of the developmental stages of *Lernaeocera*.— A. Shows the total body lengths of the measured series: ordinates represent the lengths in microns and the abscissae the growth stages in seven columns, the sexes being separated into subcolumns V–VII. Unsexed individuals as open circles, males as black circles and females as black squares. The ordinates for stage VII have been continued at right angles along the top of the diagram to include those females in which the hind body had become extended. The arithmetic mean lengths for the total individuals for each stage are shown by a horizontal line and for the separate sexes by a longer line; these values are connected by continuous and dotted lines respectively to show the mean growth-rate. The stars represent the lengths of individuals from hosts other than *Pleuronectes flesus* and are not included in the mean values. B. A similar diagram for the lengths of the cephalothorax: these show a greater variation and a slower growth rate as compared with the body as a whole. Inset: diagram illustrating the rate of increase in body length from stage to stage —see Table II column 1—symbols for sexes as above.

obtained by dividing the length of one stage by the length of the preceding stage and multiplying by 100. In Table II this is shown for *Lernaeocera* (also in Fig. 6, inset), for *Caligus centrodonti* (measurements taken from Gurney, 1934), also for two free-swimming copepods, the fresh-water *Diaptomus castor* (from Gurney, 1940, p. 283, table III) and the marine *Calanus finmarchicus* (from Marshall, 1933, p. 126).

TABLE II. PERCENTAGE INCREASE IN LENGTH OF *LERNAEOCERA BRANCHIALIS* DURING DEVELOPMENT AS COMPARED WITH THAT OF OTHER COPEPODS

| Stage | Lernaeocera branchialis (Sproston) | Caligus centrodonti (Gurney, 1934) | Diaptomus castor (Gurney, 1940) | Calanus finmarchicus (Marshall, 1933) |
|---|---|---|---|---|
| I | | | | |
| II | 131 | 114 | | |
| III | 126 | 115 | 134 | 122 |
| IV | 120 | 154 | 130 | 122 |
| | 118 | 157 | 130 | 119 |
| V | ♂ 119   ♀ 114 | ♂ 178   ♀ 154 | ♂ 120   ♀ 131 | 117 |
| VI | | | | ♂      ♀ |
| VII | 130   162 | —   — | 124   119 | —   112 |

As with *Lernaeocera*, the rate of increase in length decreases in the free-living forms *Diaptomus* and *Calanus*, and though the growth factors for the sexed forms vary rather markedly, the gradient of the curve is about the same for *Diaptomus* and *Lernaeocera*, and for *Calanus* it is more uniform though flatter. Gurney (1928) found that the growth factors for *Eurytemora velox* decreased rather rapidly from stage to stage as compared with those of *Diaptomus*. On the other hand, the rate of growth in *Caligus centrodonti*—a parasitic form more nearly related to *Lernaeocera*—increases throughout the life cycle. This increase shows two high jumps: the first is between the first and second chalimus stages when there is no discontinuity in morphological development and only a slight alteration in shape. Between the third and fourth chalimus stages in the female there is a very slight drop in the curve, but for the male there is a further increase in growth rate (but only about half the previous increment) and yet there is again no morphological gap between the two stages; and the change of body form is almost negligible. Such a contrast in the growth behaviour in two nearly related forms is difficult to explain.

It is clear from the foregoing that a discontinuity in the growth-factor curve has no necessary correlation with development: it can neither be used as an indication of abnormal moults (Marshall, 1933), nor of the suppression of certain developmental stages in the life history (inverse induction from the *Lernaeocera* results). Gurney (1928) points out that apart from the growth factor changing from moult to moult, there is a marked individual variation in the free-living copepods which he studied; this has since been confirmed by Marshall (1933) in her work on *Calanus finmarchicus*. Gurney (1940, p. 283,

table IV) shows that the growth factor varies irregularly for different parts of the body of individuals of the same sex at the same stage of development, and that these variations are not correlated with the growth factor for the body length, nor this latter with the average of the growth factors for selected parts of the same body.

When the body lengths of *Lernaeocera branchialis* and *Caligus centrodonti* are plotted logarithmically as functions of the growth stages, their difference in behaviour is at once apparent: the curve for *Lernaeocera* is by no means a straight line, but is a curve with a very gentle convexity. That for *Caligus*, on the other hand, is markedly concave—the steep gradient is, however, only developed after the first chalimus stage, and this, incidentally, is the juncture at which accelerated growth is seen in the cephalothorax of *Lernaeocera* (Fig. 6 B).

## Size Variation

From Fig. 6 A the high degree of scatter of the lengths of the various stages is apparent, even though the means of these measurements give a uniform growth curve. It is not possible to group the individuals into two or more size classes in the various stages. At the same time the degree of scatter does not increase uniformly along the stage scale (see column 2, table I) if exception be made for the stage VII females—for which the scatter is due to the operation of a continuous variate within the group—the progressive elongation of the genital segment. The differences in size of the individuals belonging to one stage cannot be explained on the basis of seasonal variation. As an example of this apparently capricious variation in the size of the adult males: an exceptionally small specimen (0·944 mm.) was taken from a flounder on 27 December 1939, while from the same fish another male was taken measuring 1·335 mm. The largest male (1·52 mm.) was found during April, but in the same month other small males were found, including one only 1·075 mm. long.

