EVOLUTION AND ADAPTIVE RADIATION IN THE MACROTHRICIDAE (CRUSTACEA: CLADOCERA): A STUDY IN COMPARATIVE FUNCTIONAL MORPHOLOGY AND ECOLOGY

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An account is given of the functional morphology, ecology, habits and – in most cases – feeding mechanisms of representatives of 13 genera of anomopod cladocerans of the family Macrothricidae.

As in the Chydoridae, habits, which often depend on anatomical specializations of great complexity, are diverse, and permit the exploitation of a wide variety of ecological niches. In general, locomotion is less specialized than in the Chydoridae and most species neither swim nor creep so efficiently as do chydorids. So far as is known only one species, *Macrothrix triserialis*, has evolved a chydorid-like method of crawling by means of the first trunk limbs but others have acquired means of locomotion peculiar to themselves. In only a few cases is the post-abdomen used for pushing, its lack of such employment and the lack of a joint between it and the trunk being primitive features.

In basic structure and arrangement the trunk limbs are similar to those of the Chydoridae and the principles involved in many of the feeding mechanisms are the same in both families. By numerous, sometimes subtle, sometimes profound modifications of the components involved, this basic arrangement has been adapted to widely differing ways of life and different functions. Many macrothricids use the first trunk limbs for food collection rather than the second as in most chydorids. This is interpreted as a primitive feature.

Acantholeberis curvirostris (figures 1–6), a frequenter of peaty pools, is primitive in several respects; for example, it lacks a headshield and is unable to push effectively with its post-abdomen, but exhibits several specializations. The antennae, which also serve as props and levers, are the principal means of locomotion, and have massive protopods flexed at about 90°. Progression is by means of intermittent 'leaps': steady swimming is not practised. Crawling by use of the first trunk limbs in a manner that

foreshadows the efficient crawling of certain anomopods is feebly developed. Food collected by the first trunk limbs is dragged into the chamber made up by these and other trunk limbs (figures 8, 9), both mechanical handling and filtration being involved in its manipulation.

Ophryoxus gracilis (figures 19, 20) is a littoral species which can swim steadily, if weakly, but spends much time on the bottom. Here it attaches itself, and crawls in a rudimentary manner by means of the first trunk limbs, whose distal lobes are provided with grasping spines (figure 28), assisted by the antennae. A striking specialization in what is on the whole a generalized animal is the presence of massive secretion-filled reservoirs in the first trunk limbs (figures 29–31) similar to those which produce material for entangling food particles in certain chydorids. Although specialized for grasping substrata (though less so than most chydorids) and for collecting food with the second trunk limbs, *Ophryoxus* exhibits both habits and morphological attributes that indicate how the trend that led to emancipation from benthic habits and ultimately to the evolution of the Daphniidae could have been initiated.

Many morphological and functional peculiarities of the minute *Streblocerus serricaudatus* (figures 32, 33 and 35) are associated with the hitherto unreported habit of burrowing into flocculent detritus. Burrowed individuals move but little, locomotion being generally restricted to that achieved by occasional rowing movements of the antennae, which are specialized for levering and not for swimming. Neither the first trunk limbs nor the post-abdomen are used for locomotion. Food collected by the first trunk limbs is dragged into the sorting chamber by trunk limbs 1, 2 and 3. Trunk limb 1 bears scraper-like spines (figure 36) on endite 3 which have no parallel in other macrothricid genera and are remarkably similar to the scrapers of trunk limb 2 of both chydorids and macrothricids. There is no respiratory-feeding current. Food is manipulated by purely mechanical means. This process is described.

Many attributes of *Drepanothrix dentata* (figures 40, 42, 44) are also associated with the habit of burrowing into flocculent detritus, which serves both as a substrate and as food. The body is wedge-shaped in two planes and provided dorsally with a friction-reducing and protective crest on both the well-developed headshield and the carapace. The animal is levered into detritus by highly specialized antennae the setae of whose two proximal endopod segments are modified for this and not for swimming. A stout spine (figures 42, 44) on each antennal protopod which sweeps away material as the animal moves forward is an important adaptation to burrowing. Neither the first trunk limbs nor the post-abdomen are used for locomotion. Burrowed individuals move but little. *Drepanothrix* can, however, still swim effectively when necessary, and can do so while inverted. The convolutions of the gut, hitherto erroneously illustrated, are made clear (figures 48–50). There is no respiratory-feeding current. Food is collected and manipulated by mechanical means.

Macrothrix laticornis (figure 56) is a benthic animal which penetrates suitable substrata by use of the antennae, but appears to be a less-persistent burrower than *Streblocerus* or *Drepanothrix*. While the principles involved in the collection and manipulation of food are the same as in these genera the limbs are specialized in different ways, in part to permit small particles to be handled (figures 63, 65). There is no respiratory-feeding current.

Unlike most macrothricids *M. triserialis* uses the highly specialized distal armature (figure 69) of trunk limb 1 for grasping and, more important, for 'hand over hand' crawling as do many chydorids. To this accomplishment, which enables it to match chydorids at their own game, its undoubted success in tropical and subtropical waters may in part be due. The principles of the feeding mechanism are similar to those employed by several other non-filter feeding species. The labrum contains enormous secretion-filled reservoirs (figure 77) which extend into the head in a manner unique among investigated anomopods.

Onchobunops tuberculatus (figures 78, 79) is specialized for steady swimming, in which it can indulge even when inverted, and for intimate association with substrata. Attachment is by means of enormous distal hooks on the first trunk limbs (figure 80), a habit unusual in the Macrothricidae. Settled individuals move forward by means of swimming strokes of the antennae, the first trunk limbs contributing little, if at all. Food is collected by scraping with trunk limb 2, as in many chydorids, and manipulated by a combination of mechanical handling and filtration similar to that of *Acantholeberis*. Enormous secretion-filled reservoirs are present in the labrum (figures 82–84).

Lathonura rectirostris (figures 91–95), a leaf-frequenter, is highly specialized for creeping over and removing food from surfaces, and can do so while inverted provided the surface can be gripped by hooklets with which unique crawling claws of the first trunk limbs (figures 97, 102–105) are provided. These are assisted by similar, scraper-like, crawling claws of the third trunk limbs (figures 97, 106, 108). The animal rests on highly specialized setae of the ventral carapace margins, which fringe the widest ventral gape of any macrothricid (figure 97).

Crawling and feeding are intimately related. Forward movement in small increments is effected by dragging with the first and pushing with the third trunk limbs. Such quadrupedal locomotion is unique within the Anomopoda. Like the post-abdomen the antennae (figure 91) play no part in crawling. Swimming by antennal movements of small amplitude and great rapidity provides efficient propulsion over short distances. There is no feeding-respiratory current. The second trunk limbs scrape up food and are the prime agents in its subsequent manipulation. Proximal endite spines of the first trunk limbs make up a grid (figures 97, 100, 101) which guards the anterior inter-limb space. The first trunk limbs lack ejector hooks.

Minute size (length about 0.4 mm) and a ventral gape that lacks fringing setae or spines are among the attributes of *Guernella raphaelis*, which appears to be of benthic habits and probably swims over suitable substrata. The arrangement of the median sorting chamber (figure 112) shows clearly that food is collected by mechanical means and that currents are not used.

Pseudomoina lemnae, which bears a superficial resemblance to *Lathonura*, also displays features that indicate possible phyletic relationships, but differs markedly in its way of life. Although only preserved material has been available it is clear that food collection, which probably takes place from the bottom or from plant surfaces, involves filtration.

Neothrix armata (figure 116) is a benthic and probably burrowing species whose morphology suggests mud-frequenting habits. Its antennae are highly specialized, probably for levering in soft mud, and the spiny armature of the carapace and head-shield probably facilitate movement in muddy situations. The trunk limbs are specialized for the mechanical handling of food particles: filtration is not employed. The second has a setose gnathobase (figure 127), unique within the Macrothricidae, and a brush-like gnathobasic seta which serve to clean the food groove and which reflect mud-frequenting habits. The first trunk limbs lack ejector hooks and the post-abdomen has no claws.

Grimaldina brazzai is a bottom-frequenting but not a burrowing species, one of whose outstanding attributes is an ability to push with its post-abdomen, which is highly specialized for this purpose (figures 128, 129). It can also swim steadily. Filter feeding is practised, filtration being restricted to trunk limbs 3 and 4.

The habits of *Parophryoxus tubulatus* (figure 130) are different from what might have been expected. It swims only feebly and is by preference a burrower into soft deposits which it penetrates by using its antennae in a way that foreshadows their use by the truly burrowing *Ilyocryptus*. Detrital particles adhere, but sparsely, to the carapace. Notwithstanding its burrowing propensities its feeding mechanism involves filtration. The outer filter plate of trunk limb 4 is better developed (figure 133) than in any other genus save *Ilyocryptus*.

Ilyocryptus sordidus (figures 134, 137) differs markedly from all other studied macrothricids in its habits and feeding mechanism. It is a non-swimming, largely sedentary, crawling and burrowing animal which extracts its food from currents set up by the exopods of the posterior limbs. It burrows by use of the antennae and post-abdomen, pushing with the latter being an unusual, and advanced, feature in a macrothricid. The ventral carapace margins are specialized for the exclusion of coarse debris from

the carapace chamber. The posterior spines are defensive and retention of old carapaces at the moult results in a hedgehog-like array posteriorly (figure 137). Other specializations for life in mud include shape, a broad headshield, a camouflaging burden of detritus (figure 137), the habit of shamming death, and the development of abundant haemoglobin in the blood.

The highly complex feeding mechanism involves the passage of particles through a protecting sieve formed by the spines of trunk limb 1 (figure 146), along a chute made up by the second trunk limbs, and either direct passage to the food groove or, more usually, entrapment in a large posterior filtering basket (figure 140) from which they are swept forward along the food groove. In limb structure, and to some extent in its feeding mechanism, *Ilyocryptus* stands closer to the daphnids than do other macrothricids.

Notwithstanding its great specializations and isolated systematic position within the family, it is not difficult to visualize the way in which, via a progenitor that had some of the attributes of *Parophryoxus* (which is not, however, ancestral), *Ilyocryptus* could have evolved.

Adaptive radiation and phylogeny are discussed. There is no doubt that the Macrothricidae is the most primitive family of the Anomopoda. A primitive feature is sometimes retained for functional reasons by an otherwise specialized species. While a meaningful account of adaptive radiation can be given, it is difficult, in some cases perhaps impossible, to establish the phyletic relationships of the various genera.

Attention is focused on certain features of the geographical and ecological distribution of macrothricids relevant to their evolution.

The monotypic genera differ so widely in structure and habits that interspecific competition is unlikely even where it is not precluded by geographical factors. Here evolutionary progress appears to have been brought about by refinement of those aspects of morphology and behaviour that lead to ever more efficient adaptation to particular ways of life.

I. Introduction

Previous papers on adaptive radiation within the Cladocera Anomopoda have dealt with *Eurycercus* (Fryer 1963) and several other chydorid genera (Fryer 1968). This paper extends the survey to the Macrothricidae which, while containing fewer species than the Chydoridae, embraces several well-defined genera of distinctive structure and habits. Representatives of 13 of these are dealt with here in varying degrees of detail on the basis of studies on their functional anatomy, ecology and habits. This covers all the genera recorded in Britain (*Echinisca* being regarded as inseparable from *Macrothrix*) and also certain exotic genera, though some of the latter, available only as preserved specimens, receive only brief mention. The methods used are the same as those described for the Chydoridae.

II. Preliminary remarks on structure and habits

The Macrothricidae is of particular interest as it contains what are undoubtedly the most primitive of extant anomopods. A primitive phyletic position is not, however, incompatible with morphological complexity, which is always of a high order within the family: in particular the apparatus used for the collection and manipulation of food is invariably intricate. That the family is primitive does not mean that any one living macrothricid retains all the primitive attributes of the ancestral anomopod, or that elaborate specializations related to different ways of life have not been evolved by individual species. Adaptive radiation has in fact been considerable and, while of less magnitude than in the Chydoridae, has given rise to such animals as *Lathonura* (§X) and *Ilyocryptus* (§XVI) which, in the complexity of their adaptations, rival the hyper-specialization seen in such chydorids as *Graptoleberis* and *Pseudochydorus*.

Like the chydorids, macrothricids are essentially bottom-frequenting animals and many of their structural specializations are associated with benthic habits. No species, however, has developed such a robust carapace as is found in the Chydoridae. While this has to some extent militated against the evolution of specializations of the ventral carapace margins such as enable these areas to establish intimate contact with various substrata, and which have played a conspicuous role in the evolution of several chydorid genera (Fryer 1968), the macrothricids nevertheless show parallel developments of these margins. Here almost all species have developed setae whose often complex arrangement has not hitherto received an explanation and which are associated with benthic habits and sometimes with highly specialized ways of life. In both families a primitive arrangement of the ventral armature is preserved in certain species. In some cases the same problem has been solved in similar ways by chydorids and macrothricids; in others different solutions have been evolved, and members of each family have also developed specializations for ways of life peculiar to themselves.

In most macrothricid genera the post-abdomen is not articulated with the trunk but is a simple reflexed extension of it, this being a primitive feature whose significance has hitherto gone unremarked and which throws much light on phylogeny. Such a post-abdomen, while it may be massive, is often virtually immobile and usually either thrusts in a desultory manner against the substratum or, more often, is not used at all for this purpose. *Grimaldina*, however, has solved the problem of swinging its post-abdomen efficiently without developing an articulation. The headshield is often feebly developed, or even completely absent – another primitive feature. In *Acantholeberis* the head is covered dorsally only with a simple cuticular pellicle. Both these features militate against efficient pushing either through vegetation, detritus or mud, as do the size, form, and particularly the orientation, of the antennae in many genera. Thus, while several chydorids show specializations of both headshield and post-abdomen for pushing through vegetation or burrowing into several kinds of substrata (Fryer 1963, 1968), the only macrothricids that have successfully exploited this suite of specializations are members of the genus *Ilyocryptus* (§XVI) which are true burrowers. Even in this genus, the trunk post-abdomen articulation is simple, the headshield small, and the antennae are used in a manner not found in the Chydoridae. Even when the headshield is well developed it is not necessarily accompanied by an articulated post-abdomen. Thus while *Onchobunops* (§IX) has the best developed headshield its post-abdomen is not articulated and is not used for pushing.

The often feeble development of these attributes has not, however, prevented the acquisition of burrowing habits by members of the family, for both *Streblocerus* (§V) and *Drepanothrix* (§VI) readily penetrate soft, flocculent organic deposits but by a method different from any used by chydorids, and which does not involve use of the post-abdomen for pushing. The same is true of *Parophryoxus* and probably of *Neothrix* but more observations are required.

Association with firm substrata is seldom intimate and most macrothricids have never evolved specialized crawling habits. In this they stand in marked contrast to the Chydoridae. To this generalization *Lathonura* (§X) is a striking exception. In several species progression is by swimming over surfaces, often in a series of 'hops', by means of the antennae, and with frequent rests on the bottom. The antennae, always relatively much larger than those of the Chydoridae, frequently show modifications of a type not seen in that family which enable a settled animal to balance and, more important, to exert leverage on the bottom. Such habits preclude the close association of antennules and substratum established in several chydorids. Furthermore, several genera exhibit a previously unconsidered antennal specialization which presented evolutionary opportunities not available to the Chydoridae (and also imposed certain limitations on locomotory possibilities), namely an approximately 90° flexure of the protopod. Much of the adaptive radiation within the family has involved the exploitation of this attribute and has taken place within limits that it imposes. The antennules are long and, in some cases (*Ilyocryptus* and an enigmatic animal mentioned in §XVII), are two-segmented. In these features the Macrothricidae generally exhibit a primitive, the Chydoridae an advanced, condition, but, as in the case of the antennae, specializations may be superimposed on basically primitive attributes.

While still essentially a benthic animal, *Ophryoxus* has attributes that could lead to emancipation from the bottom and swims more directly and persistently (though weakly) than do representatives of most genera. *Bunops* and *Onchobunops* also swim steadily, though weakly, and *Grimaldina*, which also 'hops', can do likewise, but no macrothricid is so adapted to swimming as are the daphnids, and none is planktonic.

In their major features the mouthparts and trunk limbs are essentially similar to those of the Chydoridae, and many of the principles of food collection and manipulation are the same, but in this, as in other features, there has been wide divergent specialization within and between the families.

Of the available species, *Acantholeberis curvirostris* (O. F. Müller) and *Ophryoxus gracilis* G. O. Sars exhibit various primitive features both in structure and habits and are therefore dealt with first. Each represents a monotypic genus. Although primitive, both show specializations for different ways of life – *Acantholeberis* for exploitation of the ancestral benthic habitat, *Ophryoxus* for both this and for swimming. As in the Chydoridae, an overall primitive condition is not incompatible with specialization of a particular organ or structure. Thus in both genera modifications of the alimentary canal are related to specialized mechanisms of defecation. That of *Acantholeberis* has been described elsewhere (Fryer 1970); that of *Ophryoxus* is mentioned here. *Ophryoxus* also exhibits an advanced feature in the trunk post-abdominal joint.

Although an appreciation of basic anatomy is essential to an understanding of the habits of macrothricids, little such information is available. This deficiency is partly rectified here, particularly by reference to *Acantholeberis* and *Ophryoxus* which reveal many of the basic attributes of the family. This information is given principally by use of illustrations. Although some species have been portrayed several times in taxonomic and faunistic works, sometimes with meticulous accuracy, as by Lilljeborg (1900), but often crudely, few illustrations enable a three-dimensional picture of the animal to be obtained. Sometimes the lateral view, almost always the only one given, is even misleading in this respect. Because of this, and because gross morphology is often intimately related to habits, particular attention has been paid to the illustration of the whole animal in such ways that its form can be readily appreciated.

III. The structure, habits and feeding mechanism of *Acantholeberis curvirostris* (O. F. Müller)

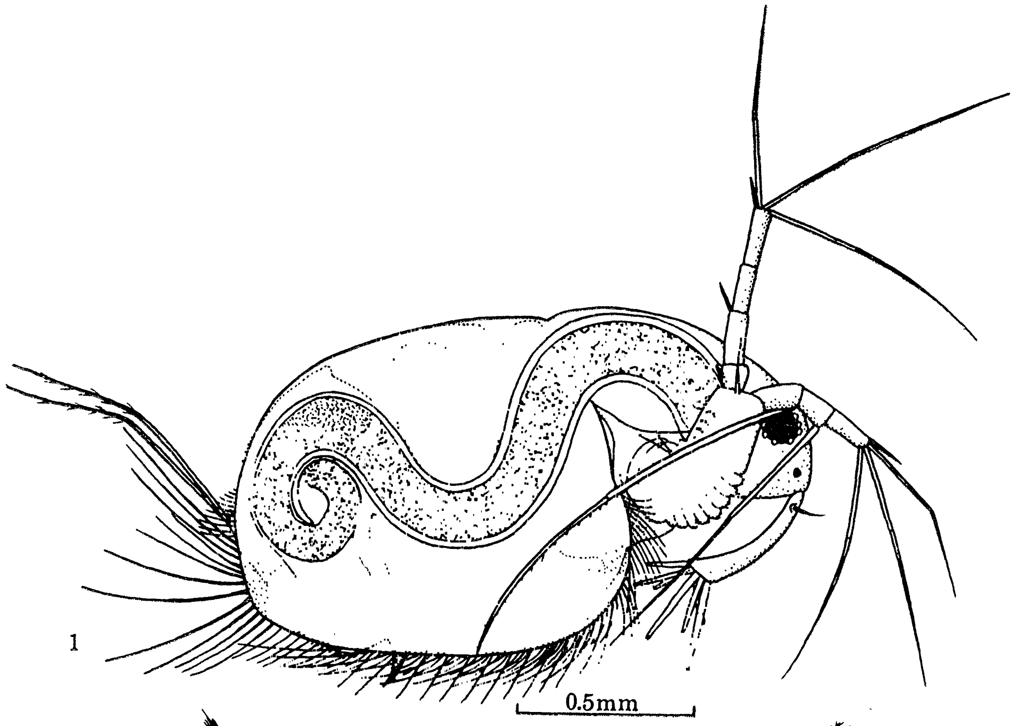
(i) *Ecology and habits*

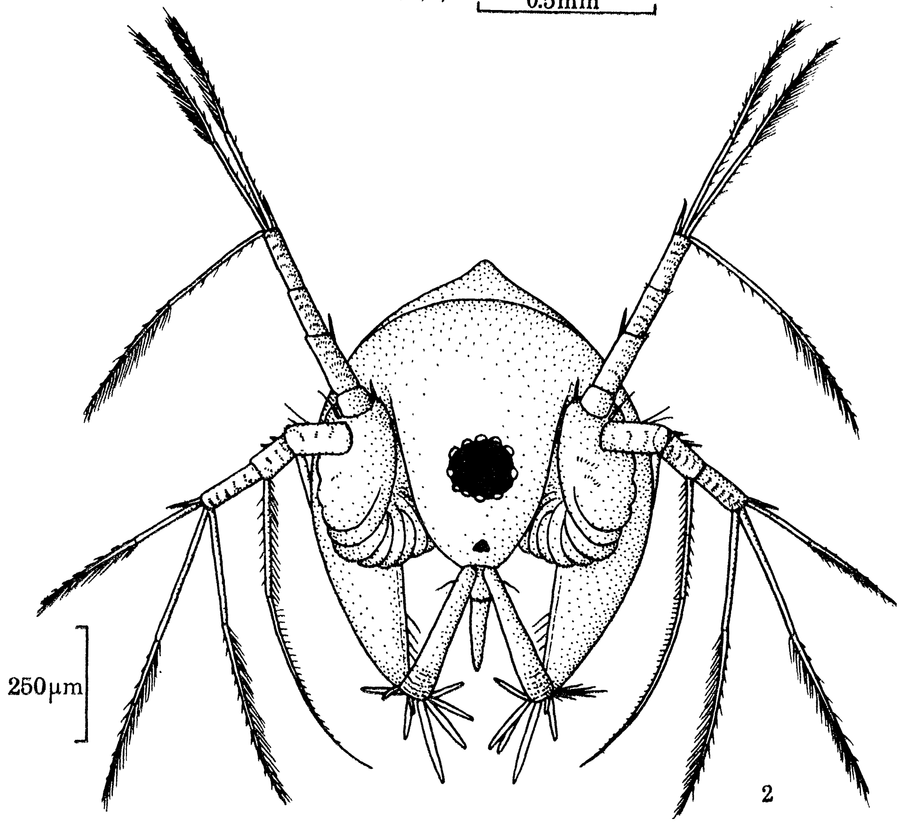
Acantholeberis curvirostris (figures 1–5), of which adult females are reputed to attain a length of up to 2 mm, but of which large British specimens are about 1.6 mm, is a characteristic species of acidic, peaty pools, especially those in which *Sphagnum* is growing. It often occurs among submerged *Sphagnum*, especially at the edges of pools and, in the Pennines, may be found even in channels occupied by dense masses of this moss. Association with *Sphagnum* is not, however, obligatory for it occurs on the peaty, *Sphagnum*-free bottoms of such pools, and in pools in which the moss is not to be found. Very shallow water seems to be avoided. These pools often occur in exposed situations, sometimes at altitudes of over 600 m (2000 ft), have a low pH and a low calcium content (pH 3.8 and 1 mg/l calcium are the lowest I have recorded but data are not available for all finds). It was, however, never found in a well-explored area of predominantly cotton-grass (*Eriophorum*) moorland in the southern Pennines (Fryer 1955), where altitudes never attain more than about 550 m (1800 ft) but where even more acidic conditions prevail (pH usually between 3.3 and 3.7) and it is possible that such conditions are beyond the limits of its physiological tolerance. In the Tatra Mountains *A. curvirostris* occurs at altitudes up to 1226 m (Litynski 1922). While most plentiful in summer and autumn a few individuals are to be found in mid-winter, even under ice.

Provided food is readily available, undisturbed individuals often spend long periods at rest and may move only a few body lengths in several hours. A resting animal often balances on the spines of the ventral carapace margins (figures 1, 5 and 18) and uses the long spines of the antennal endopods as props, though when suitable support is available it may rest at almost any angle. When resting among *Sphagnum* it sometimes even hangs by the antennal spines and setae. When necessary, or when disturbed, it swims rapidly and strongly by means of the antennae, but only a few beats are employed. These often suffice to propel it into cover, or into open water whence it sinks slowly to the bottom to alight in almost any position. Persistent swimming is not practised. Equally it is not a specialized crawler. Although when settled, ventral surface downward, on a suitable surface it at times moves forward by means of the first trunk limbs much as do many chydorids (Fryer 1968), this ability is only feebly developed and may even be in part an inevitable consequence of food collection (see §(v)). The efficient persistent crawling exhibited by many chydorids is not practised. Although the first trunk limbs often undoubtedly pull the animal forward, they are not habitually used even for gripping. This is well shown when an individual moves forward a little by this means among a mass of *Sphagnum*. After so moving it may halt, fall from the leaf, and sink. Even simple attachment would prevent this. Many observations of individuals resting on *Sphagnum* revealed that the first trunk limbs were not gripping. Although formidably armed, the antennae are not used for scrambling as they are both in certain other macrothricids and in chydorids. Likewise, although the massive post-abdomen is capable of feeble movements it appears not to be used for effective pushing. Locomotion is therefore relatively unspecialized.

Acantholeberis feeds on the flocculent detritus almost invariably present in superabundance in the habitats in which it occurs. While algal cells occur among this material they certainly contribute little to the food supply and some appear to pass unchanged through the gut, where they may remain for less than 30 min.

When advanced embryos are carried these are usually under pressure from the walls of the brood pouch. From time to time the trunk of the parent is eased ventrally, thereby increasing the size of the brood pouch, helping to ventilate it, and releasing the pressure on the embryos. When this happens the embryos begin to move their appendages rapidly. Within a few seconds the trunk is moved back, the embryos again come under pressure, and all movement ceases.

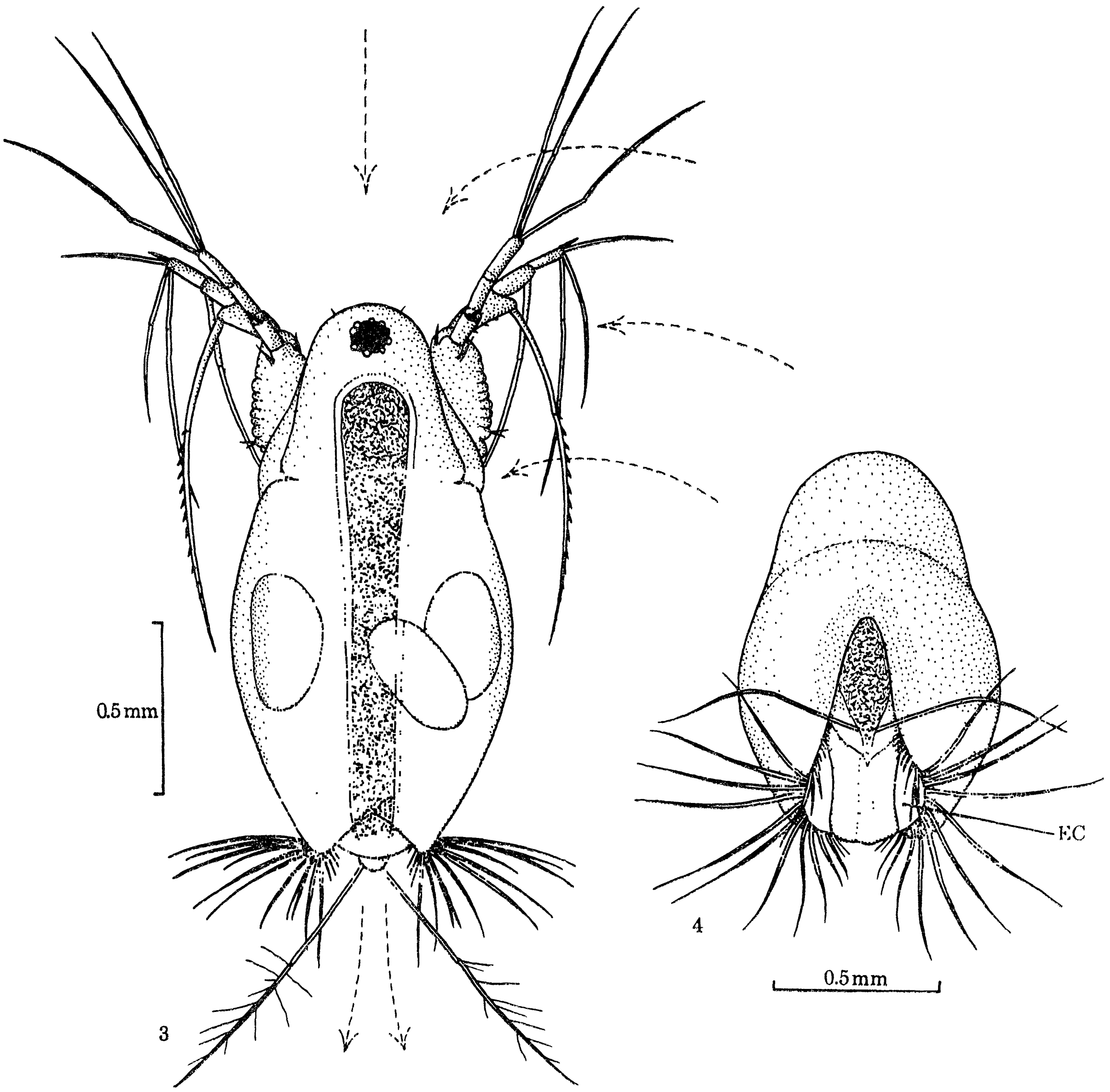




Figures 1 and 2. *Acantholeberis curvirostris.*

Figure 1. Adult female, lateral. The fine setation of the antennary setae is omitted.

Figure 2. The same, as seen from directly in front. Only on the left-hand side of the animal (right-hand side of figure) are some of the anterior members of the ventral carapace setae shown. In order not to obscure these some of the sensillae of the left antennule are omitted.



Figures 3 and 4. *Acantholeberis curvirostris*.

Figure 3. Adult female, dorsal. The fine setation of the antennary setae is omitted. Dotted lines indicate the direction of flow of currents which pass through the carapace chamber.

Figure 4. The same, from behind and slightly dorsal.

(ii) *Gross morphology*

Although the lateral view is illustrated by various authors this alone fails to convey a true appreciation of form, and in some respects is even misleading. Šrámek-Hušek (1962) gives a simple sketch of the ventral aspect; otherwise such illuminating views seem to have been ignored. Figures 1–5 portray the gross morphology of *A. curvirostris* and also introduce certain features of macrothricid morphology as a whole. Even detailed illustrations of the whole animal from several aspects may fail to make clear certain important points. For example, the very narrow ventral region of the head, while shown in figure 5, is difficult to appreciate without recourse to sections such as that shown in figure 7. The absence of a headshield – a primitive

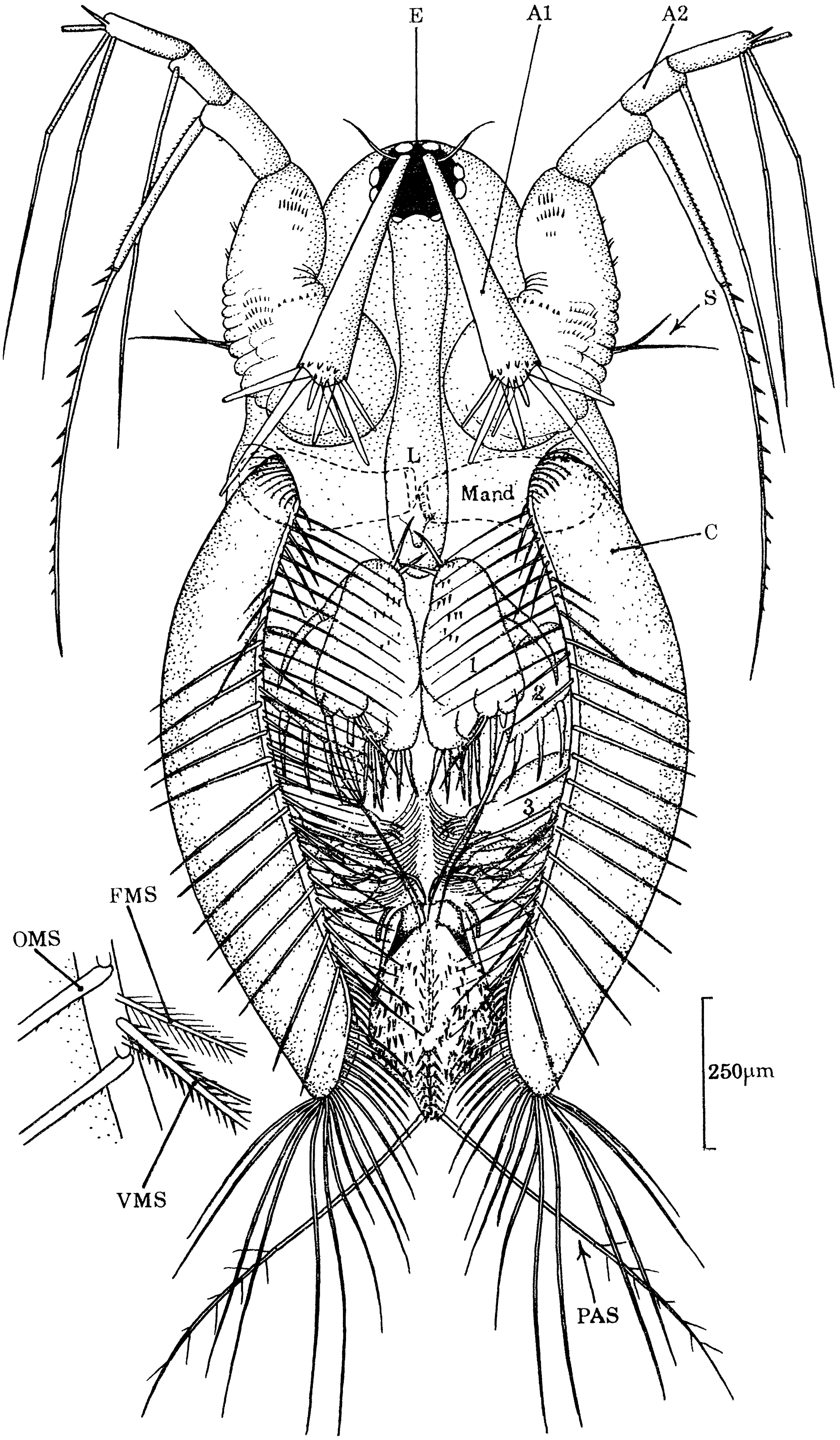


FIGURE 5. *Acantholeberis curvirostris.* Adult female, ventral. The inset shows the arrangement of the setae over much of the ventral carapace margin. Because it is directed almost vertically and lies dorsal to the endopod, the exopod of the antenna is not visible from this angle. Of the scrapers of trunk limb 2, that lying adjacent to the carapace margin is number 5. Numbers 6, 7 and 8 are obscured by the carapace.

feature – is particularly noteworthy, but a ridge above the antenna (figure 1) indicates on each side the region where the edge of the headshield becomes delimited by duplicature and outgrowth of the cuticle in other species. Neither the antennules nor antennae are protected in the manner in which, often very effectively, and always to at least some extent, they are in chydorids.

Unlike the robust carapace cuticle of chydorids that of *Acantholeberis* is thin and delicate, as is that encasing the head. Over much of the carapace of adult females the endocuticle (blue-staining with Mallory) is less than 2 μm in thickness and the non-staining, amber-coloured, sclerotized epicuticle is only about 0.5 μm thick. The head is unsuited to pushing through any but easily yielding flocculent deposits and the forwardly protruding antennae probably inhibit such penetration though they have not prevented it in certain other genera. That the massive post-abdomen (figures 1, 5 and 6) is used for only desultory pushing is of evolutionary interest and illustrates the need to observe the behaviour of the living animal as well as its structure.

The width is evident from figures 2–5, which also show the widely projecting antennae. Exploitation of narrow crevices is not possible, but movement through even dense beds of *Sphagnum* is not prohibited.

The carapace is basically a simple fold enclosing the body dorsally and laterally and with a wide gape ventrally as shown in figure 5. Anteriorly there is a wide aperture (figure 2). The posterior aperture is shown in figure 4. Only at its margins are there elaborations of the carapace. Here the inner cuticular lining, elsewhere extremely delicate, is somewhat thickened, and here the thickness of the tissues between the internal and external cuticles is greater than elsewhere (figure 18). Here arises a complex array of setae (figures 1–5 and 18) of which the long posterior group, whose arrangement is best appreciated from the dorsal (figure 3), posterior (figure 4) and ventral (figure 5) aspects, represents a specialization unique to *Acantholeberis*. These are widely splayed but not always at the same angle (cf. figures 3 and 5) and probably provide a defensive fence against small predators by increasing the effective size and by serving to foil attempts at seizure from behind.

The arrangement of setae on the anterior margins and at the anterior end of the ventral margins is apparent from figures 1 and 5. Over much of the ventral portion the armature is dominated by 13–15 long, outwardly directed, spiniform setae (figure 5 inset, OMS). Alternating with these are shorter spiniform setae (VMS) directed inwards and ventrally, and between each long and short seta is a very slender, inwardly directed seta (FMS). A row of 7 or 8 short, simple setae bridges the gap between the posteriormost of the long ventral setae and the array of posterior setae (figure 5). One of the functions of the ventral setae is to allow *Acantholeberis* to rest on but not sink into the soft flocculent deposits over which it usually occurs and on which it frequently rests (figure 18). This is largely the role of the long horizontally directed spiniform setae which also facilitate balance on *Sphagnum* leaves. The major function of the other setae is described in § (v).

Many attributes of the post-abdomen, antennules, antennae and labrum are apparent from figures 1–5. Particularly noteworthy is the almost right-angled bend near the base of the antennal protopod (figures 1 and 2) which ensures that the distal portion is directed almost vertically in a resting individual. The protopod is in fact curved in two planes as figures 1, 2 and 5 make clear. The result of this, and of the mode of their insertion, is the very characteristic orientation of the antennal rami (figures 1, 2, 3 and 5). This in turn permits specialization of the long spine of the basal endopod segment, which facilitates balance and perhaps, by granting purchase, at times assists in rapid take-off. The orientation of the antennae is such that the working stroke automatically lifts a resting animal clear of the bottom and launches it into open water in the manner so characteristic of a disturbed individual. Persistent horizontal swimming is not practised. While some macrothricids with a similarly flexed protopod coordinate the vertical (lifting) and horizontal components of antennal propulsion in such a manner as to permit this, in *Acantholeberis* steady horizontal progression appears to be precluded by the powerful lifting component. The presence of lateral sensory setae of the antennae – the analogues of mammalian vibrissae – is noteworthy and is evidently an ancient anomopod characteristic. The labrum (figures 6 and 8) is not clearly delimited from the narrow ventral part of the head, of which it is a posterior prolongation. It lacks the blade-like keel so characteristic of the Chydoridae: in its place is a simple, ventrally directed spine (figure 6, K) which guards the anterior aperture to the carapace chamber. Where the dorsal part of the trunk protrudes through the posterior aperture of the carapace chamber it is provided with protective spinules (figure 1).

(iii) *Some points of anatomy*

Figure 6 shows *Acantholeberis* in longitudinal section and reveals many of its salient anatomical features, variants of which are found in other members of the family and indeed throughout the Anomopoda. Many features are self-explanatory but particular attention is directed to the elaborate cephalic endoskeleton. In places its form changes over very short distances so that a single illustration is inadequate to reveal its full complexity. Basically it consists of a ventral plate (ENP), best developed in the antennary somite (though segmentation is here obscure) which throws out arms on each side of the oesophagus and is continuous with the suspensory system of the mandibles (SUS) and with various other suspensors and fibrils. The posterior extremity of this system is to be seen in figure 7 (END). The endoskeletal plate is particularly well developed above the oesophagus, in which region numerous oesophageal dilator muscles are inserted. There are also muscles (DAO) which unite the plate to the relatively thick cuticle which overlies the masticatory portion of the mandibles, whose function is probably to help dilate the atrium oris when necessary. Mandibular suspension is similar to that of *Eurycercus* (Fryer 1963) and other chydorids (Fryer 1968), but the spatial relation of the mandibular endoskeleton to the rest of the system is much modified in some of the latter according to the shape of the animal, especially where the assumption of a globular form has involved great foreshortening of the head. *Acantholeberis* displays a more primitive arrangement than do such species. Further fragments of the endoskeleton (END) are indicated beneath the compound

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FIGURE 6. *Acantholeberis curvirostris* as seen in longitudinal section. The section is median except that, instead of showing the full length of the gut at this level, the posterior end of the trunk, including the post-abdomen, is shown at a level nearer the observer in order to reveal the arrangemnet of some of the trunk musculature. Note especially the relatively small area occupied by the trunk limbs (TLS) (for details of which see especially figure 8), the massive nature of the post-abdomen (PA), the extensive and complex nature of the endoskeleton (ENP and structures continuous with this), the way in which the dorsal longitudinal trunk muscles (DLM) become modified in relation to trunk flexure and carapace attachment, and the enormous size of the gland cells of the labrum (LGC). The transverse mandibular muscle (TMM), here seen inserting on the posterior face of the transverse mandibular tendon (TMT), originates on the inner face of the left mandible and extends beyond the mid-line before insertion and is therefore seen in transverse section here. Because of the shape of the mandibles each masticatory surface (Mand) lies anterior to the body of its appendage, hence the noticeably posterior position of the transverse mandibular tendon, suspensors (SUS) and transverse muscles in relation to the masticatory surface.

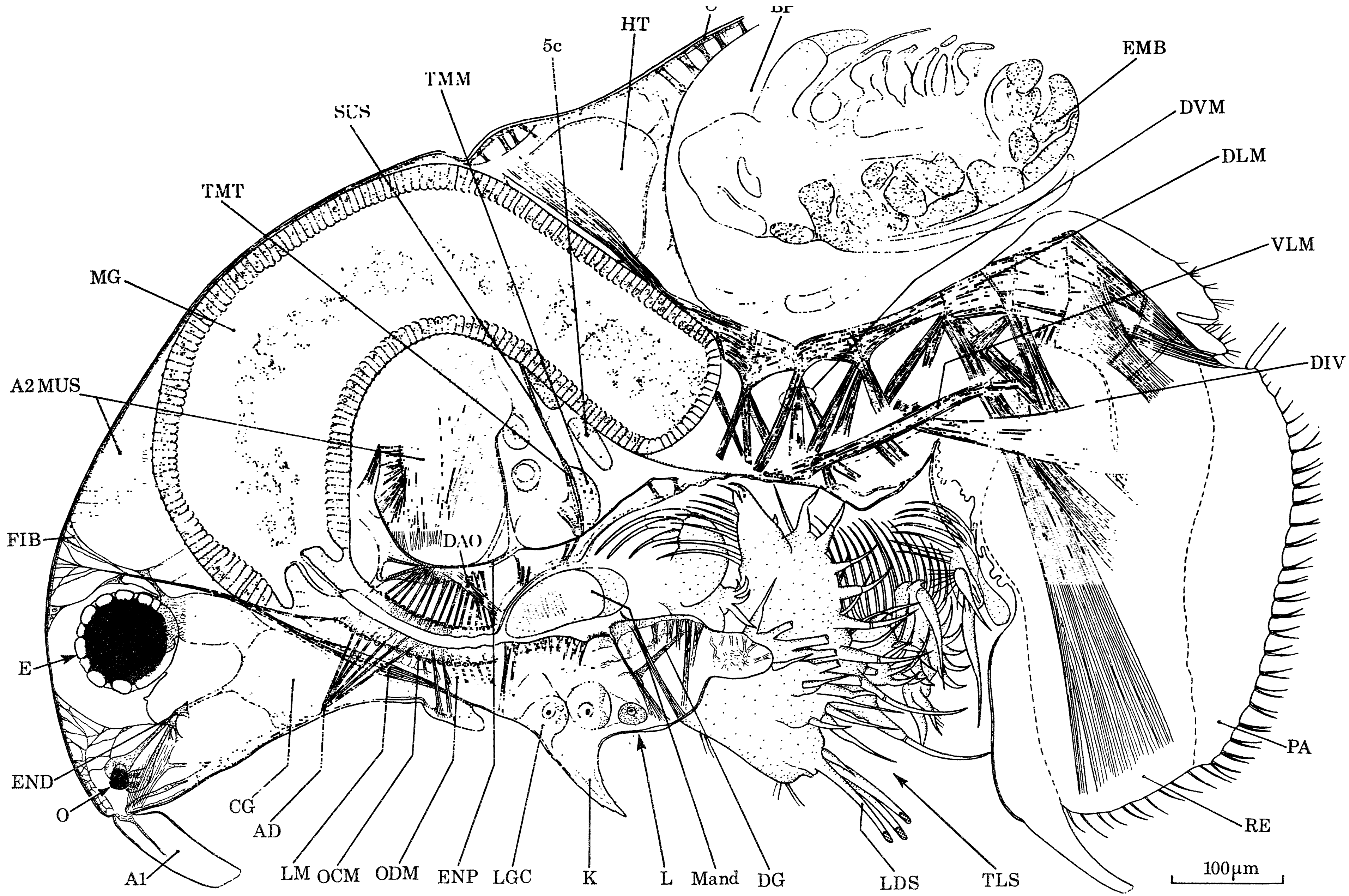


FIGURE 6. For description see opposite.

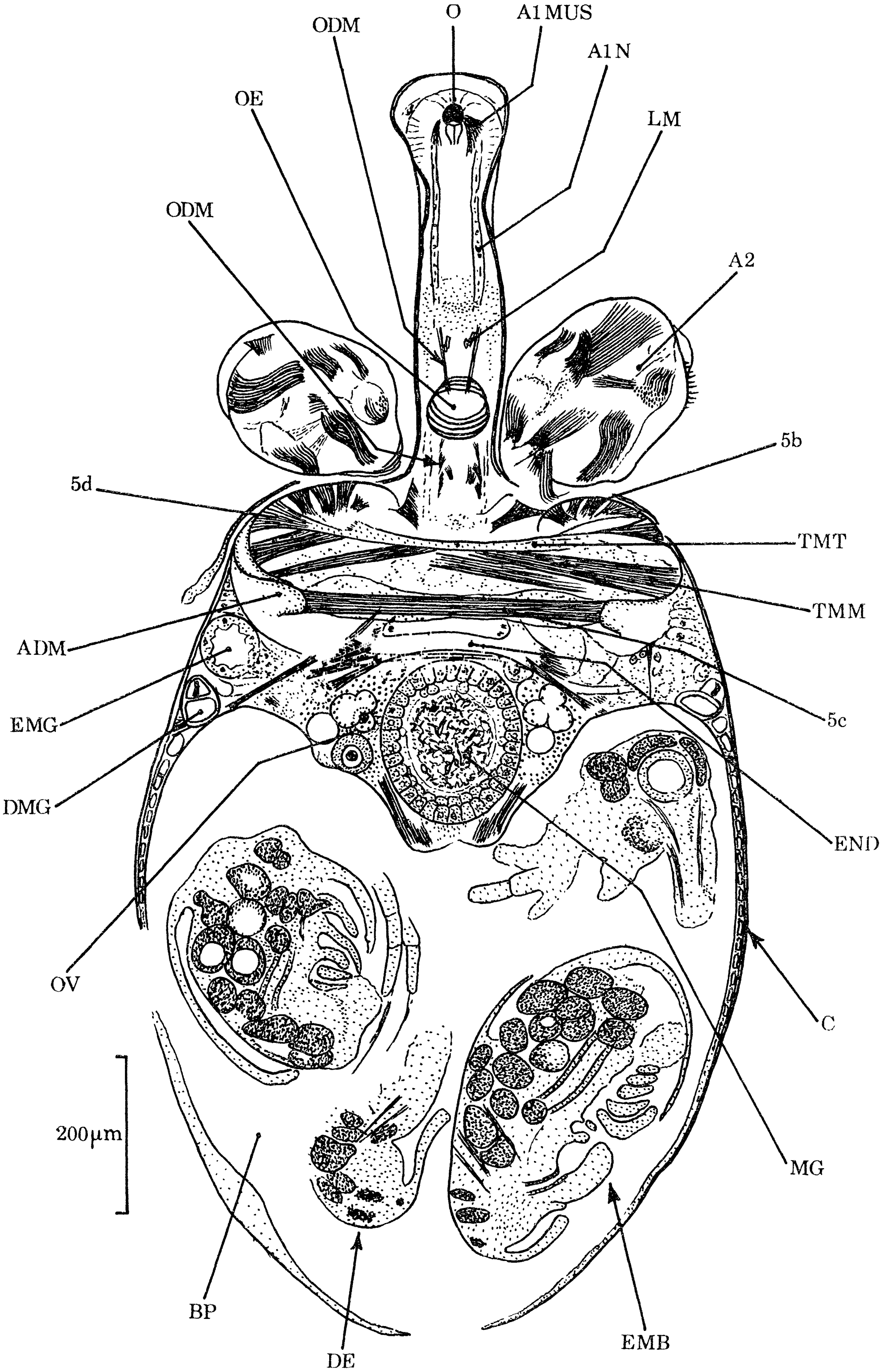


Figure 7. *Acantholeberis curvirostris.* Horizontal slice, ventral aspect, passing anteriorly through the ocellus (O) and posteriorly through the brood pouch (BP) just dorsal to the posterior arch of the alimentary canal. Thus the alimentary canal is cut only twice: through the oesophagus (OE) and, once only, through the mid-gut (MG). On the left (right-hand side of animal) the slice just includes the dorsalmost portion of the end sac of the maxillary gland (EMG). On the right the slice passes very slightly more dorsally and above the end sac. Note especially the very narrow ventral region of the head – which is not readily apparent in the whole animal – and that portion of the endoskeleton (END) in addition to the transverse mandibular tendon (TMT) which lies anterior to the sectioned region of the mid-gut. The transverse mandibular tendon is cut obliquely and therefore appears to be thick. It is in fact thin. At this level some of the antennary muscles are at or near their origin. Adjacent and more distal slices show the cavity of the sympod largely filled by muscles. The dual origin of the compound eye (DE) is apparent in one of the embryos to the rear of the brood pouch.

eye (E). These are continuous with an intricate and delicate system of fibrils (FIB) whose functions include suspension of the compound eye (E), the cerebral ganglion (CG) and the nerve cells which supply the ocellus (O).

Figure 6 also gives some indication of trunk musculature. Posteriorly metamerism is clearly apparent: anteriorly segmentation is obscured by flexure of the trunk – which facilitates the formation of a dorsal brood pouch (BP) – and by modifications related to carapace attachment. This is evident from the modification of such of the dorsal longitudinal muscles (DLM) as are shown anteriorly. Modifications of the trunk muscles for flexing the post-abdomen (PA) are evident, but the versatility of the chydorid post-abdomen is not achieved.

Of the other muscles shown, the dorso-ventral muscles of the labrum (L) are clearly seen as a continuation of the ventral series of oesophageal dilators (ODM). The muscles which depress the labrum (LM) (but which are morphologically levators) pull on a tendon which breaks up dorsally into a well-spread series of fibrils (FIB). Just below the tendon the muscles are closely associated with the mid-gut wall and are evidently attached to it but the means of adhesion is not clear. From this point, and not apparent in all preparations, a pair of tiny muscle fibres runs to the dorsal extremity of the oesophagus evidently as an additional pair of dilators. The bulge of thin cuticle adjacent and ventral to the origin of the levator muscle tendon permits hinging of the labrum. Because the compound eye is cut medially none of its muscles, which insert on the lateral head cuticle, are visible. Likewise the massive promotor and remotor roller muscles of the mandibles are located too laterally to be revealed in this figure. One of the major transverse mandibular muscles (TMM) is here seen in transverse section, as are the two 5c muscles (the terminology of Manton (1964) is used for these). Some of these muscles are seen in horizontal section in figure 7.

The post-abdomen (PA) is shown in outline only. Internal details, including the nature of the diverticulum, the suspension of the gut and the musculature of the rectum, are illustrated elsewhere (Fryer 1970).

(iv) *The trunk limbs and mouthparts*

All the trunk limbs and mouthparts are shown in face view in figures 6 and 8. These and figures 9–13 also show their relations to each other.

Morphologically each trunk limb is based on the same plan as its counterpart in the Chydoridae, but each has distinctive attributes, and some primitive features are retained. Trunk limb 1 is particularly revealing in this respect. In most chydorids the first trunk limbs are specialized for gripping and for locomotion. That such specialization is secondary and that the first trunk limbs assisted in the collection of food in the primitive anomopod will be demonstrated elsewhere. In *Acantholeberis* they retain this primitive function and also retain what appear to be extremely ancient features of anomopod and probably pre-anomopod organization. Details of the first trunk limbs are shown in figures 9, 10 and 14–16. Noteworthy features include the long, extremely finely toothed spines (LDS and SIDL) of the two distal lobes, the presence of scraper-like spines (IS1) on the inner face of endites 1 and 2 and the presence of four setae (SIL) on the inner lobe which is located near the base of the corm. Other features are either readily apparent or are referred to in §(v).