The appearance of abnormally large copepodids from time to time throughout the year on the gills of the flounder may possibly find their explanation in delayed metamorphosis. Nauplii measured at random from different hatchings in the laboratory showed very little variation in size, and the copepodids obtained from them under experimental conditions had a uniformly small size. It is conceivable that the largest copepodid (0·633 mm. long, found on 13 February 1940) was one that had moulted without metamorphosing, owing to a prolonged pelagic existence in search of a suitable host. Some little support is given to this suggestion by Gurney & Lebour (1941), who found giant larvae of littoral decapods in oceanic plankton, and hint that metamorphosis is delayed owing to the unsuitable habitat: the larvae have got lost, as it were, and when they moult they do so only to emerge as larger forms of the preceding stage.

Whether such giant copepodids give rise to abnormally large chalimids is unknown, though this may be the explanation of the large forms among the

later stages in my material (see Fig. 6 A). Attractive as this hypothesis is, it makes the explanation of the abnormally small forms all the more difficult.

### LARVAE RESEMBLING *LERNAEOCERA* FROM OTHER HOSTS

During a visit to Roscoff in September 1938 I found a copepodid and a third chalimus stage which in every way resembled *Lernaeocera branchialis*, except that their size was rather wide of the average for these stages (the specimens are marked by stars on Fig. 6 A). I hesitate to identify them with this species because they were found on the gills of *Solea solea* (L ). Since then (Sproston & Hartley, 1941 a), numbers of pleuronectids (other than *Pleuronectes flesus* and including *Solea solea*) have been examined carefully for larvae in those localities where *Lernacocera branchialis* is common, but none was found except on *Pleuronectes flesus*.

During April 1940 occasional specimens of *Cyclopterus lumpus* were brought into the laboratory, but the only copepods found on the gills of these fish were three adult males (on one fish) which resembled those of *Lernaeocera branchialis*. The only differences were very slight—in the shape of the cephalothorax —but the specimens were larger than the average for the males of *L. branchialis*. These specimens are also marked by stars on Fig. 6. No character could be found which would separate these larvae into distinct genera or even species, though the specimen referred to above (footnote, p. 455) as found by T. Scott, and since called *Saucissona lumpi* by Leigh-Sharpe, may possibly be the corresponding mature female to these males. On the other hand, it is unusual to find males on the final host, and in the present instance no females were present. The possibility that these males are conspecific with Scott's female cannot be ruled out, but if this is true the almost exact correspondence of the males with *Lernaeocera* shows that Scott's specimen can scarcely be relegated to a separate genus.

At least two examples exist in the Lernaeoceridae of the developmental forms and males occurring on the same host as the mature females: Brian (1929, p. 14) describes all the forms of *Pennella sagitta* on a single host, *Antennarius histrio*, from the Sargasso Sea. A still more surprising record is that of Stekhoven (1936 a, pp. 17–18, fig. 16), who found *Lernaeocera lusci* as a mature female in the gill chamber of *Solea solea*, the same host on which I found larval forms of *Lernaeocera* sp. at Roscoff.

Stekhoven suggests that the characters of the second maxillae may prove to be specific criteria in the genus *Lernaeocera*: an excellent suggestion, because these appendages occur well developed in the copepodid, in the free-swimming male and female, and also sometimes in the mature female (very often, however, they are broken off in this stage). I have, unfortunately, been unable to use these characters, for in all my material the appendages appeared identical —except for sexual differences—and I have not found forms exactly corresponding to Stekhoven's figures.

## SUMMARY

The morphology of a complete series of developmental stages of *Lernaeocera branchialis* is described. Seven stages are passed through before reaching the gadoid (final) host.

The structure of the mouth tube and appendages is discussed in detail and compared with those of related genera in which the resemblances are close.

The free single nauplius and copepodid stages are immediately followed by four chalimus stages on *Pleuronectes flesus*; these show some dedifferentiation though segmentation is not lost. An explanation is given for the peculiar suspensory mechanism of the chalimus.

A second dedifferentiation follows the second well-developed pelagic phase in which the adult form is attained and copulation takes place. Some irregularity is noted in the details of the retrogressive metamorphosis of the maturing female on the gadoid host.

The rate of increase in body length in *Lernaeocera* decreases regularly up to the assumption of the adult form (stage VII). In this respect it is similar to the free-living copepods *Diaptomus*, *Eurytemora* and *Calanus*, but is in strong contrast to *Caligus centrodonti* which has an increasing growth rate up to the fourth chalimus stage. In the latter at this stage there is a marked acceleration in the growth rate unaccompanied by any change in shape or any other discontinuity, whereas in *Lernaeocera* there are early discontinuities in development, yet the growth rate is continuous when expressed graphically: it is a straight line rather than a logarithmic curve as would be expected from our knowledge of the higher crustacea.

The size of the female is greater than that of the male: that of the female overlapping the male of the succeeding stage. Variations in size of the larvae in a stage group are not seasonal, and an explanation is offered for giant larvae.

Similar lernaeocerid larvae and males to those of *Lernaeocera branchialis* on *Pleuronectes flesus* were found on *Solea solea* and *Cyclopterus lumpus*. No characters of generic or specific significance could be found which would serve to separate them from *Lernaeocera branchialis* so that their identity is not determined.

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