The limb has a complex system of intrinsic and extrinsic muscles, a trace of which is to be seen in figure 9, which enable elaborate movements to be performed and confer great mobility on the limb as a whole and on the distal lobes in particular (§(v) and figure 17).

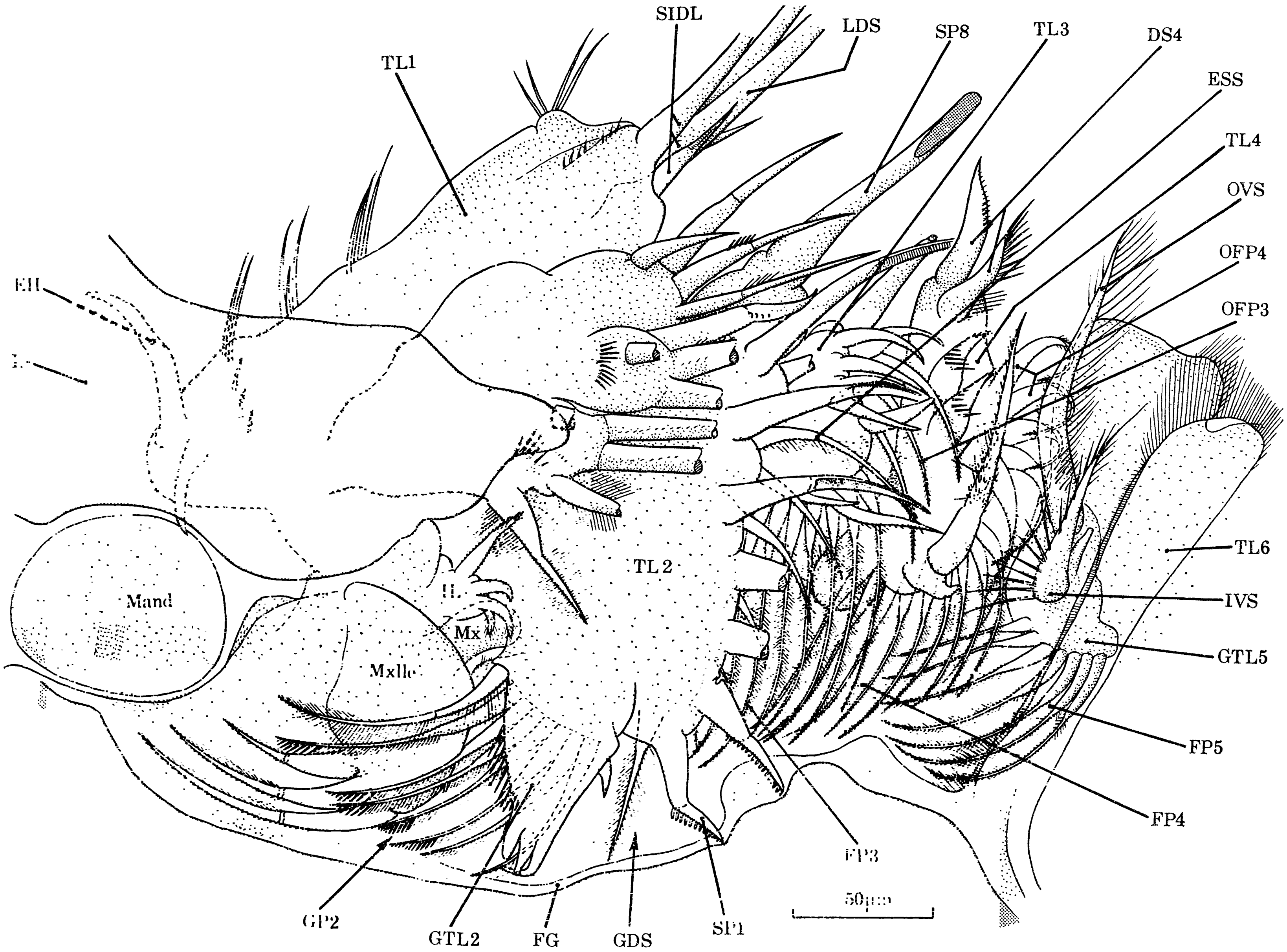
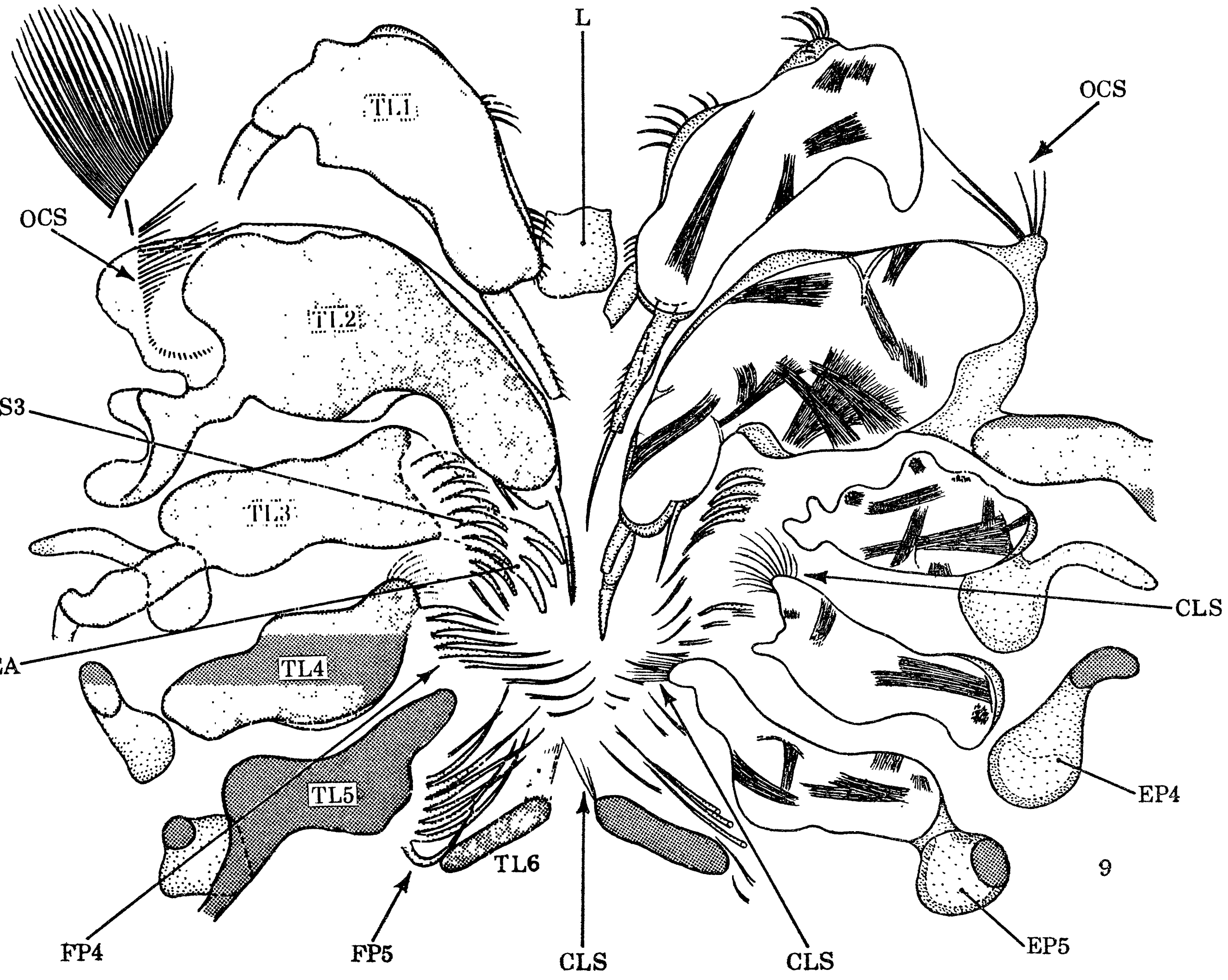
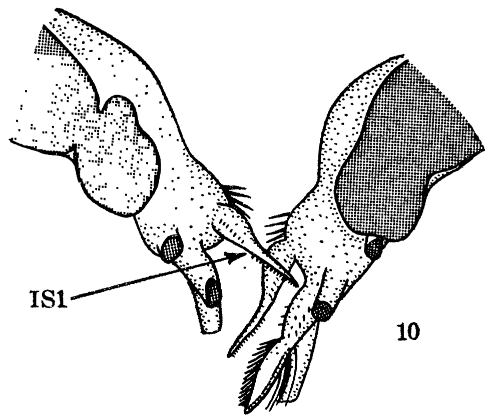
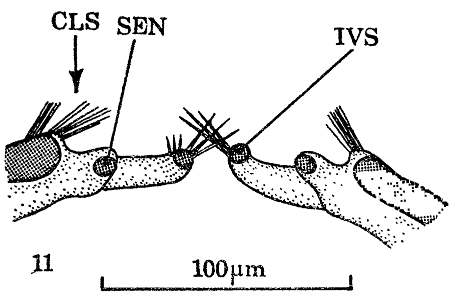


Figure 8. *Acantholeberis curvirostris*. Median longitudinal section through the trunk limbs, ventral surface uppermost. The trunk has contracted somewhat as a result of fixation, thereby causing the food groove (FG), normally more or less straight, to buckle posteriorly, and has pulled the posterior limbs forward so that their filter setae overlap the limb in front. The sixth trunk limb is shown as if transparent so as to allow the filter plate of trunk limb 5 to be seen. For further details of trunk limb 1 see figure 14.





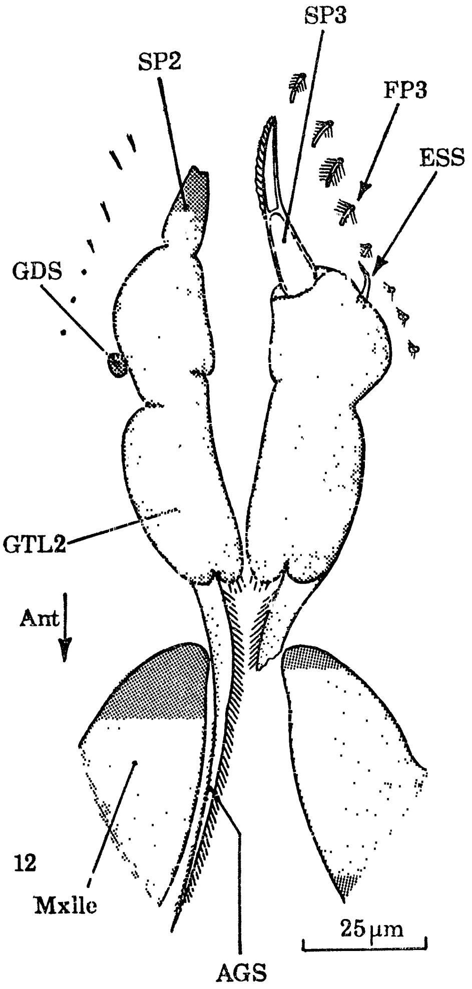


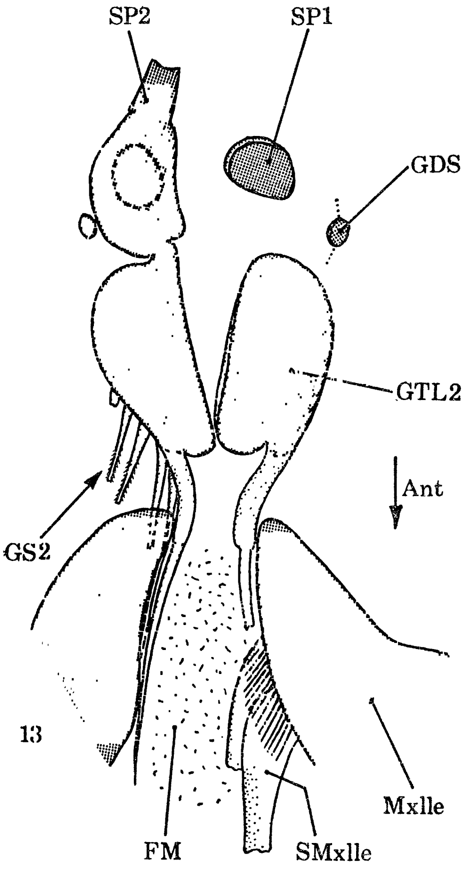
FIGURES 9–11. *Acantholeberis curvirostris.*

FIGURE 9. Horizontal section through the trunk limbs (ventral aspect), cutting more deeply at the level of trunk limb 5 than at the level of trunk limb 1. Some indication of the complexity of the musculature of the limbs is shown on the right. Part of the endite region of the right trunk limb 3 (on the left of the figure) is shown as if transparent to reveal the origin of outer and gnathobasic filter plates (FS3) whose continuity is here apparent. This limb is swung inwards a little more than its partner. Some of the spines of trunk limb 1 are omitted for clarity and although two scrapers of the right trunk limb 2 are included in the slice only one is shown. Note the cleaning setules (CLS) on trunk limbs 4, 5 and 6. The inset shows part of one of the rows of outer cleaning setae of trunk limb 2.

FIGURE 10. Horizontal section through the first trunk limbs (ventral aspect), more distal than in figure 9, to show one of the scraper-like inner spines (IS1) of each limb.

FIGURE 11. Horizontal section through the fifth trunk limbs (ventral aspect). The section cuts through the inner vertical seta (IVS) and the adjoining sensilla (SEN) of each limb but is a little too dorsal to cut the larger outer seta (cf. figure 8).





FIGURES 12 AND 13. *Acantholeberis curvirostris.*

FIGURE 12. Horizontal section through the maxillule (Mxlle) and gnathobases of the second trunk limbs (GTL2), viewed from the ventral side and cut at a level which slices through the second scraper (SP2) of the left appendage and reveals the third scraper (SP3) of the right and, on each side, the whole, or part of, the anteriormost (ventralmost) gnathobasic seta (AGS). Note how the anteriormost gnathobasic seta lies close to its partner, thereby containing the food mass in a tunnel between these spines and the food groove.

FIGURE 13. The same, at a deeper, more dorsal, level. The inclination of the two gnathobases differs somewhat and this, plus deliberate adjustments of focus, reveals the splaying out of the gnathobasic setae (GS2) on the left appendage and the position of the guard seta (GDS) of the gnathobase and the spines of the maxillule (SMxlle) on the right. The position from which the first scraper of trunk limb 2 arises is shown by a broken line on the left appendage. The food mass (FM) is indicated only schematically and lightly so as not to obscure structural features.

Each second trunk limb (figures 8 and 9) bears the basic anomopod number of 8 scrapers. In figure 8, scrapers 3 and 4 are omitted for clarity and number 8, the longest, is cut obliquely near the base. Adjacent and external to the scrapers is a row of sensory setae of which one of the more distal (ESS) is labelled. The presence of a row of setae here appears to be a primitive feature, from which condition, sometimes by loss of setae, sometimes by complex elaboration, specialized conditions have been derived, e.g. *Onchobunops* (§IX). What may represent the most proximal seta of this series (figures 8, 12 and 13, GDS) is well developed, bears two rows of spinules directed fore and aft, and is directed into the food groove. This guards the wide gap between the gnathobase (GTL2) and most proximal scraper (SP1) and is therefore designated as the guard seta.

The gnathobasic setae (GP2) are highly specialized and their very precise arrangement is of great functional significance. The anteriormost (figure 12, AGS) differs from the rest in that it lies nearer to the mid-line and close to its counterpart on the opposite limb, and by being armed on its inner face with a row of stiff setules which are directed obliquely towards their fellows on the corresponding seta of the limb of the other side. These two setae thus form a floor to the anterior end of the food groove. In certain other anomopods, e.g. *Eurycercus*, *Ophryoxus*, the anteriormost setae serve not as a floor, but as grids to prevent the lateral escape of food particles. This function they may to some extent fulfil even in *Acantholeberis* when the limb is at the very beginning of its working stroke, though their armature is not specialized for this. At their bases the remaining gnathobasic setae, whose armature includes specialized sweeping spinules near their tips, lie near to their counterparts on the opposite limb, but their tips gradually diverge as do those of the anteriormost setae (figures 12 and 13). In effect the two sets of gnathobasic setae therefore form a funnel whose wider end is anteriormost.

The second trunk limb also has a larger exopod than any other chydorid or macrothricid examined, which bears three setae and some long spinules. This is interpreted as a primitive feature. Contrariwise, the limb exhibits a specialization in the form of two rows of long fine setules (figure 9, OCS), one borne on a distinct lobe, which are directed towards the adjacent carapace. As the limb moves during the manipulation of food these sweep over the inner surface of the carapace and cleanse it. Their action may perhaps be related to the more stereotyped movements undergone by this limb than by its counterpart in many chydorids.

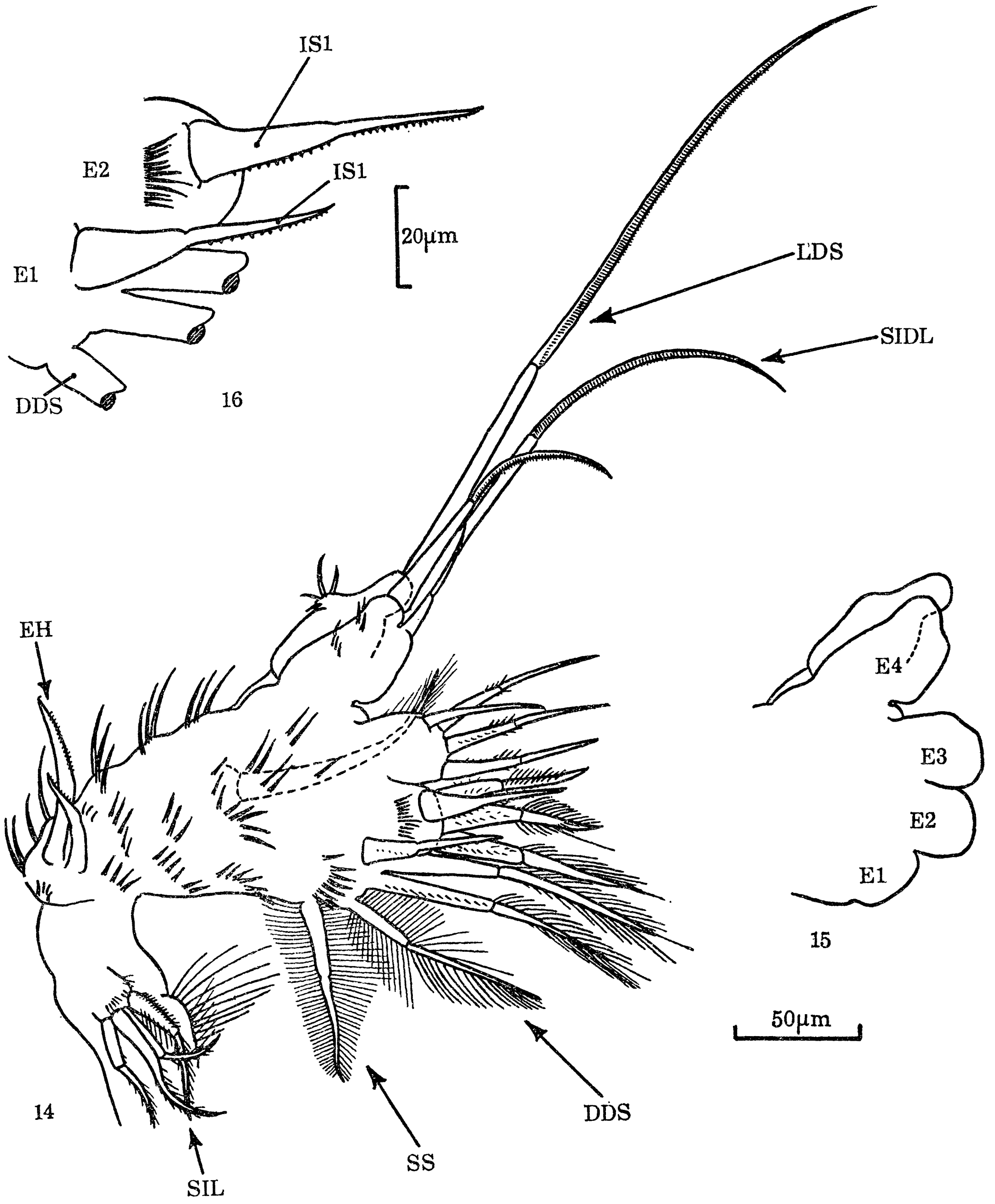
Trunk limbs 3 and 4 each bear a gnathobasic (figure 8, GP3, 4) and an outer filter plate (OFP3, 4). The endite armature of each is shown in figures 8 and 9. Trunk limb 3 bears a large exopod, well illustrated by Lilljeborg (1900), which is much larger than that of most chydorids and larger than that of several macrothricids. This is probably a primitive feature. Trunk limb 4 has a large exopod which, with that of trunk limb 5, which is also large, is responsible, with some assistance from the exopod of trunk limb 3, for setting up respiratory-feeding currents.

A sixth trunk limb (figures 8 and 9, TL6), which is a simple lobe like that of *Eurycercus* but has no vesicular epipodite, is present. Its main functions are to assist in the closure of the filter chamber posteriorly and to provide cleansing setules for adjacent filter plates.

The mandibles (figures 6 and 8, Mand) are similar in general structure and musculature to those of *Eurycercus* (Fryer 1963) and *Chydorus* (Fryer 1968). Like those of chydorids in general (*Pseudochydorus* and *Anchistropus* being partial exceptions) they exhibit marked skeletal and muscular asymmetry, the functional significance of which has been explained in detail (Fryer 1963).

The maxillules (figures 8, 12 and 13, Mxlle) have three spines and are similar to those of other microphagous anomopods.

Each maxilla (figure 6, Mx) is a simple lobe which fits into a groove excavated on the inner face of the basal portion of the first trunk limb. This location means that it lies to the outside of trunk limb 2 and enables the excretory products to be discharged into the exhalent stream which flows posteriorly on each side of the filter chamber.



FIGURES 14–16. *Acantholeberis curvirostris.*

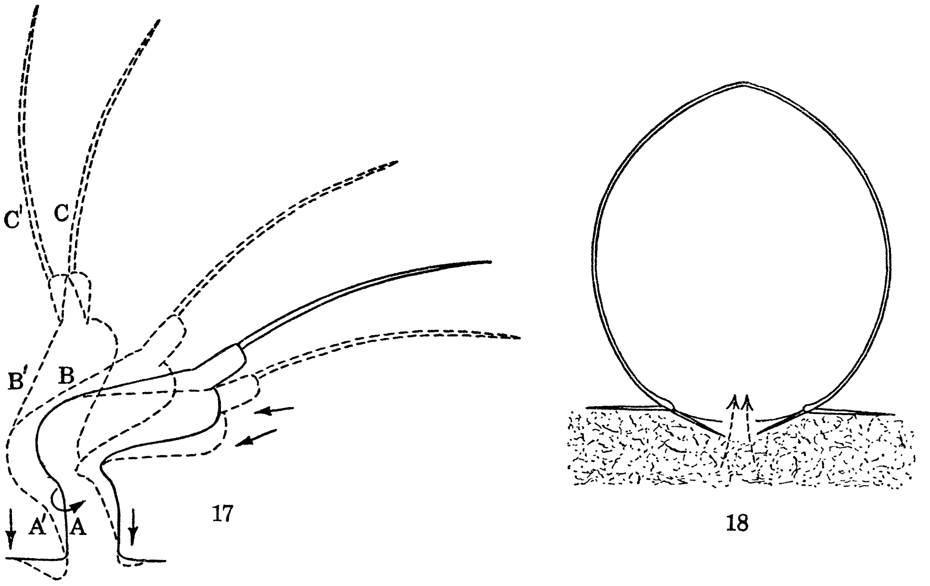
FIGURE 14. Trunk limb 1 seen from inside. Note especially the great length of the spines (LDS and SIDL) of the distal lobes, the location of the scrapers of endites 1 and 2 (for details of which see figure 16), the presence of 4 setae (SIL) on the inner lobe, and the orientation of other setae and spines.

FIGURE 15. The endites of trunk limb 1, shown without armature (cf. figure 14).

FIGURE 16. Endites 1 and 2 of trunk limb 1, seen from the inside to show the scrapers which they bear.

(v) *The feeding mechanism*

While the feeding mechanism of *Acantholeberis* shares many points of similarity with that of those chydorids which possess a well-developed filter chamber, such as *Eurycercus* (Fryer 1963) and *Peracantha* (Fryer 1968), there are some noteworthy differences. The filter chamber is a highly efficient filtering device, as is apparent from structure alone. As revealed by carmine and other particles, water is pumped briskly through it by the pump made up by the exopods of trunk limbs 4 and 5, assisted to some extent by those of trunk limb 3. Some of the currents observable from above are indicated in figure 3. Water enters the carapace chamber anteriorly and ventrally, some of that entering ventrally coming from behind the level of the filter chamber. Some suspended particles taken in anteriorly are deflected over trunk limbs 1 and 2 and then enter the filter chamber with others coming from the ventral regions. Some material inevitably enters the filter chamber in this way in nature as the animal rests on the bottom, but how much this contributes to the total amount collected is difficult to ascertain. Under some conditions it could contribute significantly: usually it is much less important than that collected mechanically by the trunk limbs.



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Figures 17 and 18. *Acantholeberis curvirostris.*

Figure 17. Diagrammatic representation of some of the movements of which trunk limb 1 is capable. Movements of the whole limb can take place in the trunk/limb 'joint' region A–A'; great mobility is granted at the 'elbow' of the limb as indicated by B–B', and the distal endites are capable of further independent movement, C–C'. Arrows indicate twisting and other movements, essentially horizontal dragging being achieved by a combination of actions.

Figure 18. Diagrammatic transverse section of an individual at rest on flocculent deposits, to show how the long, outwardly directed spiniform setae give support, and how the inward and ventrally directed spiniform setae screen the entrance to the carapace chamber posteriorly and form a grid through whose aperture restricted quantities of food material can be dragged by the long setae of trunk limb 1. The arrows indicate the approximate course of the dragged-in food, so far as it can be shown in one plane.

Acantholeberis uses the first trunk limb for collecting and manipulating food. Although this necessitates certain specializations, such utilization I believe to be primitive, and the limb in fact retains certain features which I have reason to believe were found in the ancestral anomopod. Food is collected by a reaching out of the limbs whose long distal spines (figures 6 and 14, LDS and SIDL) drag it towards the ventral aperture of the carapace chamber. This is made possible by the extreme mobility of the limb and by the great length and suitable armature of the distal spines. The limb is movable not only at its base but at the 'elbow', the latter flexibility contributing greatly to its versatility, much as does the elbow of the human arm. The trunk/limb 'joint' is extremely mobile and here, particularly anteriorly, the whole limb can be involuted to a considerable degree (figure 17), which facilitates the dragging in of food. While this seems to be permitted largely by thin trunk cuticle, some folding at the limb base may be involved, but this is extremely difficult to ascertain in life, especially as the limits of the limb cannot easily be defined. Still greater mobility is granted to the collecting spines by movements of the lobes which bear them, each of which has its own intrinsic musculature and articulates with the corm of the limb. Some indication of this mobility is given in figure 17, which, while showing the major movements involved in the collection of food, cannot reveal their full complexity. Simultaneous employment of several movements enables the limbs to be thrust out beyond the limits of the carapace chamber, permits their spines to collect even material lying anterior to the carapace as well as ventral to it, and to sweep and drag this towards the mid-line of the ventral aperture of the carapace chamber. Several grasping movements usually follow each other in rapid succession and are performed with great vigour. The long food-collecting spines tend to arch towards their partners on the opposite limb and, at least when they reach out and fail to make contact with food (which is the only time that this can be observed clearly), often cross over near their tips. This ensures that material is pulled to the mid-line.

A feeding individual may lie at almost any angle (which enables the process to be seen from many viewpoints) and, so long as the outreaching spines of the first trunk limbs continue to encounter food, often remains in one place for long periods. Should a number of sweeps fail to encounter food, this is invariably a signal to move on.

Food usually consists of loose flocculent deposits and often a large accumulation of this is seized and pulled by the first trunk limbs. Were the aperture of the carapace chamber unguarded, this would arrive as an unwieldy mass. It is prevented from doing so by the ventrally directed spiniform setae of the carapace margins (figures 5 and 18), which are stout and barbed (figure 5 inset, VMS). Such setae occur only in the region where food is pulled into the carapace chamber. More anteriorly, where they are not only unnecessary but would impede the activities of the first trunk limbs, they are absent. From a food mass so held, smaller portions can be pulled by the first trunk limbs through the gap between the rows of spiniform setae and encounter the other limbs only in a zone much narrower than the width of the ventral carapace aperture. On this material the more posterior limbs can operate; their more lateral parts, unequipped to deal with food material, are protected from what would here be its clogging effects. The very fine, inwardly directed setae of the ventral margins (figure 5 inset, FMS) yield easily to pressure and in no way impede the inward passage of food. In any case their length is such that they do not cover the main aperture to the filter chamber. Only where they overlie the first trunk limbs do those of the two margins almost meet in the mid-line (figure 5), but here they are so fine as to in no way impede the movements of these limbs. That any movement of the limbs inevitably exerts pressure on, and often deflects, these setae, suggests that they have a sensory function, passing information about the location and movement of the first trunk limbs to the central nervous system.

Movements of the first trunk limbs are not restricted to those described, nor need the two limbs move simultaneously. If material finds its way between the limbs, as is inevitable at times, it is pushed backwards and dorsally (i.e. towards the filter chamber) by alternate backward pushing movements of that part of the limb distal to the elbow. This enables the suitably located scraper-like spines of lobes 1 and 2 (figures 14 and 16, IS1) to perform these functions.

When the material grasped by the first trunk limbs is not loose, the inevitable result is that the whole animal is pulled towards it by the first trunk limbs – perhaps suggesting the way in which the habit of using these limbs for locomotion arose in the Anomopoda. Some of the forward movement produced by these limbs may be an inevitable consequence of such food-seeking activity, but progression over leaves of *Sphagnum* is at times too effective to be entirely explained in this manner. In addition to dragging towards the carapace chamber material that is to be used as food, the food-collecting spines of these limbs also bring in other material – such as filaments of algae and fragments of higher plants – which are rejected before they enter the filter chamber. Even material which superficially appears suitable as food may be pulled from a food mass, arrive at the entrance to the filter chamber and then be rejected, passing near the claws of the post-abdomen as it departs. Whether this is related to palatability or to the state of fullness of the food groove is unknown.

The rest of the armature of the first trunk limbs also plays some part in forcing food towards the food groove, but exactly how much is difficult to assess. Certainly the collecting spines are the most important holders of material after it has been collected, and play an important part in pressing it against the distal parts of the more posterior limbs, but the other armature inevitably assists in this process.

Movements of the second trunk limbs are more stereotyped than in most chydorids. While this restricted versatility may be partly primitive, some of it is imposed by the carapace setae which prevent much of the direct scraping seen in many anomopods (see figure 5). Trunk limb 2 is near the beginning of its working stroke in figure 5; near its end in figure 8. As it swings its scrapers describe an arc, the most distal (no. 8) sweeping first ventrally beneath the carapace, towards whose inner wall its fine comb is directed, and towards the mid-line, then, as it approaches the end of its stroke, dorsally towards the filter chamber. Thus when the limb is part way through its swing its distal scraper has access to the ventral aperture and, as its endite articulates with the corm and has its own intrinsic musculature, it can reach out to the food mass. Such outreach, which can be observed in animals held in a compressorium but is extremely difficult to detect in an unrestricted feeding individual, would enable this scraper to whisk food directly from a substratum, but its role in this respect is probably slight. It and its companions, however, play an important part in the transfer of food from the aperture of the carapace chamber to the filter chamber. The way in which they do so is essentially the same as that described for several chydorids (Fryer 1963, 1968).

At times the second trunk limbs make one or a few deliberate movements of varying amplitude. At others they move regularly and rhythmically as do trunk limbs 3, 4 and 5, but with very small amplitude. Deliberate movements are concerned with pushing and dragging food into the filter chamber and, at a later stage, with its movement along the food groove (see below), small movements apparently with the latter only.

That the third trunk limbs make regular movements is of particular interest. In no investigated chydorid except *Disparalona* do these limbs swing regularly (Fryer 1968). In *Disparalona* this movement takes place in non-feeding as well as in feeding animals. *Acantholeberis*, however, is usually feeding, and apparently non-feeding individuals may at times extract particles from the respiratory-feeding stream. One consequence of the regular swing of these limbs is that material entering the filter chamber is dragged and pushed along its way by their distal armature and, somewhat deeper in the filter chamber, is forced towards the food groove by the heavy gnathobasic armature, the longest spine of which is clearly shown in figure 8, where it lies more or less horizontally and reaches back over trunk limb 4.

The regular activity of the third trunk limbs is accompanied by movements of equal regularity and greater amplitude by the fourth limbs. These include a component that swings the endite armature more or less transversely along an arc towards the mid-line and food groove, as is typically the case in the Chydoridae (Fryer 1963, 1968). The action of the distal armature of limbs 3 and 4 helps to break up food masses as well as to convey them to the filter chamber.

Currents flowing through the filter chamber assist the mechanical propulsion of food material thus described. Although it is often difficult to assess the relative effectiveness of the two methods there is no doubt that mechanical propulsion plays the leading role in the movement of large masses. However, currents suck material against the gnathobasic filter plates of trunk limbs 3, 4 and 5 and the outer filter plates of limbs 3 and 4, which together comprise the filter chamber. The rhythmic swing of all these limbs, including trunk limb 5, which is not concerned with the mechanical handling of food near the entrance to the filter chamber, conveys material ever nearer to the food groove and forward. Filter plates are cleaned in the usual manner by cleansing setules – clearly apparent on several limbs in figure 9, CLS – and material eventually arrives in the food groove. Thence it is swept forward; from the posterior end by the tips of the gnathobasic filter setae of trunk limbs 5, 4 and 3; more anteriorly by elements of trunk limb 2. Some large food particles in fact never find their way to the posterior end of the food groove but are forced directly into its more anterior portions by the heavy armature of the more anterior appendages. The importance of trunk limb 2 in sweeping food forward is readily apparent from figure 8, in which it is near the end of its working stroke. That the more proximal scrapers serve as rakes which drag and sweep food from well back along the food groove is clearly shown. Material is carried forward by these scrapers to a position from which, on the next swing of the limb, the gnathobasic armature can sweep it within range of the maxillules. The importance of the guard seta (figure 8, GDS) is now readily apparent. It is in this region that the biggest accumulations of food collect in the food groove and it is for the transfer forward of these that the equivalents of the gnathobasic filter setae of the more posterior limbs are specialized for sweeping, especially at their tips. All save the anteriormost are so modified (figure 8, GP2). The nature and orientation of the anteriormost of each of the second trunk limbs (§(iv)) is such that they combine to form a floor beneath the food string to prevent it drifting out of the food groove. The other setae push not only with their tips but also over the whole of their inner faces. This is an inevitable consequence of their arrangement for, forming as they do a funnel whose mouth lies anteriorly (§(iv)) and whose throat is blocked by the gnathobase of the limb (figure 13), they and the gnathobase, which terminates in sclerotized spines (figure 8), inevitably sweep forward accumulations of material as they make their working stroke. On their return swing they equally inevitably leave behind their load. Thus little material has the opportunity to slip out of the food groove. Any that should do so, however, is prevented from slipping between trunk limbs 1 and 2 by the screening seta (figures 8 and 14, SS) of the former. The gap is often smaller than that present in figure 8 where the first trunk limb is not pulled in to its maximum extent. The spine adjacent to the screening seta (figure 14, DDS and, cut short, figure 8) must also prevent the drift of material away from the food groove and, as the first trunk limb undergoes remotion, will also wipe across the inner face of trunk limb 2 and sweep any stray material to the food groove, but this is almost impossible to observe in the living animal.

No mention has been made of entangling secretions during this account. That such secretions are produced by the labral glands is almost certain. However, although large gland cells are conspicuous in the labrum, and ducts are present, in no section have secretions been observed exuding from them in the manner so often demonstrated in several chydorids (Fryer 1963, 1968). In a few sections, however, typical ribbons of coagulated secretions were found in the vicinity of the labrum. As no secretion-filled reservoirs are present in any of the trunk limbs, these almost certainly emanated from the labral glands, as in many anomopods, but absolute proof is lacking. It may be that labral gland secretions are produced less copiously by *Acantholeberis* than by such a chydorid as *Peracantha* which collects finer particles. As in certain chydorids (e.g. *Eurycercus*), the inner lobe of trunk limb 1 (figure 8, IL) is so located that it must deflect, and perhaps actively wipe, labral gland secretions towards the food groove.

Large food masses are often manipulated by the distal portions of the trunk limbs without entering the filter chamber. The first limb drags them towards limbs 2 and 3, whose distal elements dislodge material and force it into the filter chamber and also move the main mass posteriorly. After this has passed posterior to the fourth limbs it is pushed away. When the mass is of a suitable shape the action of the distal armature of the trunk limbs sometimes rotates it, during which process pieces are removed from it. The tips of moss leaves are sometimes taken deep into the filter chamber and there apparently cleaned before being ejected.

Relatively large pieces of material frequently arrive at the postero-ventral part of the filter chamber only to be rejected in whole or in part in the vicinity of the fourth trunk limbs. Although often observed, the limb movements involved are so rapid and complex that the exact means of rejection is uncertain. It could be accomplished by reversal of the action of the endite armature of trunk limb 3 which, especially if this took place as trunk limb 4 was on its back stroke, would push material out of the filter chamber in the vicinity of the fourth trunk limbs as observed. Some rejected material certainly leaves the filter chamber at a level posterior to the endite spines of trunk limb 4, and a subtle twist of the corm of this limb may enable those spines to reverse their working movement. Whatever the exact movement, a rejection mechanism operates posteriorly.

Rejected material mostly leaves the carapace chamber near the claws of the post-abdomen, but usually these play no part in the ejection process. Occasionally very feeble movements of the post-abdomen assist, but nothing comparable with the powerful swing which removes excess food in chydorids has been seen.

Acantholeberis seems not to allow the posterior escape from the filter chamber of unwanted large masses by opening the posterior 'gate' formed by the vertical setae of the fifth trunk limbs – a simple expedient practised by certain chydorids. This may be related to the often unwieldy nature of the masses rejected which could prove inconvenient if allowed to slip posteriorly with the exhalent current, and to prevent whose backward passage by this means the very long spinules of the innermost vertical seta of trunk limb 5 (figures 8 and 11, IVS) seem to be specifically developed.

As in chydorids excess material can be ejected from the food groove anteriorly by the ejector hooks (figures 5, 8 and 14, EH) of the first trunk limbs. These are, however, used less frequently than in many chydorids; perhaps because so much material is rejected posteriorly and only the requisite amounts are pushed to the food groove. This device, however, is extremely effective when required. Once, part of a long algal filament, probably collected while entangled among other food, had passed between the mandibles and up the oesophagus and was clearly seen extending around the anterior curve of the mid-gut while its other end still protruded from the carapace chamber. Although partially rejected several times, the mandibles continued to feed it into the alimentary canal until most of it had entered. Eventually, however, by a repeated series of rejection movements the whole filament was dragged out of the gut and kicked away. In another case an inorganic particle was pushed into the food groove and reached the mandibular region. From here it was ejected by the ejector hooks, pushed backwards and ventrally between the second limbs – probably assisted by reverse movements of these – and appeared to be ejected at the level of the fourth limbs by movements of the third.

(vi) *Conclusions*

While one of the most generalized of extant macrothricids, *Acantholeberis curvirostris* exhibits several specialized features. The powerful leaps of which it is capable are related to the form of the antennae, of which the 90° flexure of the protopod is particularly important. Crawling is practised in only a rudimentary manner and association with surfaces is transient. Thrusting with the post-abdomen is not used for locomotion. The ventral carapace armature prevents sinking into the flocculent deposits on which the animal often rests and also screens the wide ventral aperture of the carapace chamber and restricts the entry of food – mostly flocculent material – to a narrow region. Food is collected by the first trunk limbs, passed to the filter chamber by limbs 2, 3 and 4 assisted by currents set up by exopods of the posterior limbs. The filter chamber is made up by gnathobasic filter plates of limbs 3, 4 and 5 and outer filter plates of limbs 3 and 4. From this chamber food enters the food groove and is pushed to the mouthparts by the tips of the gnathobasic filter plates and, more anteriorly, by the non-filtratory gnathobases of the second trunk limbs.

IV. THE FUNCTIONAL MORPHOLOGY AND HABITS OF *OPHRYOXUS GRACILIS* G. O. SARS

(i) *Ecology and habits*

Unlike that of many macrothricids, the functional morphology of *Ophryoxus gracilis* (figures 19 and 20) has already received attention. In a pioneer study, Eriksson (1934) gave an account of the feeding mechanism which revealed the basic principles involved, but his complex presentation is inadequately illustrated and difficult to follow. While the present investigation was in progress, and after work had been done on *Ophryoxus*, Sergeev (1970*a*, *b*) published a well-illustrated account of the functional morphology and feeding mechanism of this species which amplified the work of Eriksson and threw much new light on limb morphology (see also Sergeev 1972). Information given here is therefore much abbreviated and concerns particularly those features, often of evolutionary interest, not touched upon by Eriksson or Sergeev. Illustrations are given of features not described by these workers. These also reveal certain basic attributes of macrothricid anatomy not mentioned for *Acantholeberis*.

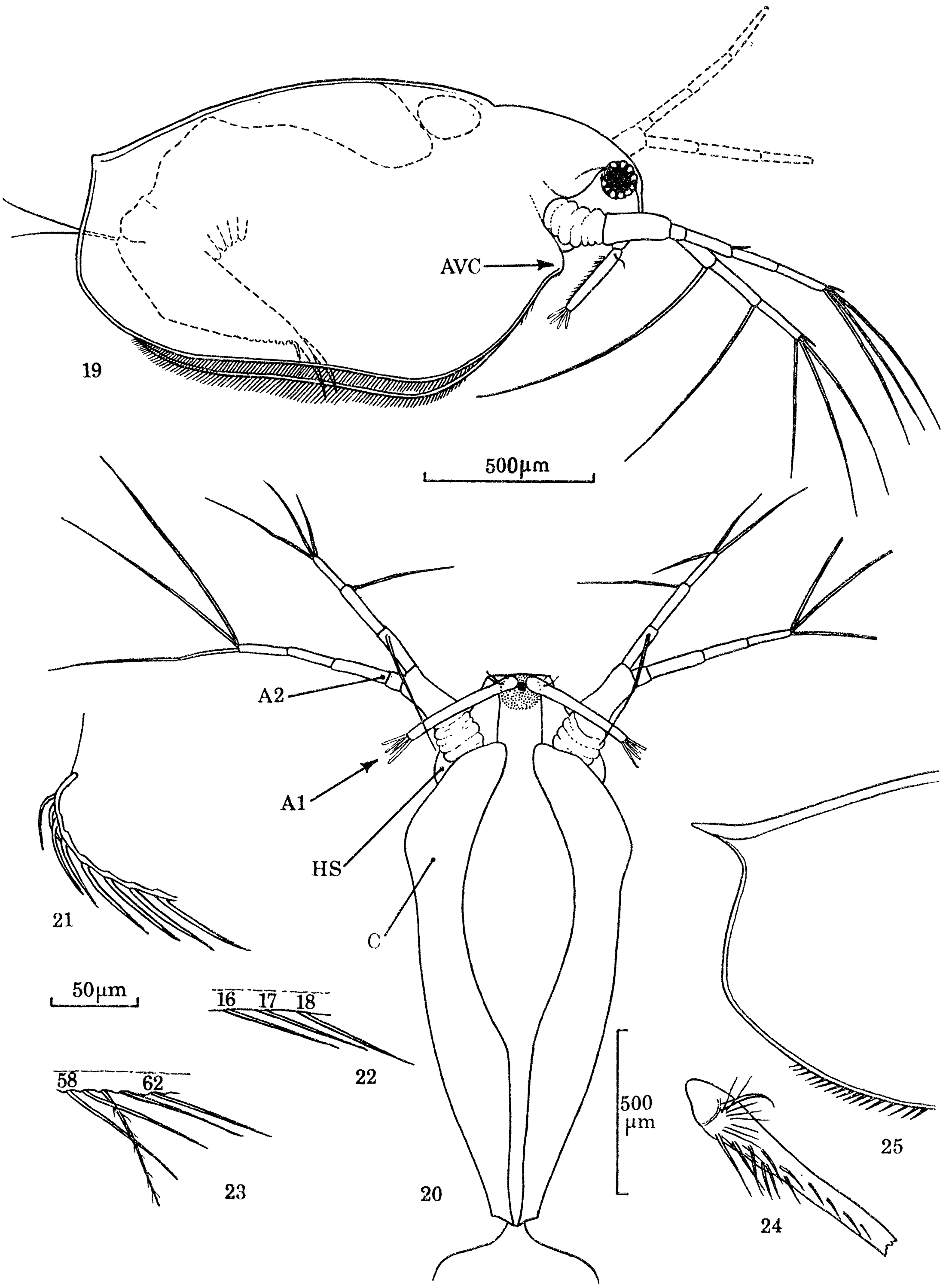
O. gracilis (length to about 2 mm) has a circumpolar distribution. In the Old World it is a characteristic northern form and is possibly stenothermous. In North America, however, what is probably a distinct race or geographical subspecies extends south at least to latitudes comparable with southern Italy. In Britain it is known only from lochs in the Great Glen of Scotland. Material for the present study was obtained from Inchnacardoch Bay, Loch Ness, where Scourfield (1904) recorded it more than 60 years earlier and where a flourishing colony still exists, from an adjacent shore in this lake, and from two lakes in the U.S.A. In all cases it occurred in the littoral region; otherwise the habitats differed considerably. Loch Ness is a soft-water loch (pH 6.0, Ca^{2+} 2.5 mg/l in the one sample analysed), and here *Ophryoxus* occurred among mixed vegetation in sheltered situations and was also found in small numbers along an exposed rocky shore. In Lake Lacawac, Pennsylvania, it was collected among sparse mixed vegetation near a shoreline of raised bog over a bottom whose organic content ranges from 60–70 %, where the pH is usually about 5.4, and where, in summer, temperatures may rise briefly to 30 °C. Dr Clyde E. Goulden has found it numerous in vegetation-free areas on an essentially sandy bottom (organic content as low as 0.01 %) in the same lake. Lawrence Lake, Michigan, is a marl lake (Ca^{2+} content 55–70 mg/l) and very different. Here *Ophryoxus* occurred in a dense and almost pure stand of *Najas flexilis* (Willd.) Rostk. & Schmidt growing on a marly bottom where the annual pH range is from 8.2 to 8.4 and where temperatures rise to at least 26 °C in summer.

As Sergeev (1970*b*) makes clear, *O. gracilis* spends much time resting on or moving slowly over the bottom or over plant surfaces. Nevertheless one of its outstanding attributes is its ability also to swim freely, as noted by Birge as long ago as 1892 and confirmed by Sergeev. This it does slowly and feebly but more persistently and less erratically than any other macrothricid examined save *Onchobunops* and perhaps *Grimaldina*. It is also a more persistent swimmer than any chydorid. In this it demonstrates in a rudimentary manner a habit whose evolutionary potential has been exploited by the Daphniidae in ways which will be discussed elsewhere.

There is a more intimate relation between the ventral carapace margins and the substratum than in *Acantholeberis*, and *Ophryoxus* does not lie on the bottom in the disorientated manner so frequent in the former. It can swim with the ventral margins parallel to the vertical walls of a glass vessel and settle there, head upwards, without apparent difficulty. No other observed macrothricid performs this feat but Sars' account (1900) of *Iheringula paulensis* G. O. Sars suggests that this species can possibly do so. In nature *Ophryoxus* must be very efficient at settling on leaves or stones. When at rest the essentially straight antennal protopod usually lies parallel to the substratum and is directed forward and somewhat outwards (figures 19 and 20). It can, however, be raised to about 45° with the horizontal. The rami extend forwards and, very markedly, outwards, the endopod being directed much as in *Acantholeberis* (figures 2, 3 and 5), the exopod more laterally.

Crawling is by means of the first trunk limbs, aided at times by the antennae. In this respect *Ophryoxus* differs from most macrothricids and shows parallels to chydorids, but the crawling is of a rudimentary kind and usually involves no more than pulling the body towards the material grasped by the first trunk limbs and somewhat forward. Persistent crawling by means of these limbs has not been observed. The spine of the basal endopod segment of each antenna (more slender than in *Acantholeberis*) makes contact with the substratum. When necessary one antenna can be used while the other remains stationary, enabling the animal to turn in a small compass. In this respect the antennae of *Ophryoxus* resemble those of the Daphniidae in structure, those of the Chydoridae in function. Eriksson (1934) and Sergeev (1970*b*) refer also to pushing by the post-abdomen in this connexion and this occurs at times, although only rarely in my experience. I have, however, seen the post-abdomen extended many times as a trapped individual attempted to free itself. Although certainly mobile, the post-abdomen is not specialized for pushing, but may well be used at times to assist negotiation of obstacles.

The food consists of bottom material or material growing or settling on plant leaves. The guts of individuals from Loch Ness contained many diatoms among the detritus and very small quantities of inorganic matter.



FIGURES 19–25. *Ophryoxus gracilis*.

FIGURE 19. Adult female, from Loch Ness, lateral. Note the straight antennal protopod. The antenna indicated by a dashed line shows the position, determined photographically, at or near which the appendage normally rests before making a swimming stroke.

FIGURE 20. The same, ventral. The antennae are in the resting position. The shape of the body has been determined photographically and the outline of the embayment sketched in from a preserved specimen.

FIGURE 21. The anteriormost spines of the carapace margin. (Seen from inside.)

FIGURE 22. Spiniform marginal setae a little more posteriorly.

FIGURE 23. Setae which fringe the embayment.

FIGURE 24. The antennule, showing the armature of the posterior face. Terminal sensillae omitted.

FIGURE 25. The posterior end of the carapace of a specimen from Lawrence Lake, Michigan, U.S.A., for comparison with the Loch Ness form, showing the more accentuated posterior-dorsal spine and the sparser, rather stouter, and more widely separated, ventral setae.

(ii) *Some points of morphology*

General form is shown in figures 19 and 20. The carapace is less wide than in *Acantholeberis* and the whole animal more slender (compare figure 20 with figures 3 and 5). Sergeev (1970*b*) mentions that the carapace is elongate and thin and relates these attributes to the habit of swimming. The carapace is indeed very delicate, being conspicuously thickened only at the ventral margins and to some extent along the mid-dorsal rib, which provide a frame for the whole. This frame is lightly sclerotized. Strength is given to the lobes by a slightly thickened and predominantly hexagonal pattern of reticulation which is more conspicuous in the Scottish than in the North American material. American animals from both populations examined have a better developed posterior-dorsal spine (figure 25) than those from Loch Ness (figure 19), and here there is light sclerotization which extends anteriorly some way in the mid-dorsal line. In ephippial females thickening and sclerotization extend along the mid-dorsal line to form the dorsal ridge of the very primitive ephippium (Fryer 1972). In both Scottish and American populations juveniles have a relatively longer posterior-dorsal spine than adults.

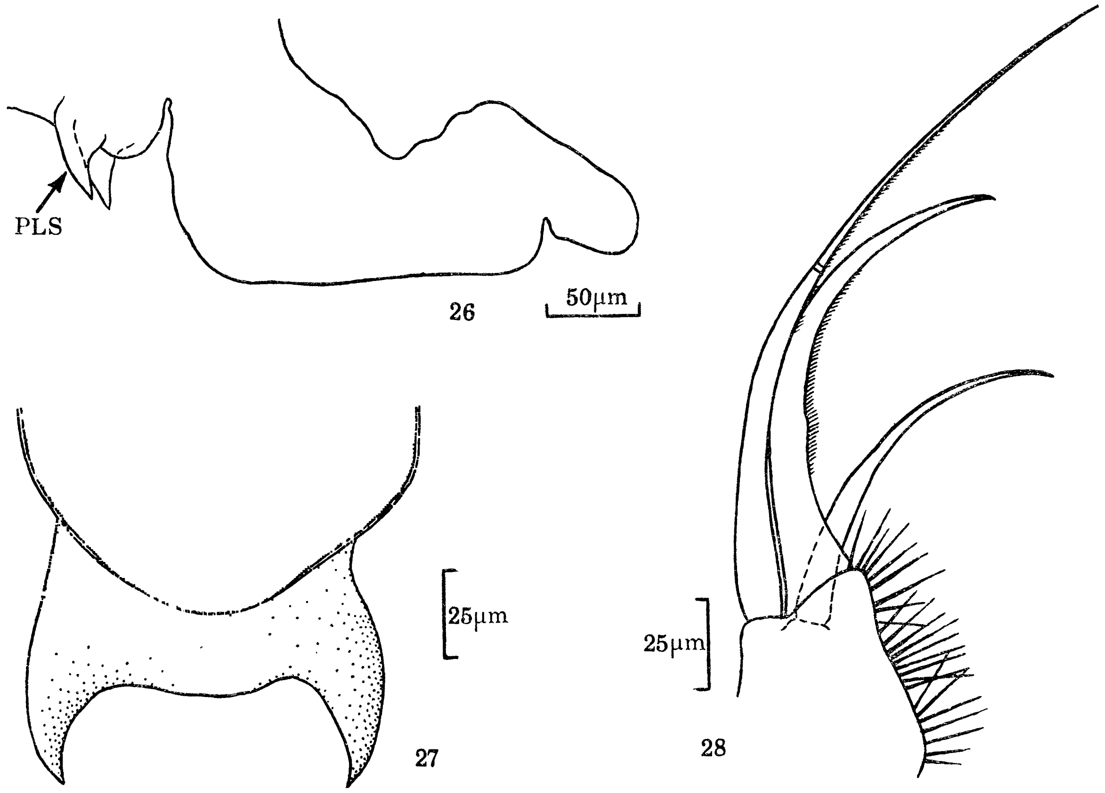
The ventral aperture, while wide, is much less so than that of *Acantholeberis*, and its margins closely approach each other in the posterior third of the carapace. They thereby convert the posterior portion of the carapace chamber into a tubular structure, through which the exhalent current passes to be discharged via a narrow lens-like posterior aperture. This is in strong contrast to the wide posterior aperture of *Acantholeberis*. That portion of each ventral margin that makes contact with the substratum when the animal is resting or scraping up food is more or less straight in both the horizontal and longitudinal planes.

The ventral armature is much simpler than in *Acantholeberis* and its component spines and setae show little differentiation except in length and stoutness. These, about 140 in number in the Loch Ness form, extend in a close-set row from the anterior ventral corner, which is conspicuous but very dorsal in position (figure 19, AVC), almost to the broadly rounded posterior ventral corner. The anteriormost (figure 21) are smooth curved spines; behind these they are successively longer and straighter (figures 22 and 23). Those which line the wide aperture adjacent to the trunk limbs are the longest in the entire series and are directed ventrally and inwards. Many of these are armed with a few stiff setules (figure 23). Those comprising approximately the last quarter of the series are short setae. Posterior to these, and extending along the inner face of both the ventral and posterior carapace margins, is a row of fine slender spinules. The short anterior margins are unarmed.

Although the number of spines and setae on the ventral margins is to some extent size-related, the Loch Ness animals display almost twice as many such structures as do the available North American specimens. This, other small differences, and apparently different temperature tolerances, suggest that geographical races or subspecies have evolved.

Unlike *Acantholeberis*, *Ophryoxus* has a distinct headshield (figures 19 and 20, HS). This is much less developed than that of chydorids but approaches the condition seen in such a daphnid as *Daphnia pulex*. Its lateral expansions overlie the bases of each antenna thereby offering some protection. More important from a functional point of view is that, while small, the lateral expansions are sufficient to impose restrictions on the swing of the antennae during promotion. Comparison with *Acantholeberis*, however, tends to exaggerate this in a misleading manner as the almost vertical position of the exopod of the antenna of *A. curvirostris* – a position never achieved in *Ophryoxus* – is due in large measure to flexure of the protopod.

The slenderness of the antennae and their long rami (figures 19 and 20, A2) are related to swimming abilities, as is the nature of the setae which arise distally on the two proximal endopod segments. While they help a crawling animal to balance, the latter are not particularly specialized for this function and are more similar to their homologues in the swimming Daphniidae than to their counterparts in *Acantholeberis* and several other macrothricids.



FIGURES 26–28. *Ophryoxus gracilis.*

FIGURE 26. Labrum and pre-labral spines as seen somewhat obliquely to reveal how the latter lie side by side.
FIGURE 27. Transverse section of the ventral part of the head to show the pre-labral spines.
FIGURE 28. Armature of the inner distal lobe of trunk limb 1.

Particularly striking when compared with that of *Acantholeberis* is the straightness of the antennal protopod (cf. figures 1 and 19). This reflects different habits: swimming in *Ophryoxus*, association with the bottom in *Acantholeberis*. The straight protopod of *Ophryoxus* and the extension of the rami in essentially the same plane ensure that the antennae swing from such a position that they propel the animal forward in the horizontal plane. The vertical component of the propulsive force, so great in *Acantholeberis*, while here small is nevertheless sufficient to enable the animal to maintain 'altitude'.

An antennule is shown in figure 24. The array of setae on the posterior-inner portion represent a specialization superimposed on an otherwise primitive structure.

Anterior to the labrum are two projections – here called pre-labral spines – that lie side by side (figures 26, PLS and 27). Their function is unknown but probably protective. The labrum lacks a keel.

The trunk limbs, illustrated by Lilljeborg (1900) and Sergeev (1970*a*, *b*), are similar in basic features to those of *Acantholeberis* and make up a similar filter chamber (Sergeev 1970*a*, *b*). An outstanding difference is in the armature of the inner distal lobe of trunk limb 1 (figure 28), here modified not for dragging in food as in *Acantholeberis* but for gripping the substratum.

(iii) *The alimentary canal and defecation*

The alimentary canal of *Ophryoxus* is specialized in several ways; it is convoluted, has anterior caeca (being in this respect unique in the Macrothricidae) and a modified rectal region associated with a specialized mechanism of defecation. That a non-coiled gut is probably primitive will be discussed elsewhere. The development of anterior caeca in a single genus within a family has a parallel in the chydorid *Eurycercus*. This feature is general in the Daphniidae.

In the rectal region of the gut there is a part muscular- part glandular-walled swelling located near the proximal part of the post-abdomen. This receives the ribbon of faeces passing backwards along the canal. The ribbon has a smaller diameter than that of the swelling. The first portion to enter the empty swelling after an act of defecation passes to its posterior end, beyond which it cannot go. Subsequent passage of material into the swelling forces the ribbon to bend and finally collapse in a convoluted pile such as is formed when toothpaste is squeezed into a heap from a tube. Material is forced into the swelling until it is full, and defecation follows. The post-abdomen is swung backwards, but only a little, so that the anus, here located on its morphologically dorsal margin, discharges the faecal ribbon into the exhalent current which carries it backward through the posterior aperture of the carapace chamber. Because the rectum holds a considerable mass of material the faecal ribbon is long. In *Acantholeberis* the anus is located distally, the post-abdomen is protruded so that the anus discharges outside the carapace chamber, and no faecal material passes through the posterior aperture of the carapace chamber.

Defecation is followed by vigorous anal drinking (cf. *Acantholeberis* in Fryer 1970), 30 or more gulps following each other in rapid succession, especially in the case of the first 20 or so. During a limited number of observations adults defecated at approximately 3–5 min intervals, juveniles more frequently, the rectum being apparently filled in about 1 min in one case.

(iv) *Feeding*

The feeding mechanism of *O. gracilis* has been described by Eriksson (1934) and Sergeev (1970*a*, *b*). Both emphasize that two methods are involved. Eriksson describes *Ophryoxus* as being 'gleichzeitig ein Partikelfänger und ein Schlammfresser', and Sergeev describes feeding under two heads – active scraping and filtering. Although Eriksson describes pure filtration (and rejection) of unicellular algae by animals supplied with these in a dense suspension, and although, like such chydorids as *Eurycercus* (Fryer 1963) and *Peracantha* (Fryer 1968), *Ophryoxus* can undoubtedly extract particles from suspension, only under exceptional circumstances can the use of this machinery alone contribute significantly to the total amount of food collected. The filtering apparatus, however, comprises an integral part of the food-collecting machinery and to describe two separate means of collection obscures this important point.

In nature the bulk of the food is undoubtedly scraped from some substratum, as is made clear both by the habits of the animal (§ (i)) and by the nature of the gut contents. The first trunk limbs are used for gripping material over which the animal crawls. Both Eriksson and Sergeev refer to the dual function of the distal armature of these limbs – attachment, and the drawing of material towards the ventral aperture of the carapace chamber. While, as will be

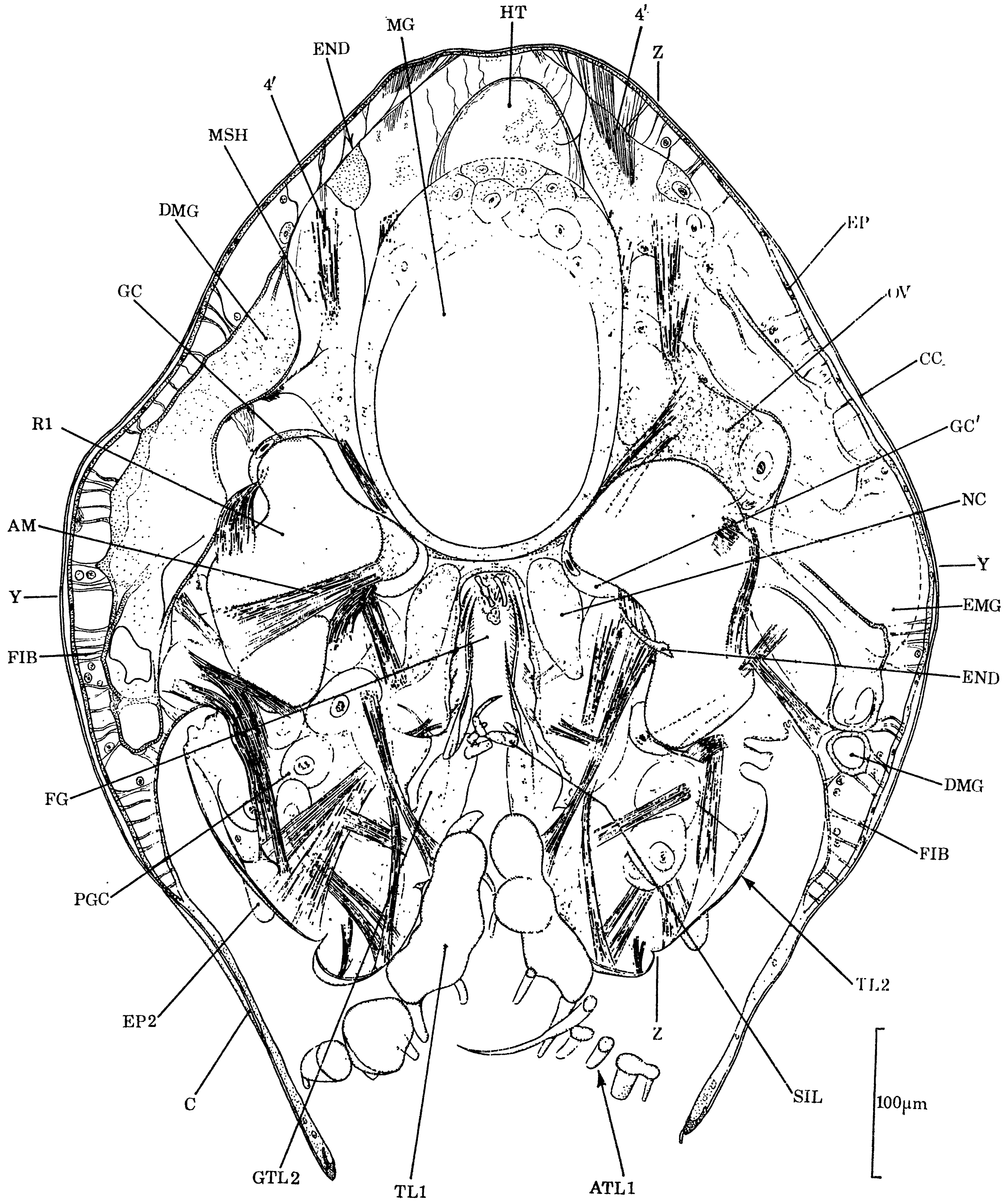


FIGURE 29. *Ophryoxus gracilis*. Transverse section through the second trunk limbs as seen from in front. The section is very slightly more anterior on the left (r.h.s. of the animal). It also cuts through the setae of the inner lobe of trunk limb 1 (SIL) and through the extremities of some of the distal endites of trunk limb 1, no internal details of which are given. There are in fact no muscles in this portion of the limb.

Note especially the enormous secretion-filled reservoirs (R1) and the gland cells (GC) associated with them, which, is inferred, are the source of the secretion. In one of these cells (GC′) a secretion reservoir is evident. Note also the extensive nature of the tubule of the maxillary gland, the extreme posterior margin of whose end sac (EMG) is shown on the right and whose full extent (as ascertained from the next section anteriorly) is indicated by a dashed line.

The extreme complexity of the muscular system of the second trunk limbs is clearly revealed by those muscles represented in this section. The remotor roller muscles (4′) of the mandible run obliquely forward from the portion shown, through the somite of trunk limb 1, and insert on the posterior margin of the mandibles. Only part of the carapace adductor muscle (AM) is shown on the left. Very slightly more anterior it is more massive and inserts particularly on the cuticle of the inner face of the carapace adjacent to the maxillary gland, which, as in this section, is slung by numerous fibrils from the carapace. Note also the extensive use of endoskeleton (END), e.g. dorsally and near the limb base on the right, and of suspensory fibrils (FIB), the presence of enormous glandular cells within the cavity of the limb (PGC), the great depth of the food groove (FG) which sinks beneath the ventral nerve cords (NC), and the extreme anterior extremity of the ovary (OV) which is sectioned on the right and skimmed on the left.

For ease of comparison the approximate plane of figure 30 is indicated by YY and of figure 31 by ZZ.

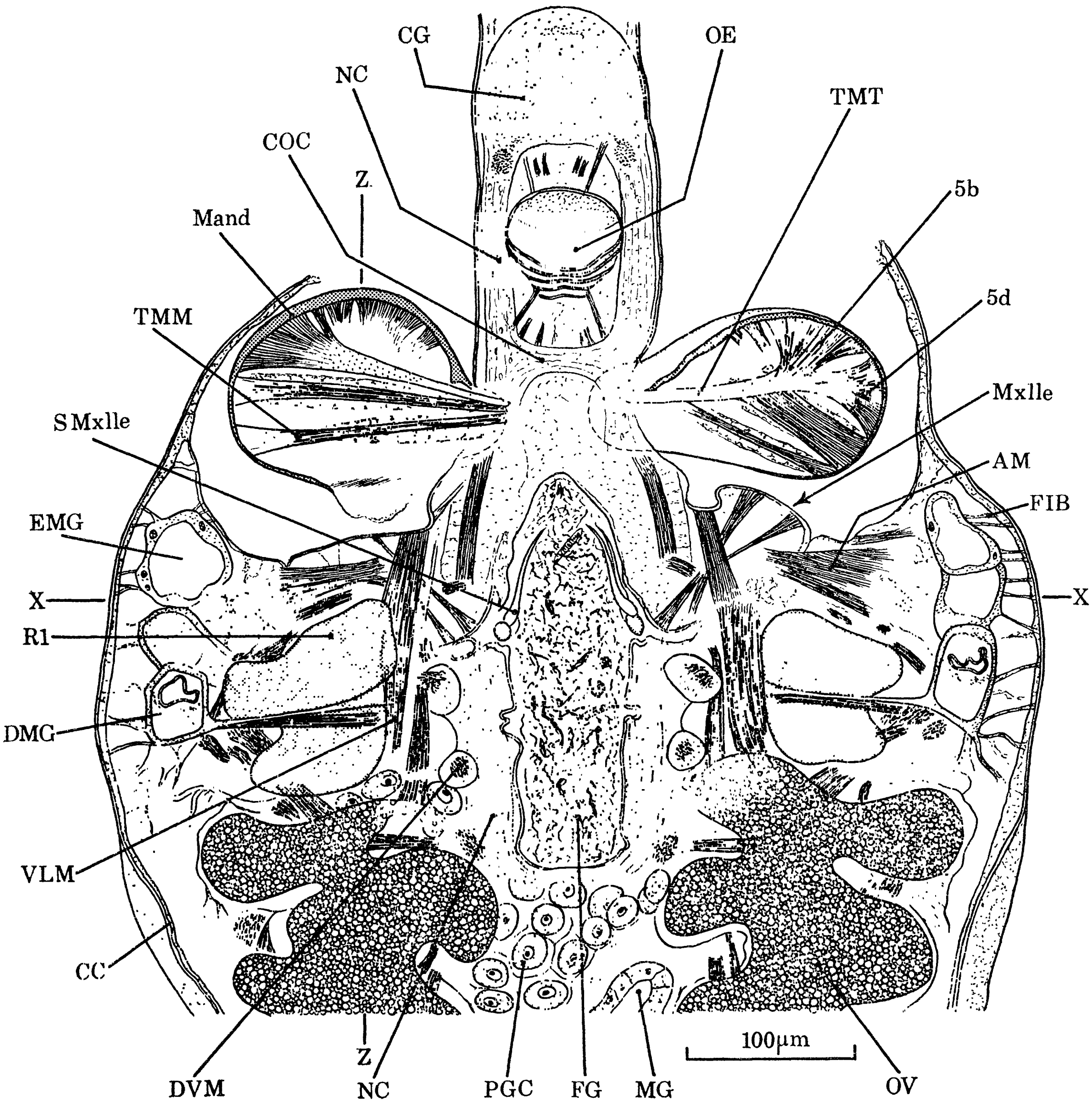


Figure 30. Horizontal section of *Ophryoxus gracilis* cut a little dorsal to the masticatory region of the mandibles and viewed dorsally. This shows specifically the secretion filled reservoirs (R1) which open on the first trunk limbs, but also reveals many basic features of the anatomy of a primitive macrothricid. Note especially the depth of the food groove (FG) which actually sinks between the ventral nerve cords (NC), of which a transverse commissure is seen, the location and extent of the maxillary glands, whose end sac (EMG) and part of whose duct (DMG) can be seen, the extent of the ovaries (OV) of which only the yolk-filled portion is seen here, the narrowness of the ventral part of the head (cf. *Acantholeberis*), the massive nature of the mandibles (Mand) and the asymmetrical nature of their transverse musculature. At this level the full complexity of neither the trunk musculature nor the extrinsic limb musculature is apparent but some muscles can be seen.

The section cuts across the upper limits of the posterior portion of the secretion-filled reservoirs slightly more dorsally on the left than on the right. The anterior portion rises and extends inwards and forwards, continuing dorsally as a narrowing, finger-like projection of its inner anterior corner, which terminates at the level of the alimentary canal, alongside which it lies (see also figure 31). Ventrally each extends some way as a voluminous sac which narrows to give rise to an anterior tube which extends into the first trunk limb.

What is almost certainly the duct of the left maxillary gland is seen just behind and lateral to the spines of the maxillule, but is unlabelled. The delicate carapace has become distorted posteriorly so that the epicuticle is here seen in face view.

For ease of comparison the approximate plane of figure 29 is indicated by XX and of figure 31 by ZZ.

discussed elsewhere, a primitive function of the first trunk limbs was almost certainly food collection, the association of *Ophryoxus* with a substratum is now sufficiently intimate inevitably to reduce this role, and the predominant function is that of attachment in both stationary and crawling animals. When an individual is settled on an unstable substratum, grasping by means of the first trunk limbs may still pull food material towards the carapace chamber, but reaching out specifically for this purpose, so characteristic of *Acantholeberis*, is not practised. This difference is directly related to the degree of association with substrata in the two animals, both of which are accurately described as benthic. Although the more able and more specialized swimmer, *Ophryoxus* has also developed the more intimate association with the substratum.

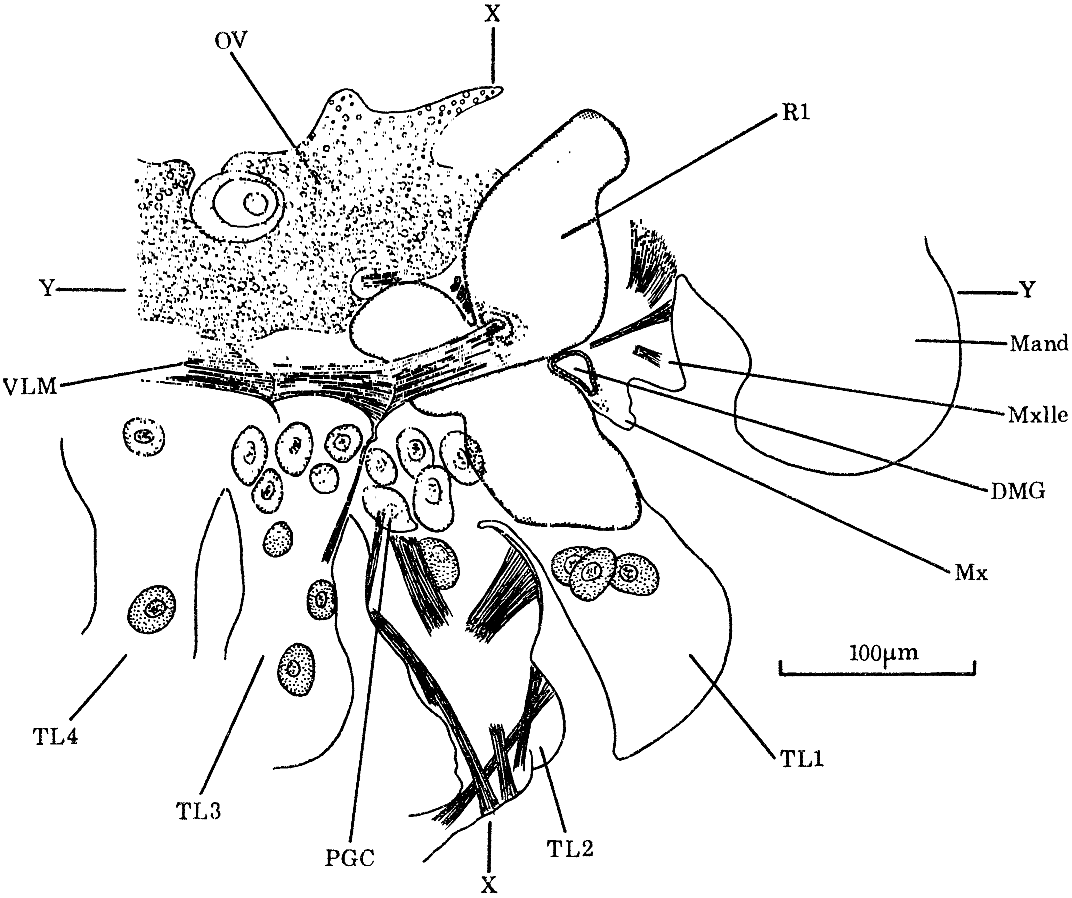


FIGURE 31. *Ophryoxus gracilis*. Longitudinal section, left of the mid-line and seen from inside, through the anterior trunk limbs to show the extent of the secretion-filled reservoir (R1). Such muscles as are visible in trunk limb 2 at this level are shown but otherwise most are omitted. The distribution of parenchymatous gland cells (PGC) within the limbs is, however, shown. The ovary (OV) here contains mostly yolk but a single egg cell is present. Note also the duct of the maxillary gland (DMG), seen here just as it bends ventrally to pass into the minute maxilla (Mx) which is often very difficult to detect in anomopods. The duct passes directly away from the observer and into the plane of the paper before turning dorsally. For ease of comparison the approximate plane of figure 29 is indicated by XX and of figure 30 by YY.

Whether they receive material brought towards them by the first trunk limbs or, more usually, collect it directly by their distal scrapers, the second trunk limbs transfer food to the filter chamber with the assistance of the endite armature of the third and fourth pairs. These and subsequent events are described (sometimes in ways which are not easy to follow) by Eriksson and Sergeev. In general, the mechanism is remarkably similar to that described in detail for *Eurycercus* (Fryer 1963). Indeed these two animals are more similar in this respect than is *Eurycercus* to several other chydorids, or *Ophryoxus* to certain macrothricids described in this paper. The similarity is basically phyletic, but convergence is also involved.

A matter not mentioned by either Eriksson or Sergeev is the use of entangling secretions. Although the involvement of labral gland secretions is not proven, typical labral gland cells are present, and in some preparations accumulations of secretory material can be found in them. More striking are enormous secretion-filled reservoirs in the vicinity of the first trunk limbs such as occur in some, but by no means all, chydorids (Fryer 1962, 1963, 1968). These are here reported for the first time for the Macrothricidae. The reservoirs (R1) are extremely irregular in shape, but their form and location can be appreciated from figures 29–31, which also illustrate several important features of macrothricid anatomy. They extend backwards into the basal region of the second trunk limbs, anteriorly almost to the level of the mandibles, and dorsally to the vicinity of the ventral wall of the alimentary canal. Each opens on the anterior face of the respective first trunk limb, proximal to the 'elbow' and not far from the labrum, much as do their homologues in such a chydorid as *Alonopsis* (Fryer 1968, figures 6 and 14) but, although many animals have been sectioned, in no case has discharge from the aperture been observed in the way it frequently has in certain chydorids. In only two preparations has discharged secretory material been seen. In one case this almost certainly, in the other it probably, came from this source, and not from the labrum. In this species fixation evidently causes closure of the aperture rather than exudation of secretory material. Optically and in its reaction to Mallory's stain the secretion is the same as that in the homologous reservoirs of *Alonopsis*.

(v) *Discussion*

While there is little in Sergeev's morphological account with which I would disagree, I would place an entirely different emphasis on the evolutionary significance of his, and my own, findings. Sergeev's conception of the evolution of *Ophryoxus*, and therefore the Anomopoda, is based on a derivation from a ctenopod ancestor. Implicit in this is a belief that benthic habits are secondary, and he is indeed explicit on this point when, in discussing the trunk limbs, he says: 'The evolution of a bottom-dwelling way of life and of active feeding resulted in the changes in the structure of the trunk limbs. The limbs of the second pair demonstrate an example of extensive change.' In his reference to 'active feeding' Sergeev contrasts the mechanism used by *Ophryoxus* with the pure filtration employed by ctenopods. I do not believe that bottom dwelling is a derived habit in anomopods. On the contrary there is abundant evidence, both morphological and ecological, to show that such habits are primitive. Likewise, as I hope to show elsewhere, I do not believe that the second trunk limbs 'demonstrate an example of extensive change'. On the contrary, comparative studies indicate that, in its basic features, this limb is an example of extreme conservatism which reflects persistent habits. These habits appear to have played a major role in the adaptive radiation of the Anomopoda.

Again, in describing certain setae of trunk limb 1 Sergeev refers to them as having 'lost the appearance typical for filter appendages'. Comparative studies indicate that no setae on this appendage could ever have been filtratory. Sergeev also accepts Eriksson's belief that the inter-limb spaces between the first three pairs of limbs have lost their role of 'suction chambers', again implying a function that, in the sense implied, I believe never existed.

While possessing certain specializations for a benthic way of life *Ophryoxus* nevertheless exhibits both habits and morphological features that indicate how the trend that led to the evolution of the swimming, filter-feeding Daphniidae could have been initiated. The significance of this, which will be mentioned elsewhere, is completely obscured by the hitherto generally accepted view that anomopods are derived from ctenopods. Eriksson (1934), however, recognized the impossibility of this. On this point I am in complete agreement but differ from him in my conception of the origin of the Anomopoda.

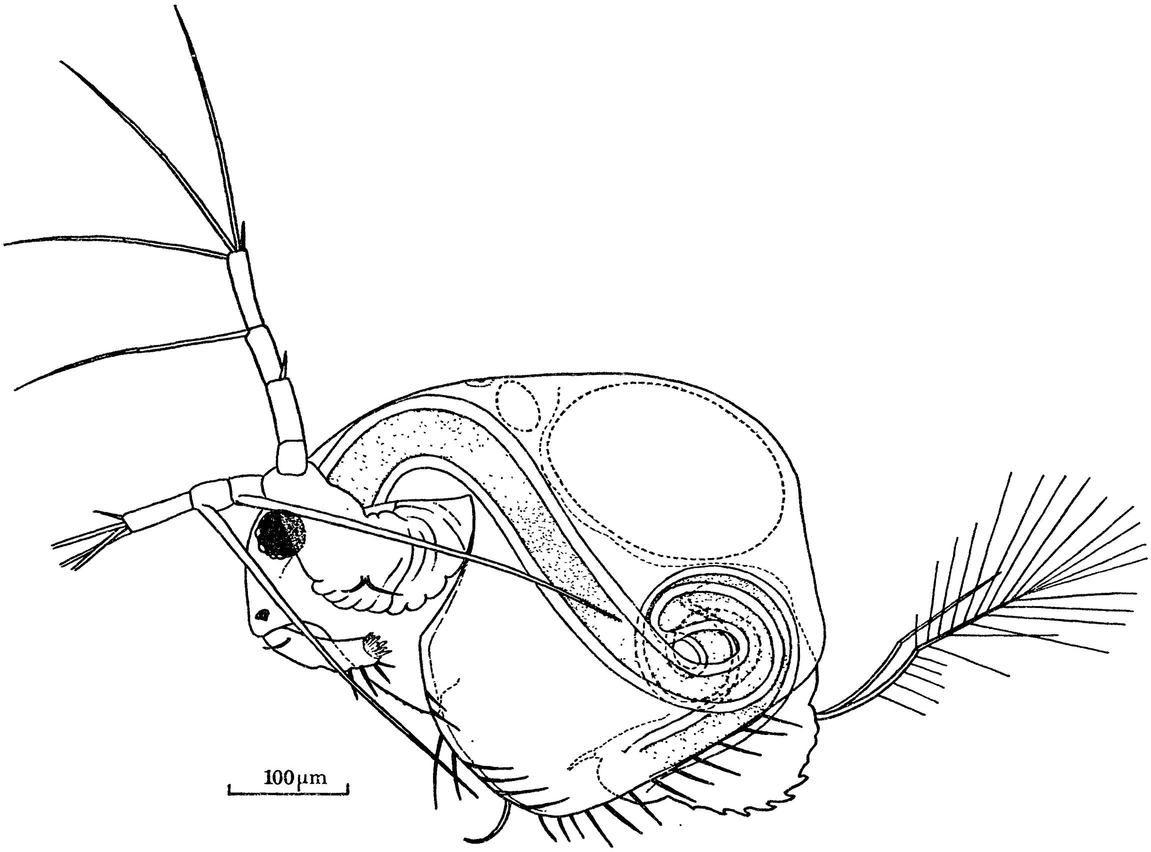
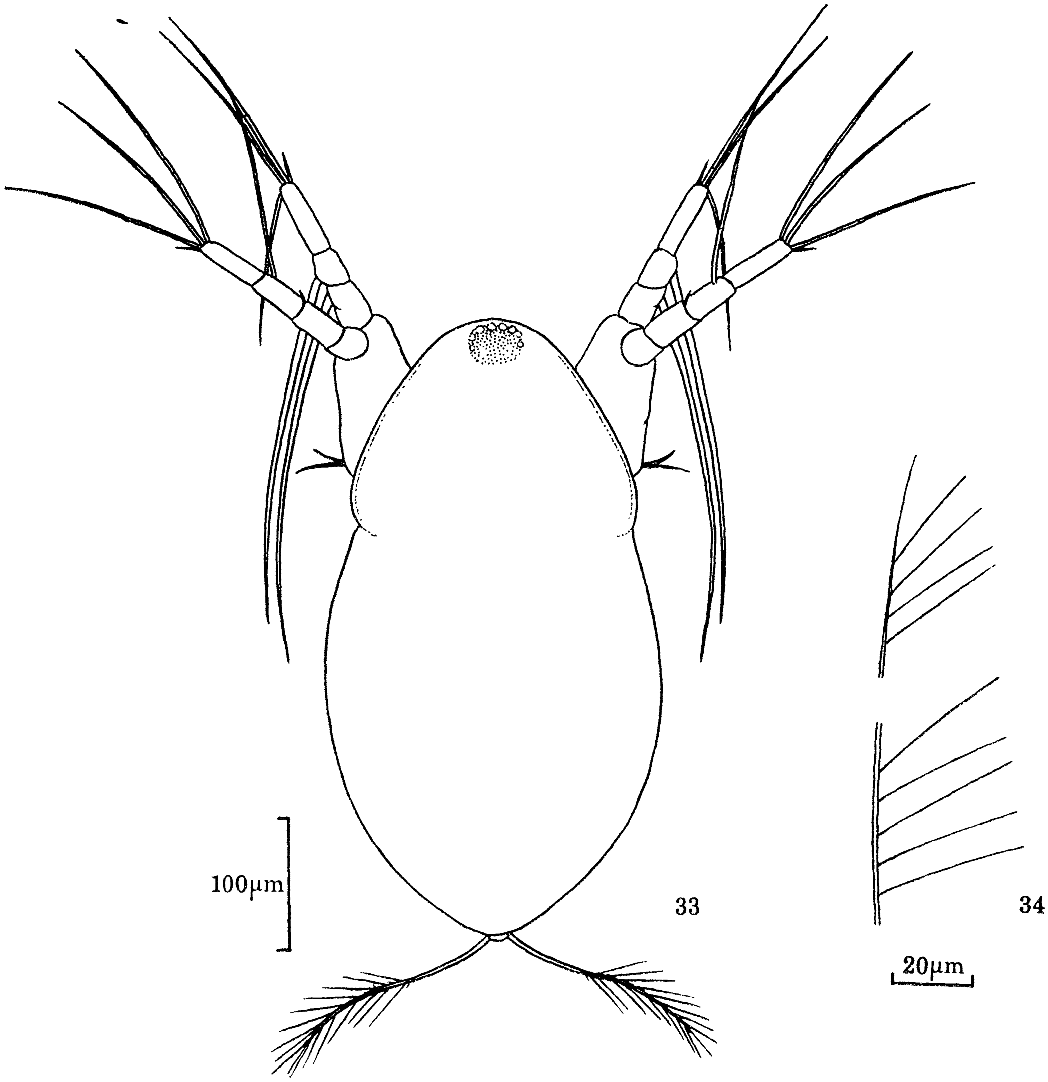


FIGURE 32. *Streblocerus serricaudatus*. Adult female, lateral. Note the long spine of the outer lobe of trunk limb 1 protruding ventrally.

(vi) *Conclusions*

Ophryoxus swims steadily, but weakly, when necessary, and spends much time on the bottom to which it attaches itself and over which it crawls in a rudimentary manner by means of the first trunk limbs, assisted by the antennae. While in several respects anatomically generalized, its specializations include massive secretion-filled reservoirs in the first trunk limbs, mid-gut caeca, and a rectal diverticulum.

Although itself specialized for association with substrata *Ophryoxus* exhibits both habits and morphological attributes that indicate how the trend that led to the emancipation of the Daphniidae from such habits could have been initiated.



FIGURES 33 AND 34. *Streblocerus serricaudatus.*

FIGURE 33. Adult female, dorsal.

FIGURE 34. Details of the ventralmost of the distal endopod setae of the antenna.

V. THE STRUCTURE, HABITS AND FEEDING MECHANISM OF *STREBLOCERUS SERRICAUDATUS* (FISCHER)

(i) *Ecology and habits*

Streblocerus serricaudatus (figures 32, 33 and 35), adult females of which never exceed about 0.6 mm in length and are usually considerably smaller than this, is the smallest British macrothricid and one of the smallest members of the family. The non-European *S. pygmaeus* G. O. Sars is even smaller, which suggests that small size is one of the specializations of the genus. While rather rare in Britain *S. serricaudatus* is widely distributed, especially in northern and western areas. In the English Lake District it is sometimes plentiful in small, particularly boggy, pools, and small tarns of rather diverse character but on whose bottom there is an accumulation of flocculent organic matter and where somewhat acidic conditions usually prevail. I have found it also in boggy pools in North Western Scotland and in Ireland.

Although not hitherto recognized as such, *Streblocerus* is a true burrower. Only when this is realized can the significance of some of its outstanding attributes be fully appreciated. Although it swims when necessary – though slowly and jerkily – by preference it moves but little and remains hidden among detritus. Into flocculent deposits it penetrates quickly and with ease when these are provided. A large number of individuals introduced to a small cell on the bottom of which is a 1 or 2 mm layer of suitable detritus rich in organic matter burrow into it and completely disappear from view within about a minute provided the cell is not brightly illuminated from below (cf. *Drepanothrix*, p. 183). Burrowing is effected solely by means of the antennae. In contrast to most chydorids, *Streblocerus* makes no use of the first trunk limbs for locomotion (§(iii)). Movements of ensconced animals are infrequent, are often effected by single, seldom more than a few, strokes of the antennae and are followed by relatively long intervals at rest.

As in the case of most macrothricids the food consists to a large extent of the flocculent organic material among which *Streblocerus* lives. While unsuitable material can certainly be rejected, true selection is unproven, but in some cases considerable numbers of diatoms – some considerably larger than the diameter of the mid-gut – and other algae have been seen in the alimentary canal. Protrusion of the post-abdomen is not involved when defecation takes place.

(ii) *Gross morphology*

Seen dorsally the animal has a strikingly nauplius-like appearance (figure 33). The width is variable (cf. figures 33 and 35 which are drawn from different individuals), rotundity being correlated in part with distension of the brood chamber in older females.

Incipient development of a head shield is shown very clearly. Anteriorly the head is encased in a complete cylinder of cuticle to which the antennules remain attached at ecdysis and with which the cuticle of the labrum is continuous ventrally. More posteriorly there is a lateral extension of the cuticle which, becoming apparent at about the level of the eye, is distinctly developed towards the region where it meets the carapace (figures 32 and 33).

The dorsal and lateral contours of the carapace are rounded. There is no flat ventral region (figure 32) – a reflexion of the lack of association with the surface of substrates – and the whole animal tends to be somewhat wedge-shaped. The ventral aperture is shown in figure 35. Each rim has a simple flange and is armed with spiniform setae whose arrangement, while similar to that of *Acantholeberis* (figure 5), is much simpler, for functional reasons. The flange continues along the anterior margin, narrowing dorsally (figure 32). Each valve is strengthened by light cuticular thickening based on a hexagonal pattern.

The anterior aperture of the carapace chamber is largely closed by the wide labrum which lacks a keel (figure 35, L). Such closure is necessary in a form with burrowing habits and contrasts markedly with the situation in the non-burrowing *Acantholeberis* in which a wide gap exists at each side of the narrow labrum (figure 5).

The post-abdomen (figures 32, 35, PA) has widely divergent setae (PAS) which are highly specialized and provided with extremely long setules (figure 32).

The alimentary canal is coiled posteriorly in a complex manner (figure 32) that enables it to be almost twice as long as would be the case were it straight. This specialization is seen particularly in benthic anomopods – all chydorids and some macrothricids – but not in the truly open water daphnids and bosminids where the extra weight involved may be a disadvantage. This may be an asset in benthic species. It also permits the storage of larger quantities of food than does a shorter gut, which may facilitate survival should food ever be scarce and may improve the efficiency of digestion.

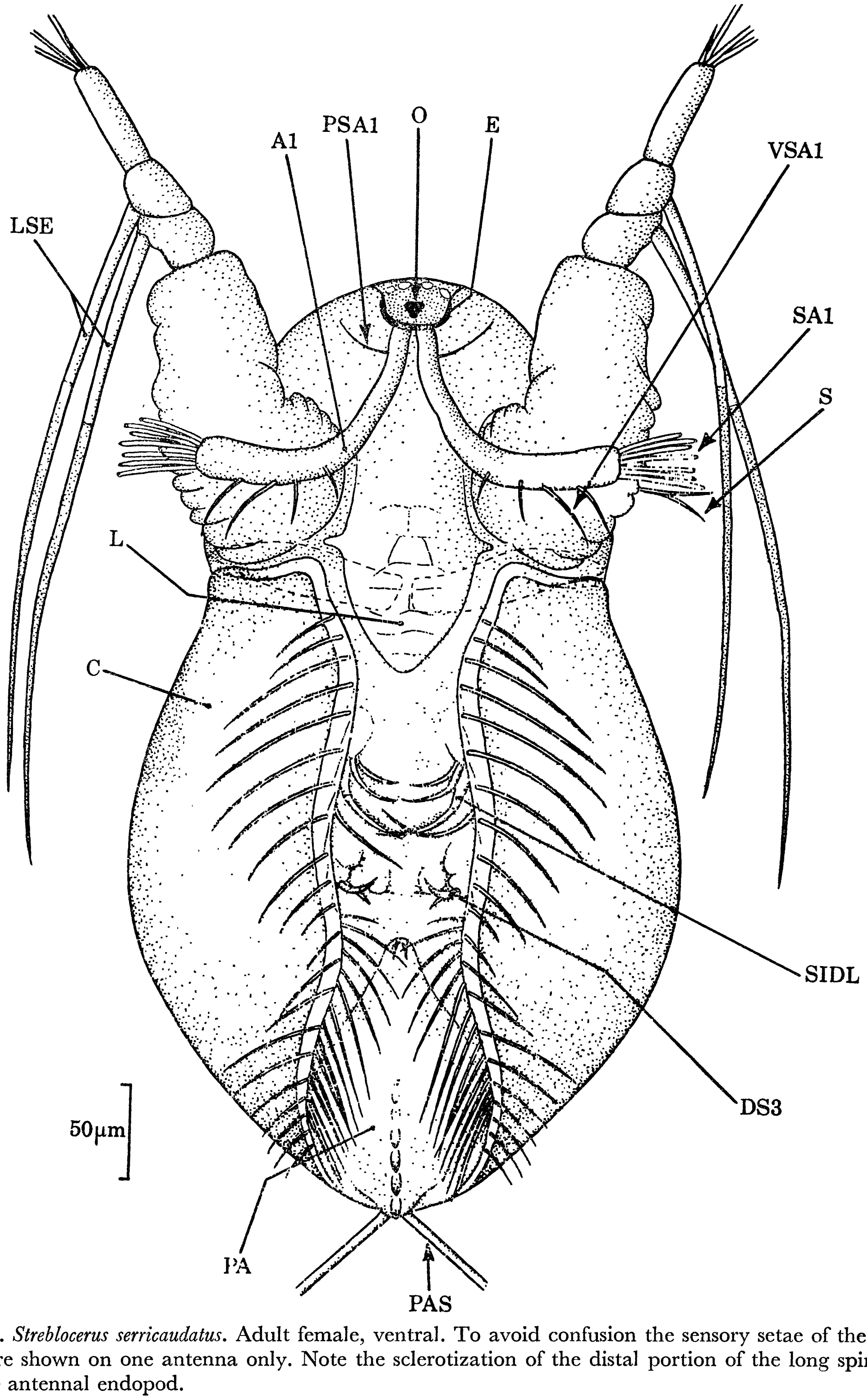


Figure 35. *Streblocerus serricaudatus*. Adult female, ventral. To avoid confusion the sensory setae of the antennae (S) are shown on one antenna only. Note the sclerotization of the distal portion of the long spines (LSE) of the antennal endopod.

(iii) *Locomotion*

The antennal movements responsible for penetration into deposits are essentially those used for swimming. In effect *Streblocerus* 'swims' into and through deposits, though individual antennal movements of burrowed animals may be modified according to immediate needs. The antennae are specialized by the modification of the distal seta of each of the two proximal endopod segments into a stout levering spiniform structure (see especially figure 35, LSE). Although the position of a former joint is still detectable the two portions are ankylosed. Distal to the joint region the entire structure is heavily sclerotized. In *Acantholeberis*, while both setae are represented, only the proximal is highly modified for propping and levering (figure 1) and is much longer and stouter than its more distal homologue. Here both are equally developed. Modification of these setae in relation to burrowing habits, while superficially small, is of profound significance in the life of *Streblocerus*. On the endopod they are aided by a stout terminal spine and to some extent by the stout basal portion of one of the three terminal natatory setae. The seta of segment 3 of the exopod also has a stout proximal portion, and this and stout spines borne distally by segments 2 and 4 also assist movement among detritus.

The distal section of each so-called natatory seta is extremely slender and flexible and armed ventrally with a row of long, widely spaced and exceedingly slender setules (figure 34). Of the three terminal setae of the exopod, the two ventralmost are armed only with such setae, and the same is true of their homologues on the endopod save that a few slender, shorter, more closely set setules occur dorsally on the median seta. All the other setae of both rami are similarly armed ventrally but have in addition shorter, fine and more close-set setules towards the proximal end of the distal portion, and rather coarser setules on the proximal portion. Such an arrangement is not typical of true natatory setae and, while these setae assist the animal to swim, they are so slender and flexible and bend so easily through a wide angle when they encounter obstacles during burrowing that a sensory function also seems possible. Certainly their extreme flexibility is an adaptation to burrowing. Stiff natatory setae would be a liability.

An important adaptation to burrowing is the slow speed at which the antennae operate. The heaviest loads can be borne at the slowest speeds of muscular contraction. Slow speeds also mean that the antennal muscles can operate at higher mechanical efficiencies and more easily develop maximum power (which in a muscle is achieved when contraction is at about 0.3 times the maximum speed) than when used for swimming, which demands repeated, relatively rapid beats. Further, as the antennae are not required to beat many times in succession they can presumably make a supreme effort should this be required without paying the same penalty for the pause for recovery – sinking – as would a swimming form.

Notwithstanding its serrated nature (from which the specific epithet is derived), and the fact that it can swing through a small arc, the post-abdomen is not used for pushing as the animal burrows. The serrations, which are somewhat sclerotized and may be defensive, are located proximally – much the least effective position if the post-abdomen were to be used as a lever – and such feeble swings as have been seen were used only to clear detritus from the posterior-ventral region of the carapace.

As *Streblocerus* moves among deposits its body may be orientated in any possible position and food is collected as readily when the animal is lying inverted, or at some oblique angle, as when it is dorsal surface uppermost. Although not immediately evident as it plunges through detritus, the ventral surface is kept predominantly against suitable material, this giving the best purchase for the antennae. The antennules (figures 32 and 35, A2) sample the material immediately in front of the food-collecting apparatus. For this, in addition to the terminal sensillae (SA1) and the proximal sensory seta (PSA1), they are provided with four ventral setae (VSA1), presumably tactile, a specialization not seen in the Chydoridae where, in general, adaptations to bottom dwelling habits are greater than in the Macrothricidae. Such setae bear the same relation to the substrate as those of certain benthic cyclopoid copepods (Fryer 1957*b*) and presumably function in a similar manner.

(iv) *The nature and arrangement of the trunk limbs and the feeding mechanism*

A feature of the trunk limb complex of *Streblocerus* which has a profound influence on the feeding mechanism is the reduction of the exopods of trunk limbs 4 and 5, which form pumping paddles in *Acantholeberis* and several other macrothricids as well as in most chydorids. Because of this no current flows either through the carapace chamber or through what, in many species, is the filter chamber. Filter feeding is therefore impossible, and there is no respiratory current. Nevertheless the basic plan of the trunk limbs common to the Macrothricidae and Chydoridae is clearly recognizable, and some of the movements of the limbs are of the same kind as those used by species in which the feeding mechanism includes a filtering component.

The first trunk limbs follow the basic plan but are highly specialized distally. Here there is an array of long, curved spines, one on the outer, 3 on the inner (SIDL), distal lobe (shown orientated as in life in figures 32 and 35) just as in *Eurycercus* (Fryer 1963, figure 23), *Alonopsis* (Fryer 1968, figure 7) and several other chydorids.† In life that of the outer lobe usually protrudes well outside the carapace chamber (figure 32). Furthermore, the two spines of endite 3 (figure 36, SE3) have the unique distinction of being modified as scrapers, which so resemble those borne on the second trunk limbs of many chydorids and macrothricids that, seen in isolation, they would be immediately identified as such. Their evolution is a remarkable example of convergence in limb armature in accordance with functional needs. Phyletically this would appear to be a natural development of the primitive function of the limb. Endite 2 also bears a large spine (SE2) which, while it barely qualifies as a scraper, has a row of minute denticles proximally. The scrapers are so orientated that their teeth are directed ventrally and are somewhat offset; perhaps as a load-spreading device. Adjacent to them are two very delicate thin-walled sensillae (figure 36, S3).

What is probably the homologue of the scraper-like inner spine of endite 2 of *Acantholeberis* is indicated (IS1). The homologue of the scraper of endite 1 is present in exactly the same position as in *Acantholeberis* (see figures 14 and 16) and is similar in general form but very delicate and so minute that if denticulation is present it cannot be detected by an oil-immersion lens.

Three setae, all similar to the two most distal setae of this endite of *Acantholeberis* (figure 14), are present on endite 1, but there is no screening seta.

The second trunk limbs follow the basic plan. Each bears eight scraper-like spines (5 being shown in figure 37) of which the six innermost are clearly modified for dragging material into

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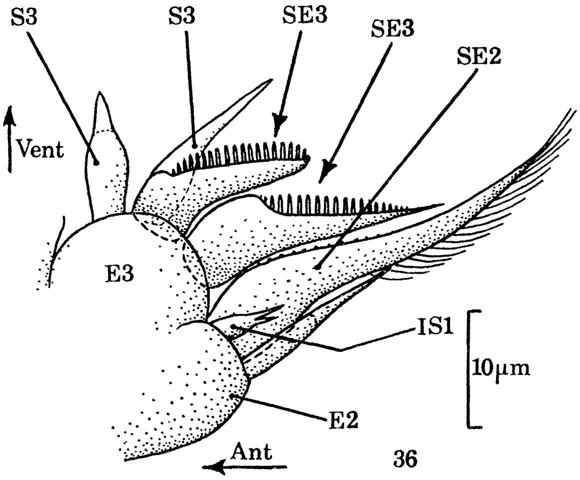
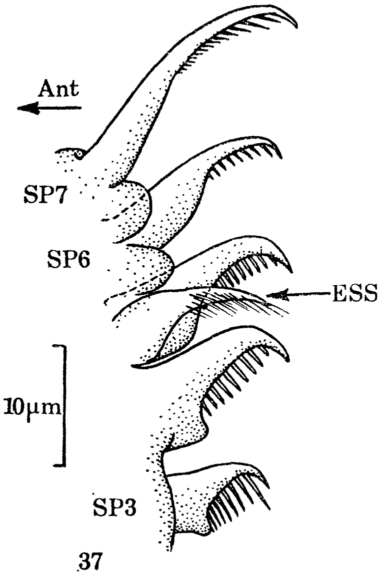
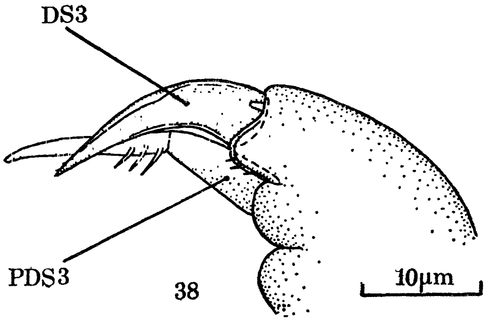
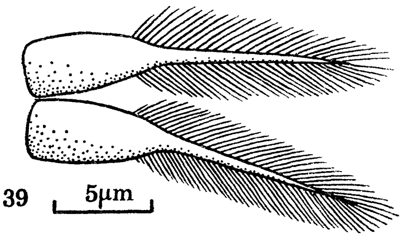
† *S. serricaudatus* may exhibit dimorphism here. In two individuals the spine of the outer lobe was armed with fewer, stouter denticles than is the case in most animals examined, and the inner lobe bore not 3, but 4 spines, the additional spine being short. One of these individuals at least had only three ventral setae on the antennule.

the inter-limb chamber which, following the usage applied to the chydorid *Leydigia* (Fryer 1968), is here called the sorting chamber. The two distalmost (numbers 7 and 8), and especially the most distal and lateral, are so orientated that their teeth encounter food masses as they swing medially and dorsally across the ventral aperture of the carapace chamber. Adjacent to, and to the outside of, scrapers 1 and 5 is a delicate sensory seta (figure 37, ESS).









FIGURES 36–39. *Streblocerus serricaudatus.*

FIGURE 36. The scrapers of the distal part of the corm of trunk limb 1.

FIGURE 37. Scrapers 3–7 of trunk limb 2, seen from the outside.

FIGURE 38. The distal armature of trunk limb 3 (cf. figure 35).

FIGURE 39. Two of the series of setae of trunk limb 3 which make up a fence homologous with the outer filter plate of filter feeding species.

The gnathobase bears five anteriorly directed spiniform setae which form a pushing complex as they do in *Acantholeberis* (figure 8) and in such chydorids as *Alonopsis*, *Graptoleberis* and *Leydigia* (Fryer 1968, figures 7, 82 and 146 respectively) in which, for various reasons, the gnathobasic plate is used solely for pushing and not for filtering. The anteriormost seta bears a row of exceedingly fine setules, the posteriormost a few long setules discernible only with difficulty by means of an oil-immersion lens, and the rest are apparently unarmed save for a bristle-like setule at the joint of numbers 3 and 4.

As in certain chydorids, a pair of distal spines on each of the third trunk limbs is modified for food collection. In *Streblocerus* these spines are the best developed armature of the limb. Of the two, the distalmost is a somewhat hook-like, sclerotized scraper (figure 38, DS3) which in life arches across the ventral aperture of the sorting chamber towards its homologue of the opposite limb (figure 35). Its companion (figure 38, PDS3) is less stout, less sclerotized and less scraper-like. The rest of the limb, while much reduced, still reveals remnants of structures present in macrothricids such as *Acantholeberis* (figure 8) and chydorids such as *Eurycercus* (Fryer 1963, figure 32) in which this limb is well developed. The corm bears a row of 7 setae arranged one above the other which clearly represents the outer filter plate of many chydorids and macrothricids whose feeding mechanism involves filtration. As filtration is not involved here, the structure of these setae (figure 39), their location and arrangement, all clearly reveal that the absence of a respiratory current is a derived condition. The corm also bears five setae of which the most proximal is sensilla-like, and of which the most distal certainly belongs to a different endite from the rest. The gnathobase bears six short pushing setae which bear the usual relation to the food groove. Setules have been detected only on the posteriormost. Three minute setae represent the heavy gnathobasic armature of more robust species. The exopod is reduced to a small flap.

The fourth trunk limbs exhibit marked reduction but the basic plan is still clear. Each corm carries four spines which stand one above the other and are directed medially, but these are all small. Proximal to these are two small setae on the gnathobase. The gnathobasic plate is reduced to four minute setae directed towards the food groove. The exopod – a large pumping plate in many species – is reduced to a small flap which, like the setae it bears, can nevertheless be homologized with that of its relatives.

The fifth trunk limbs are much reduced. The gnathobasic region is obsolete and, as in certain chydorids (Fryer 1968), the gnathobasic plate has been lost. Here the functional reasons are the same as those which prevail in *Graptoleberis* and not those which obtain in *Alonopsis* and others. The armature of the much-reduced corm consists of two vertical-standing setae of which the outer is the longer. Both are armed with setules, though these are less elaborate than in some filter feeding species. Although two setae are present in *Alonopsis* (Fryer 1968, figure 13) the reduction is more similar to that seen in *Graptoleberis* (Fryer 1968, figure 82) where only a single seta remains. The lack of any current-producing device is reflected in the drastic reduction of the exopod.

As their structure clearly indicates, the first trunk limbs serve for food gathering. They have no role in locomotion. Like their homologues in *Acantholeberis* they are very mobile and very versatile, the outer distal lobe, and therefore its spine, having virtually universal mobility. The orientation and armature of the curved setae of the outer lobes are such that they can be extended beyond the limits of the carapace chamber and drag flocculent masses within it. The outreach of the outer seta (figure 32) is especially noteworthy. Its orientation is such that it can be hooked around a food mass which is then dragged inwards and forward by flexure of the corm and by indrawing of the basal part of the corm beneath the level of the trunk cuticle. The scrapers of the corm are so located as to facilitate further indragging at a deeper level. Their structure suggests that they may at times serve as true scrapers, and such a use has possibly been seen on one occasion when a filamentous structure was being handled, but persistent scraping has not been observed and must be seldom called for when the animal is living in soft flocculent deposits. Material collected often consists of large tangled masses which are pulled against the grid comprised of the setae of the carapace margins, the resistance provided by which allows manageable quantities to be torn free by the first trunk limbs.

Material brought within reach is dealt with by the second trunk limbs, whose movements are more vigorous and of greater amplitude than those of any other limb. Their movement involves a swing towards the mid-line and inward by the distal portion of the corm and a well-marked forward component by the gnathobasic region which swings the gnathobasic spines along the food groove. From the resting position scrapers 8, 7 and 6, and to some extent 5, swing inwards. Their deeper lying companions (figure 37) serve essentially to drag material towards the food groove. Their structure is well suited to deal with tangled flocculent masses.

Swings of the second seem always to be accompanied by movements of the third trunk limbs, of whose distal spines the stout, sclerotized, hook-like structure is specialized for pulling in the material collected (cf. the scraping function of its homologue in certain species). As their amplitude of movement is greater than that of the third pair, the second trunk limbs give the impression of sliding down the latter and inevitably carry towards the food groove material originally dragged by the distal spines of the third pair. The setae equivalent to those of the outer filter plate of trunk limb 3 make up a fence on each side which prevents food from escaping backwards, a role they can fulfil in the absence of a current. Any material passing through the gap between these two plates – and if there is any such it is certainly a very small proportion of the total collected – must inevitably be pushed towards the food groove by the fourth trunk limbs. These move in time with limbs 2 and 3 and have the basic chydorid–macrothricid action, but are here of scant importance in the manipulation of food. Thus, except ventrally, material is dragged towards the food groove almost entirely by the second trunk limbs and is subsequently rammed towards the mandibles by their gnathobasic spines. The maxillules presumably assist in the usual manner but this has not been observed.

The mandibles roll briskly – a rate of 177 rolls/min was maintained for well over a minute, 181/min for 50 s and *ca.* 200/min for 15 s. As in other anomopods muscular asymmetry swings the right mandible through a greater arc than the left. Furthermore the arc swung by the masticatory portion of the left mandible is in a somewhat different plane from that of the right and swings medially as well as forwards, thereby granting a degree of adduction. At rest the mandibles have in fact a relatively wide gape, yet meet towards the end of their swing. Such action, if not effective for crushing, must help to pass material forward to the atrium oris.

Labral gland secretions are almost certainly employed but have not been conclusively demonstrated. No other possible source has been revealed for secretions found adjacent to the labrum and passing up the oesophagus of sectioned animals. In an individual held in a compressorium, which had no access to particulate matter, a trace of what could scarcely have been other than such a secretion passed up the oesophagus with each of several waves of peristalsis. This material could be seen for some time at the anterior end of the mid-gut but gradually disappeared.

In the main body of the labrum is a conspicuous dorso-ventral muscle, much larger than the more distally located dorso-ventral muscles. On occasion this contracts rhythmically as the mandibles swing. This suggests that the topographically dorsal surface of the labrum, which is covered with soft, thin cuticle and bears spinules in places, at times makes regular movements to manipulate food and, by enlarging the cavity in which the mandibles lie, helps to suck food forward. While manipulative movements of the labrum are a regular feature of anomopod feeding mechanisms, rhythmic muscular contractions are unusual. They are, however, reported in the cephalocaridan *Hutchinsoniella* (Sanders 1963). These powerful muscular contractions are also perhaps concerned with the extrusion of labral gland secretions.

(v) *Conclusions*

Streblocerus serricaudatus is a true burrower into flocculent deposits where it leads an almost sedentary existence. Locomotion is by means of the antennae alone, which are specialized for levering rather than swimming. Food is collected by the first trunk limbs and passed mechanically into the sorting chamber by trunk limbs 1, 2 and 3. Trunk limb 1 is uniquely specialized in bearing two scraper-like spines on endite 3. Currents are not used and collected material is passed forward along the food groove by mechanical means.

VI. THE STRUCTURE, HABITS AND FEEDING MECHANISM OF *DREPANOTHRIX DENTATA* (EUREN)

(i) *Ecology and habits*

Drepanothrix dentata (length to *ca.* 0.8 mm: figures 40, 42 and 44), which occurs throughout the cool temperate zone of the holarctic region, is rather rare in Britain but widely distributed, especially in northern and western areas. In the English Lake District it is sometimes plentiful in similar situations to those frequented by *Streblocerus serricaudatus*, with which it sometimes coexists. I have also found these species together in Ireland. Its main requirement seems to be an accumulation of suitable flocculent organic detritus which may, however, cover a firm bottom. That such situations tend to be acidic is perhaps fortuitous, and Flössner (1972), who gives its pH range as 4.5–8.5, and reports its occurrence in waters whose calcium content ranges from 4.8 to 70 mg/l, refers to its independence of water chemistry.

Like *Streblocerus* it enters deposits essentially by 'swimming' into them and habitually does so at the first opportunity. Securely ensconced in detritus it moves only occasionally. Individuals have been seen to remain perfectly still for more than 6 min. When to a cell of area about 2.6 cm^2 and provided with a 3 mm deep layer of flocculent organic detritus 52 *Drepanothrix* were added, within a few minutes all disappeared from view. Although these animals were present at a density of 20 per square centimetre, the detritus appeared devoid of life when viewed from above, so effectively were they hidden and so infrequently did they move. This infrequent movement was confirmed by observations from below with an inverted microscope and indicated that they seldom penetrated to a depth of 3 mm (though a deliberate retreat from a glass surface may be involved), but certainly burrowed to 2 mm at times (at least 3 times their own height). From such detritus they are not easily driven by intense illumination from below even though, as befits a burrower, they are negatively phototactic.

The surface sediments frequented by *Drepanothrix* (and *Streblocerus*) are highly flocculent and therefore permit easier penetration than deeper, more compact, layers. Further, such material presents an enormous surface area for the development of bacteria which may be important in the diet of this and other anomopods. Recent work has also confirmed that, as one would expect, the chlorophyll content of lacustrine sediments is greatest, and the amount of lignin (indigestible) as a percentage of the total organic matter is least, near the surface (Hargrave 1970), which indicates that the richest feeding grounds for burrowers are near the sediment/water interface.

The food consists of the organic detritus among which the animal lives, and defies precise definition. Defecation takes place at frequent intervals in a feeding animal; for example, eight short faecal ribbons were exuded with intervals of 35, 25, 22, 25, 20, 30 and 45 s between discharges. Faecal ribbons are not pushed away by the post-abdomen, but may be moved posteriorly by movement of excess material being dragged into the carapace chamber and backward by the first trunk limbs. There is no danger of reingestion as there is no respiratory-feeding current (§ (iii)).

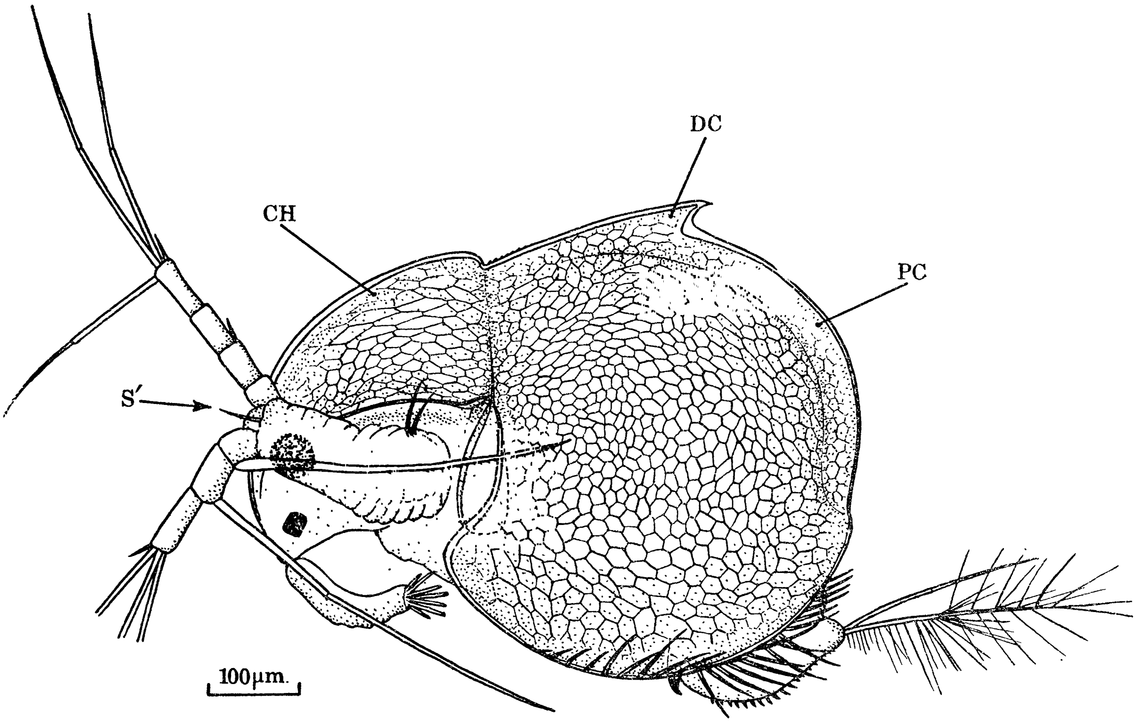
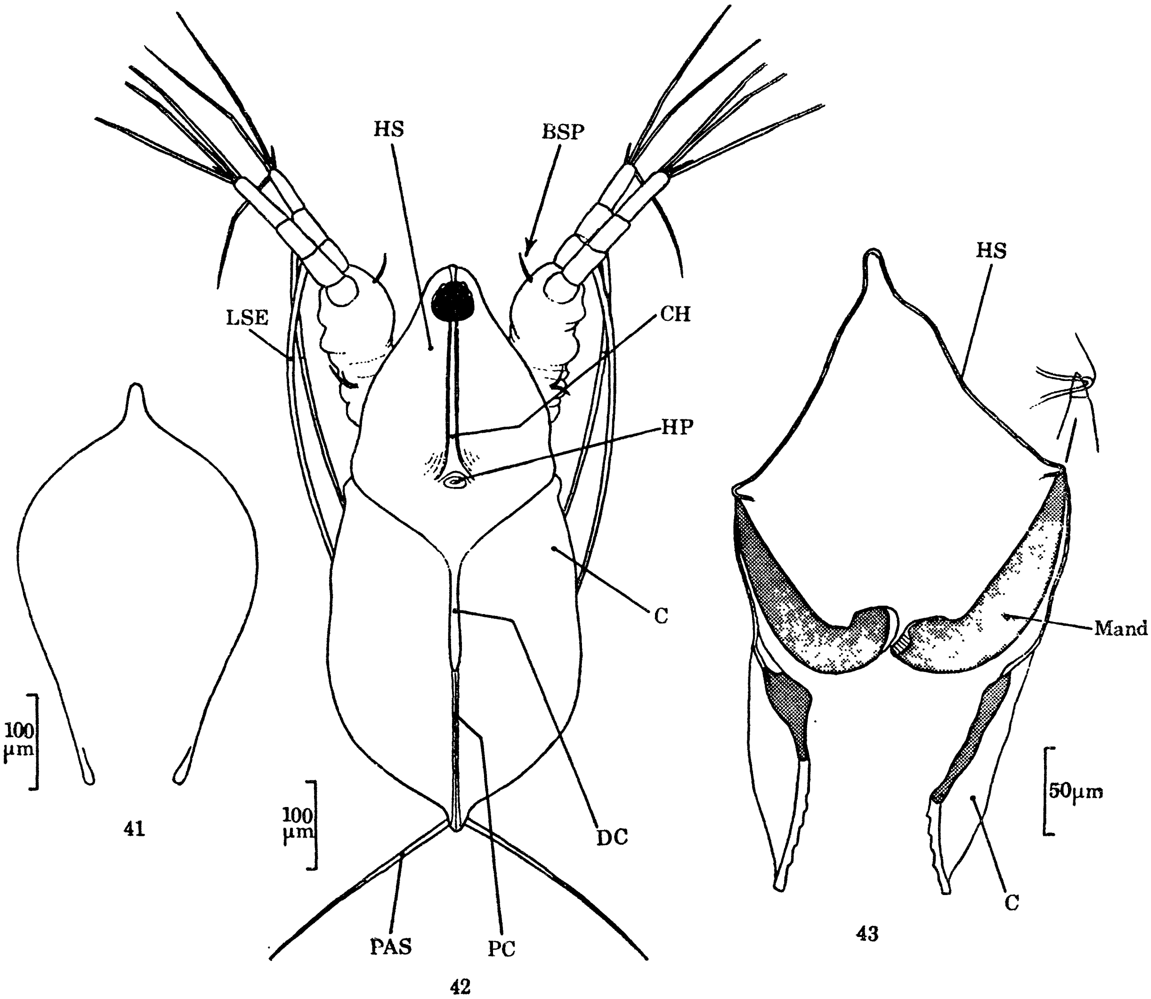


FIGURE 40. *Drepanothrix dentata*. Adult female, lateral.

(ii) *Some aspects of morphology with especial reference to burrowing*

Drepanothrix has many morphological adaptations to burrowing. The body is wedge-shaped in two planes (figures 40 and 42). The head is provided with a headshield (HS) – an advance on the condition in *Acantholeberis* – which, very narrow anteriorly, widens gradually, and has a dorsal protective crest (CH). Functionally continuous with this is the toothed crest of the carapace (DC) from which the specific name is derived, behind which a lower crest (PC) continues to the posterior limit of the carapace. These crests hold clumps of detritus clear of the headshield and carapace and, by reducing the area of contact, reduce frictional resistance to burrowing and, inevitably, reduce wear and tear, though the latter may be of no great importance. The stiff spines of the ventral carapace margins (figures 40 and 44) also deflect material and reduce frictional resistance laterally. In a swimming individual forward progression is accompanied by a lift of the head end. Whether this is always the case when the antennae are used for burrowing is difficult to ascertain, but even a small lift, which certainly occurs at times, is advantageous in that force is exerted through the dorsal crest of the head, and more delicate ventral structures are protected. As penetration proceeds the wedge is driven deeper, its maximum width being at the point where the carapace crest forms a ‘tooth’. Behind this it narrows (as it does also in width) and here resistance is negligible though a small crest still grants protection dorsally.

Posterior carapace setae, such as those of *Acantholeberis*, would be a disadvantage in a burrower and none are present in *Drepanothrix* (or *Streblocerus*), but very delicate elongate setules have been developed on the sensory setae of the post-abdomen (figure 40).



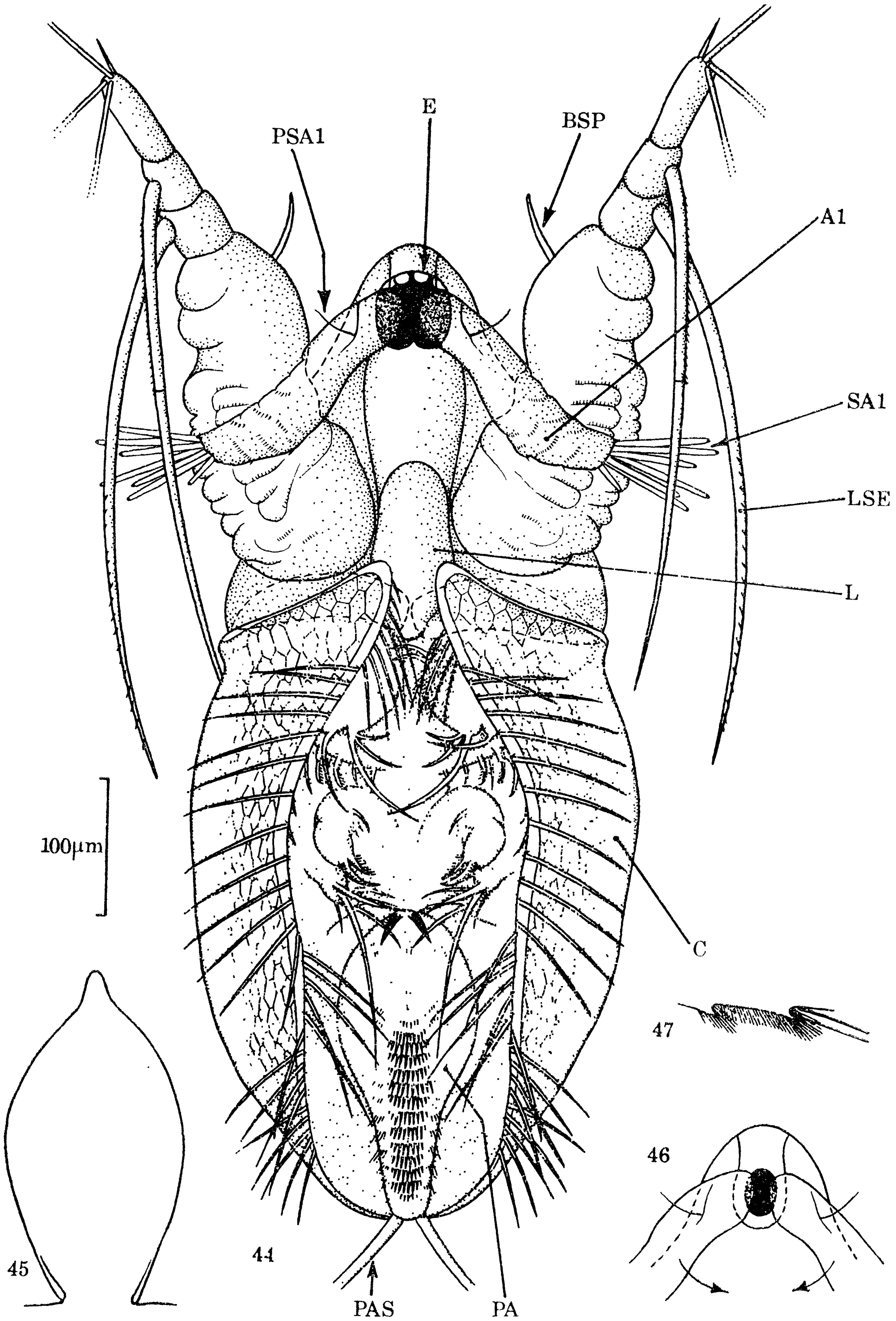
FIGURES 41–43. *Drepanothrix dentata.*

FIGURE 41. Outline transverse section posterior to the tooth of the dorsal crest of the carapace.

FIGURE 42. Adult female, dorsal. Note especially the location of the burrowing spines (BSP) on the protopod of the antennae.

FIGURE 43. Outline transverse section through the mandibular region. The inset shows the mandibular articulation as seen by deeper focusing.

The carapace is more strongly reticulated than in *Streblocerus* and the ventral gape a little wider but, as befits a burrower, narrows anteriorly, to embrace the narrow keel-less labrum (cf. the wide gaps at each side of the labrum of *Acantholeberis* and the plugging of the gap by a wide labrum in *Streblocerus*). The antero-ventral corners can be drawn closer together than they are in figure 44, and here the ventral aperture is guarded on each side by a row of inwardly directed setose setae.



FIGURES 44–47. *Drepanothrix dentata.*

FIGURE 44. Adult female, ventral. The lateral sensory setae of the antennae are, in this view, largely obscured by the terminal sensillae of the antennules and are omitted for clarity. Because of the darkly pigmented eye, the ocellus, which lies directly above it, cannot be seen clearly (see figure 46). The distal setae of the antennal endopod rise towards the observer. Some of the spines of the corm of trunk limb 1, which can be seen in this view, are omitted for clarity.

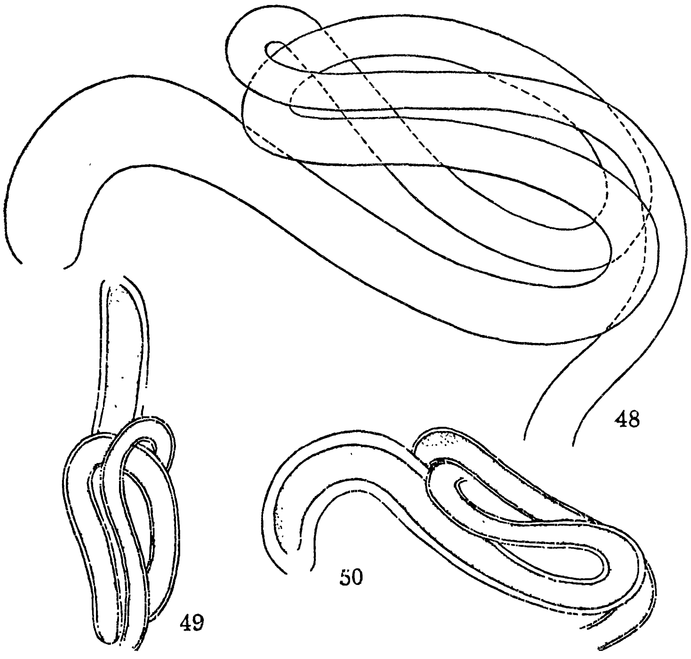
FIGURE 45. Outline transverse section in the vicinity of trunk limb 2.

FIGURE 46. Anterior extremity of head, focused at a more ventral level than in figure 44, to show the relation of the antennules to the head, and the location of the ocellus. Arrows indicate movements of which the antennules are capable.

FIGURE 47. A portion of the ventral carapace margin (lateral) near the anterior end of the row of spines.

The antennules can be swung towards each other during burrowing (figures 44 and 46) and tucked dorsally beneath the antennae. This and their curvature ensures that they do not interfere with movement through detritus. There are no ventral setae on the antennules such as occur in *Streblocerus.*

The antennae are provided on their endopods with levering spines (LSE) as in *Streblocerus.* They also have an additional specialization – a short stout spine on the protopod (figures 42 and 44, BSP) here called a burrowing spine. The structure (S′) visible in figure 40 is not this spine but a sensory seta. As the antennae swing backwards and outwards the burrowing spines sweep away the flocculent material in which the animal lives, thereby facilitating penetration. As in *Streblocerus,* slow antennal movements enable the muscles concerned to operate with great mechanical efficiency, develop their maximum power, and cope with heavier loads than can antennae used for swimming, which entails rapid movements. The antennal exopod lacks a seta on segment 3 such as is present in *Streblocerus* (cf. figures 32 and 40). The so-called natatory setae are provided with long, exceedingly slender, widely spaced setules similar to those of *Streblocerus* (figure 34).



FIGURES 48–50. *Drepanothrix dentata.*

FIGURE 48. Diagrammatic representation of the coiling of the alimentary canal.

FIGURE 49. Alimentary canal, dorsal, as seen in the living animal.

FIGURE 50. Alimentary canal, lateral, as seen in the living animal.

As is apparent from its lateral aspect — adequately illustrated in several taxonomic works (see, for example, Lilljeborg 1900) – the post-abdomen is quite unsuited to pushing. Its broad union with the trunk and its short, morphologically dorsal, surface render it both incapable of swinging through an arc greater than about 90° and of exerting leverage. It can swing only feebly and is not used for pushing as the animal burrows.

Although the coiled alimentary canal has been illustrated by several authors, all published illustrations are incorrect and misleading, showing as they do a gut coiled into an elongate S.

In fact the gut is extremely specialized and has three posteriorly and two anteriorly running limbs. As these overlie each other, the full complexity cannot be seen in either the dorsal (figure 49) or lateral (figure 50) view. A diagrammatic representation (lateral) with the coils pulled dorsally to allow their course to be shown is given in figure 48. Such complexity, greatly increasing the gut length, is a specialization of the same kind as, but more exaggerated than, that encountered in *Streblocerus*. No posterior diverticulum or anterior caeca are present.

(iii) *The nature and arrangement of the trunk limbs and the feeding mechanism*

The first trunk limbs, whose distal armature is seen in figure 44, are similar to those of *Acantholeberis* (figure 14), every seta and spine of every endite having its homologue, the differences being largely of proportion. The similarities extend to inner scrapers (figure 51) of endites 1 and 2 which are located exactly as in *Acantholeberis*. Although more slender and provided with longer spinules than those of *Acantholeberis*, their general form is still clearly the same. The inner lobe bears only two setae, a large setose brush and a more slender companion.

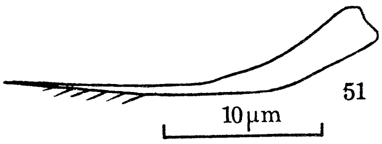
The second trunk limbs are similar to those of *Streblocerus* though the seta adjacent to scraper 1 is spiniform and denticulate and directed towards the food groove as in *Eurycercus* (Fryer 1963, figure 25). The gnathobase has six stout pushing setae directed anteriorly along the food groove (figure 52). On at least the posteriormost, each side is armed with a row of exceedingly fine 'filtratory' setules detectable only at high magnifications. Minute 'dots' can be resolved on the other setae, presumably indicating the former origin of similar setae. The four anteriormost are armed distally with sweeping spinules.

The third trunk limbs have well developed distal and greatly reduced proximal regions. Distally there are two curved spines suitably armed for grasping the flocculent material that serves as food (figures 44 and 53, DS3). Proximal to these are two smaller, somewhat similar spines. There are in all seven other, mostly hook-like, spines (ES3) on the corm exclusive of the gnathobase, all small, and four stiff setae (OGS3) that make up a fence in the position occupied by the outer filter plate of many filter feeders (figure 53). Although not used for filtration these are armed with filtratory type setules but these are exceedingly fine and can be detected only at high magnifications.

The gnathobase (GTL3), which is bluntly rounded and liberally provided with setules, lacks a filter plate or its equivalent, the armature here being reduced to a single seta (GS3) adjacent to which is a long seta (LS3) homologous with that element of the heavy gnathobasic armature that is modified for so many purposes in the Chydoridae – the sweeper of *Disparalona*, the brush seta of *Graptoleberis*, and others described elsewhere (Fryer 1968). The exopod (EX3) is relatively well developed, being larger than that of trunk limb 4; an unusual condition directly related to the absence of a respiratory-feeding current.

The fourth trunk limbs (figures 54 and 55) are better developed than in *Streblocerus*. The vertical standing endite spines (ES4) lie in line with a spiniform seta of the gnathobase (SG) adjacent to which is a papillose seta. A row of four setae (OGS4) – absent in *Streblocerus* – represent the outer filter plate of many chydorids and macrothricids. Although not used for filtration these bear filtratory type setules. Notwithstanding the statement of the meticulous Lilljeborg (1900) that 'ein Maxillärprocess fehlt', there is in fact a row of four gnathobasic setae (GP4) directed into the food groove (figure 55). A small plate (EX4) bearing two setae is all that remains of the exopod, the dominant element of the limb in many species.

Proximally trunk limb 4 is in certain respects better developed than limb 3. This is unusual



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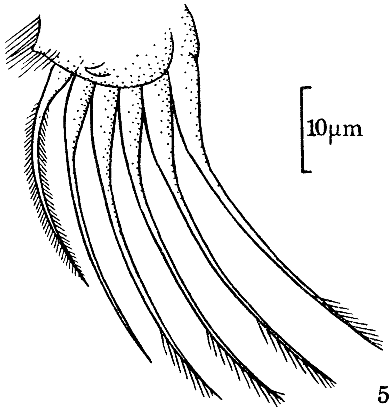

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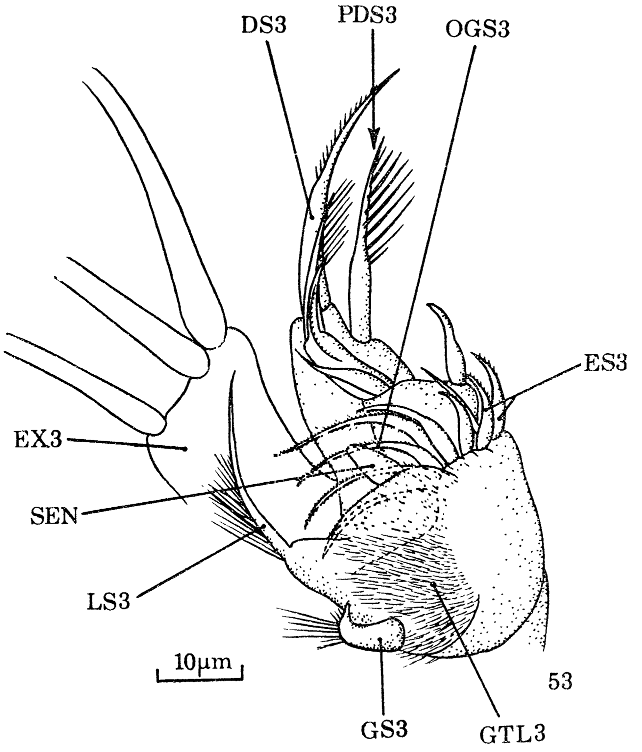

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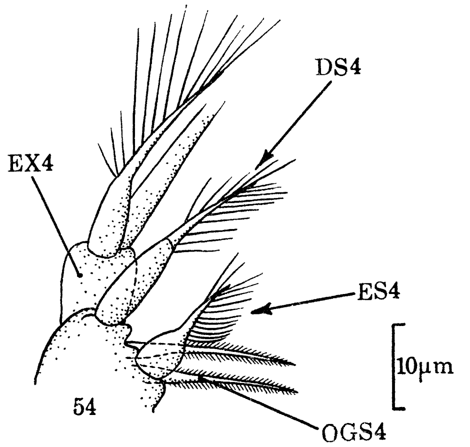

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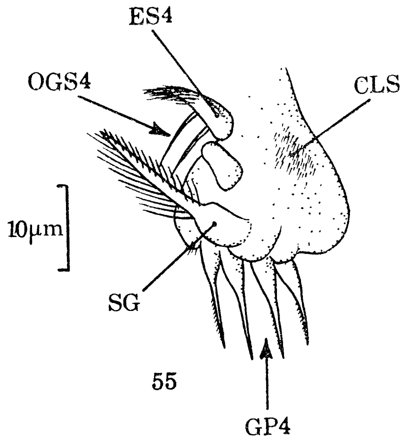

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Figures 51–55. *Drepanothrix dentata.*

Figure 51. Inner scraper of endite 1 of trunk limb 1. This is homologous with the scraper of *Acantholeberis* shown in figure 14 and not with either of the distal scrapers of trunk limb 1 of *Streblocerus*.

Figure 52. Gnathobasic setae of trunk limb 2. Note how these are modified for sweeping.

Figure 53. Trunk limb 3 orientated so that the gnathobase lies nearest to, and the distal spines of the corm furthest from, the observer. Note the absence of any fence of gnathobasic setae directed into the food groove and the setose nature of the gnathobase. Note also that, although this species does not use filtration, it has a fence of 'filter setae' (OGS3) in the position occupied by the outer filter plate of many species that do so.

Figure 54. Distal portion of trunk limb 4 showing the two most distal spines, part of the fence of 'filter setae' (OGS4) and the reduced nature of the exopod.

Figure 55. Basal portion of trunk limb 4 orientated to show the gnathobasic plate.

as reduction generally proceeds from behind forward. The persistence of the outer fence (OGS4) is also noteworthy.

Trunk limb 5 is reduced to little more than the usual pair of vertically directed setae.

The feeding mechanism is essentially similar to that of *Streblocerus*. As in that species no currents flow through the median chamber, filtration is therefore impossible, and food is manipulated entirely by mechanical means. The first trunk limbs reach out, drag in food masses, and sometimes hold them, but they lack the specialized scrapers seen in *Streblocerus*. As in that species, the second trunk limbs dominate the operation, moving very vigorously with a regular and powerful swing. By virtue of folding of the cuticle proximally and contraction of powerful extrinsic muscles there is a definite withdrawal of the limb into the carapace chamber as food is dragged in, which has been seen particularly clearly in this species. The specialized distal armature of the third trunk limbs assists in the dragging of food into the sorting chamber. Whether these appendages ever collect material independently or operate only on that dragged within their orbit by the first pair (which is often inevitable) is uncertain. More proximally (figure 53) the armature is better developed than in *Streblocerus* for helping the second trunk limbs to move food towards the food groove, and this is equally true of all the armature of the fourth limbs, which is basically similar to that of many macrothricids and chydorids. Whether the minute gnathobasic setae of the fourth limbs actively move food particles forward or act merely as a fence is not clear but any active role must be small. Movements of the third trunk limb gnathobases inevitably sweep material forward, but the absence of true pushing setae and the setose nature of these gnathobases suggest that such particles as are swept are small items that have evaded the main forwarding mechanism represented by the gnathobasic setae of trunk limb 2, and that the role of the third gnathobase is as much that of cleansing as of contributing to the movement of food particles. That the fourth trunk limb retains a patch of cleaning setules (figure 55, CLS) indicates that cleansing of the equivalent of the outer filter plate of trunk limb 3 is necessary although filtration is not practised. This function is fulfilled for the equivalent plate of trunk limb 4 by the highly setose vertical setae of the fifth trunk limbs whose size probably reflects this need rather than the necessity of sealing the sorting chamber posteriorly.

Anteriorly the situation is typical. The steeply inclined mandibles (figure 43), roll persistently and can maintain a rate of 122 rolls/min for well over 2 min. Secretions are employed for entangling the food anteriorly, but the evidence that these emanate from the labrum, while good, is only circumstantial.

(iv) *Conclusions*

Many attributes of *Drepanothrix* are associated with the hitherto unreported habit of burrowing into flocculent detritus which serves both as a substrate and as food. The body, wedge-shaped in two planes, is driven into detritus by highly specialized antennae which, in addition to having the two proximal endopod setae modified for levering and not for swimming, are provided with a stout spine on the protopod which sweeps away material as the animal moves forward. Neither the first trunk limbs nor the post-abdomen are used for locomotion.

There is no respiratory-feeding current. Food is collected and manipulated by purely mechanical means, the process being essentially as in *Streblocerus* but there are many specific differences.

VII. THE STRUCTURE, HABITS AND FEEDING MECHANISM OF *MACROTHRIX LATICORNIS* (JURINE)

(i) *Ecology and habits*

Although almost cosmopolitan in distribution, *Macrothrix laticornis* (figure 56: length to about 0.65 mm) is rare in Britain and material has been obtained only from a tarn (Berrier End) at the northern fringe of the English Lake District. Here, in the shallow littoral region over a bottom that is somewhat sandy but covered with flocculent organic detritus, there is a persistent population which, however, is sometimes reduced to very small numbers.

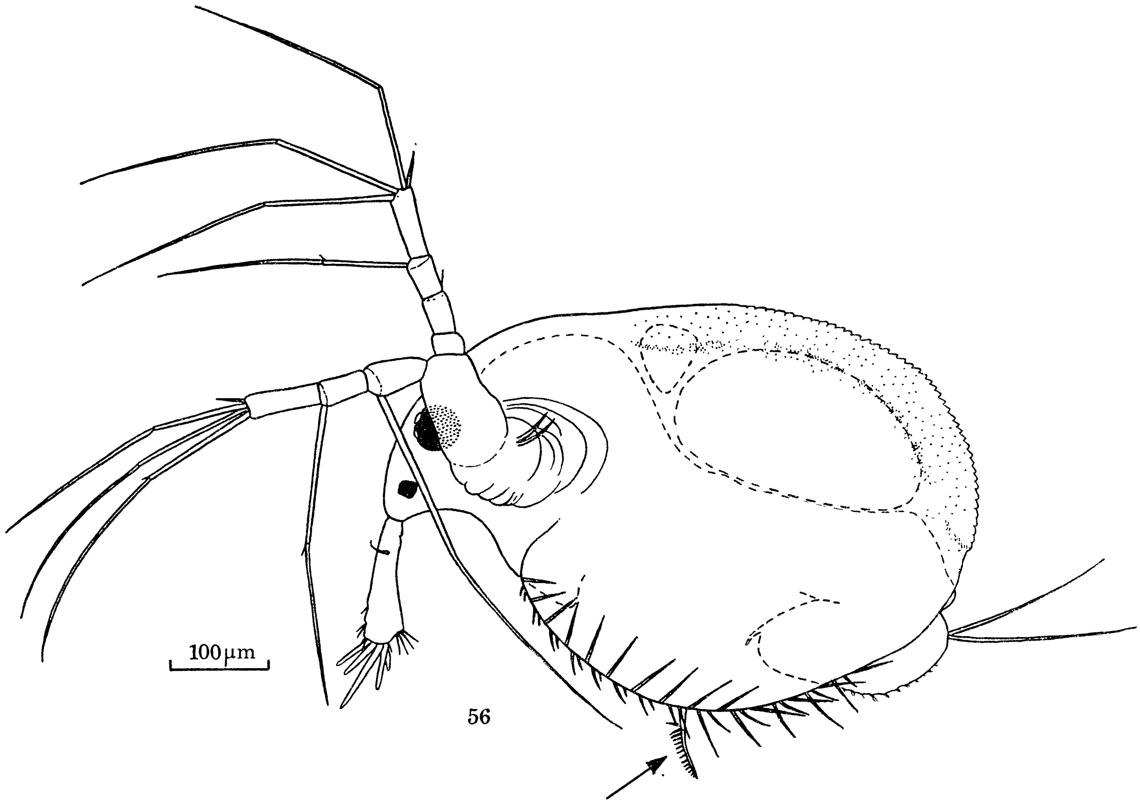
Because highly relevant to the specialized feeding habits, the habitats in which others have found this species merit consideration. Lilljeborg (1900), who says that *M. laticornis* is very common in Sweden, states categorically that it is found 'immer auf schlammigem Boden', which is what its feeding habits would lead one to expect. Almeroth (1916) and Obermayer (1922) likewise categorize it as a mud-dweller and Wagler (1937) and Herbst (1962), summarizing others, both say simply 'liebt Schlammboden'. By contrast, Johnson (1951) found it over bottoms that were sandy or composed of sandy silt, silt, and soil, but which may well have been covered by a thin layer of fine organic mud as was the sandy bottom from which my own material came. Flössner (1972) says that *M. laticornis* 'bewohnt den schlammigen Grund...seltener auf Sandboden', and that it is to be found also among *Potamogeton.*

Like many other macrothricids *M. laticornis* rests on the bottom and moves but little if undisturbed. Progression is by means of the antennae alone and the animal swims in a series of short 'hops'. Usually a small number of beats – not infrequently a single beat – move the animal forward, but when necessary more persistent swimming can be practised which takes it along a course which, while made up of a series of shallow arcs, is basically straight. While it tends to rest on the specialized setae of the ventral carapace margins (§(ii)), though these margins are not straight, and to use the long setae of the basal segment of the antennal endopod as props, this is not invariably so and, like *Acantholeberis*, it may rest in other positions. The tendency to rest ventral side down is, however, stronger than in *Acantholeberis*. Like several other macrothricids it penetrates flocculent deposits, but probably to a less extent than *Streblocerus* and *Drepanothrix*. When moving among deposits it lies at any angle. Propulsion is here also by means of the antennae alone, which then display greater versatility than when used for swimming. Crawling by means of the first trunk limbs is not practised and the post-abdomen, which moves only feebly, is not used for pushing.

The food consists of detritus. As material has been available from one locality only, too much weight cannot be placed on this but the detritus was brownish green in colour and, in general, consisted of very fine particles. That this is usual – though not necessarily invariable – is, however, indicated by the feeding mechanism (§(iii)). A few larger particles – 'sand grains' – reflected the nature of the underlying substratum and a few green algae were also present as were, in one specimen, two long slender hooks of unknown origin. When the animal is about to defecate the post-abdomen is protruded a little and a short faecal ribbon is ejected to the ventral side of the carapace.

(ii) *Gross morphology*

The lateral view (figure 56) gives no indication of two of the most striking features of the animal – a dorsal carapace ridge similar to, and when viewed from the appropriate angle as conspicuous as, that of the chydorid *Graptoleberis*, and, in the material studied, an anterior



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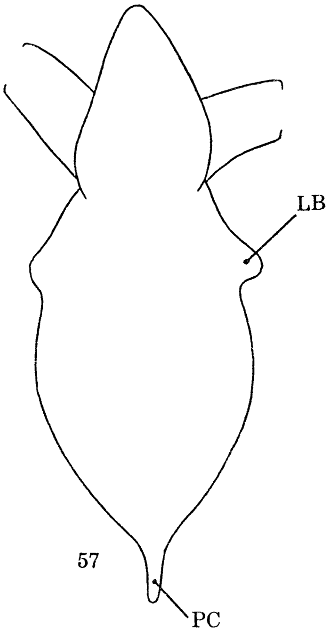

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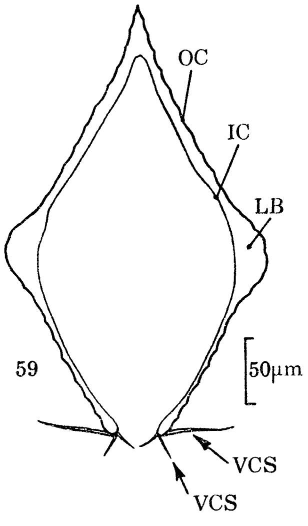

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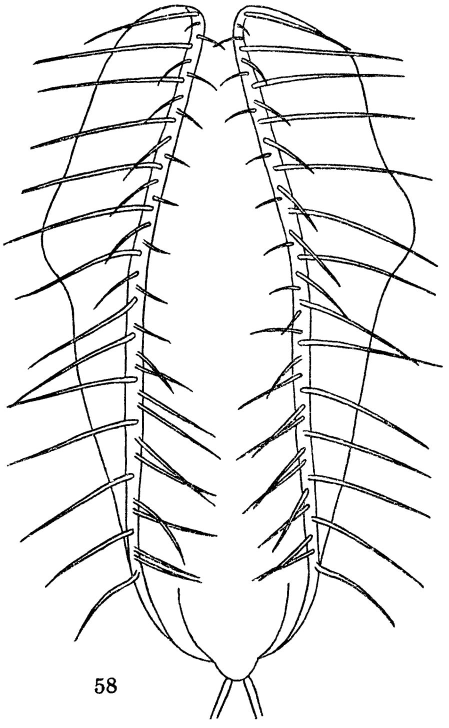

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FIGURES 56–59. *Macrothrix laticornis.*

FIGURE 56. Adult female, lateral. From this aspect the lateral bulges are not apparent. The dorsal ridge is indicated by stippling.

FIGURE 57. Dorsal outline to show the lateral bulges and the posterior end of the dorsal ridge.

FIGURE 58. The armature of the ventral carapace margins, ventral. Note that in this individual there is a malformation of the right valve. Lateral spines 8 and 9 are a little closer together than should be the case and only one spine lies between them.

FIGURE 59. Transverse section of the carapace in the region of the lateral bulges showing also the arrangement of the ventral marginal setae. The region between the thick outer carapace wall and its thin cuticular lining is for the most part occupied by fibrils and blood spaces; in the vicinity of the bulge by other tissues and organs (see text).

lateral bulge on each side of the carapace (figures 57–59, LB). The dorsal ridge, formed by a pinching of the dorsal part of the carapace lobes into an inverted V or sharp U, extends forwards to the posterior margin of the head, where it divides into two arms, and backwards to the posterior extremity of the carapace. Its dorsal edge is finely serrated. Besides lending strength to the otherwise delicate carapace (compare the simple dorsal cuticular ridge of *Ophryoxus*) it possibly serves to some extent for defence against small predators, may also function as a keel to promote stability during locomotion (compare the cuticular keel of such chydorids as *Acroperus* and *Camptocercus*) and almost certainly represents, and probably functions as, an incipient version of the structure described for *Drepanothrix.* The anterior end of this V girder has also been utilized as a firm site of origin not only for both the remotor and promotor roller muscles of the mandibles but by some of the posterior antennal muscles. This hitherto ignored morphological feature is thus of great functional significance. A first step towards the development of such a dorsal ridge is apparent at the anterior end of the otherwise evenly arched carapace of *Acantholeberis* (figure 2).

The lateral bulges are indicated in figures 57–59 (LB). Although mentioned by Lilljeborg (1900) these appear never to have been illustrated, except by Motas & Orghidan (1948) who assigned their material to what they described as a new species, *M. bialatus*, largely on this account. The other features used to differentiate this species from *M. laticornis* are within the range of individual and geographic variation of the latter and I have therefore little doubt that *M. bialatus* is a synonym of *M. laticornis.* Flössner (1972) adopts the same view but makes no reference to the lateral bulges.

Individual and racial differences in the degree of development of the bulges evidently exist, for in material from Surrey provided by the British Museum (Nat. Hist.) they are, in general, less conspicuous than in the Cumbrian population, and in some individuals are only weakly developed. The degree of development is not size-related. That racial variation exists is also indicated by the original description of Jurine (1820), whose material came from the vicinity of Geneva and who, apart from Motas & Orghidan, appears to be the only observer to illustrate the animal from above. No bulges are shown.

The bulges house the tendons into which the lateral extremities of the carapace adductor muscles almost imperceptibly fade and, more laterally, the fibrils into which these tendons break up and insert on the inner face of each bulge. This device spreads the load of these muscles over a wide area and also ensures that during their contraction they exert their pull on the inside of a dome – a self-bracing and rigid configuration – which is better able to resist buckling than is a flat surface. The cuticle here is a little thicker than that of the adjoining parts of the carapace and the endocuticle faintly sclerotized. Such a device, analogous to the system of load-spreading fibrils that carries the suspensory ligaments and remotor roller muscles of the mandibles of *Eurycercus* (Fryer 1963), suggests that particularly powerful contractions of the carapace adductor muscles have to be borne, perhaps when the animal penetrates deposits. Other macrothricids have an equally delicate carapace but no such device. Anteriorly the bulges also house some of the fibrils which suspend the distal portion of each maxillary gland. Much larger projections arise more posteriorly in *M. pennigera* Shen, Sung & Chen and cannot therefore house part of the carapace adductor system and are probably not homologous. The same is true of the lateral bulges present in the daphnid *Simocephalus lusaticus* Herr; otherwise they are without counterpart among anomopods.

The ventral carapace margins are not straight (cf. the straight margins of the specialized

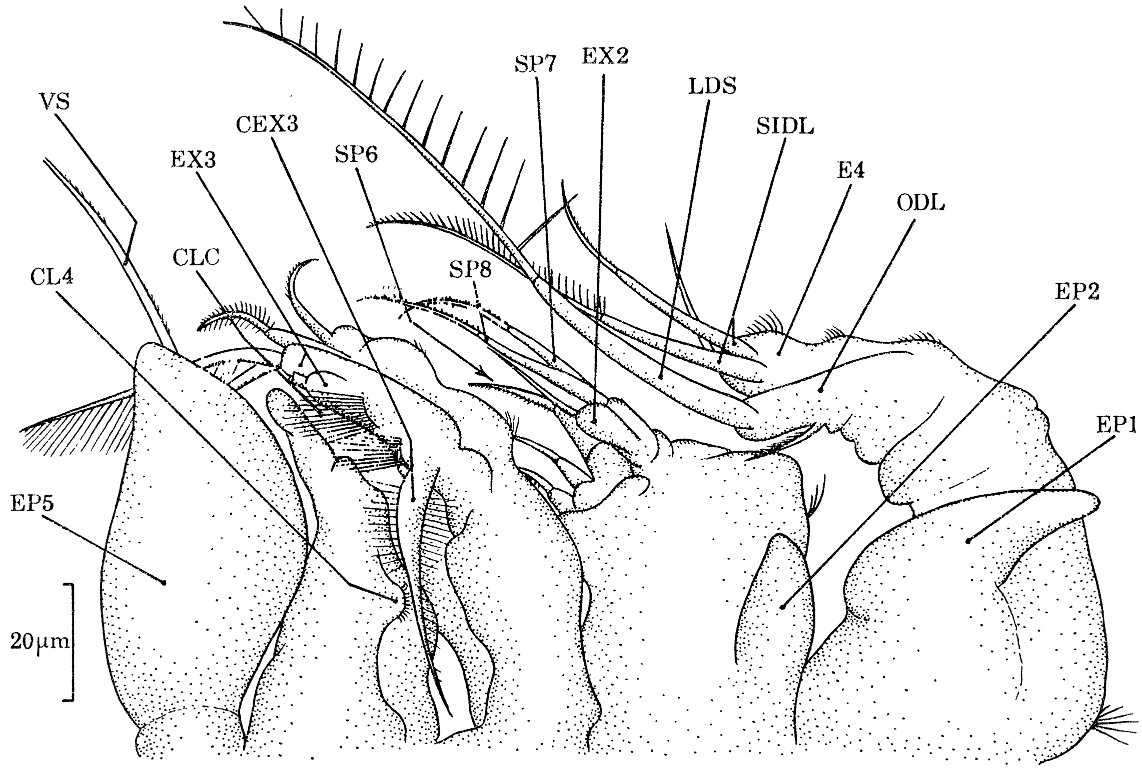


FIGURE 60. *Macrothrix laticornis*. Trunk limbs seen from the outside to show the enormous length, and the armature, of the spine of the outer distal lobe of trunk limb 1 (LDS) and the slender, elongate nature of the outermost lobe itself (ODL); the complementary nature of the two distalmost scrapers (8 and 7) of trunk limb 2 (SP8, 7); the distal armature of trunk limb 3; the enormous epipodites of trunk limb 1 (EP1), and especially of trunk limb 5 (EP5); the cleaning seta (CEX3) and combs of setules (CLC) of trunk limb 3, and the cleaning lobe (CL4) of trunk limb 4 which clean the inner wall of the carapace. The setules on trunk limb 4 are directed towards the observer and thus appear much foreshortened. Scraper no. 4 of trunk limb 2, which is in fact partially obscured by a portion of trunk limb 3 that lies nearer to the observer, has been revealed by drawing this limb in optical section at a deeper level in order to show the relation of various structures more clearly. The wide gap between trunk limbs 1 and 2 is occupied at a deeper level of focusing by that part of the corm of trunk limb 1 which lies distal to the 'elbow' and is directed largely posteriorly. Armature of trunk limb 4 that is present distally is omitted for clarity.

FIGURES 61–66. *Macrothrix laticornis*.

FIGURE 61. Distal extremity of trunk limb 1 from inside. Note that the long spine (LDS) of the outer distal lobe is cut short.

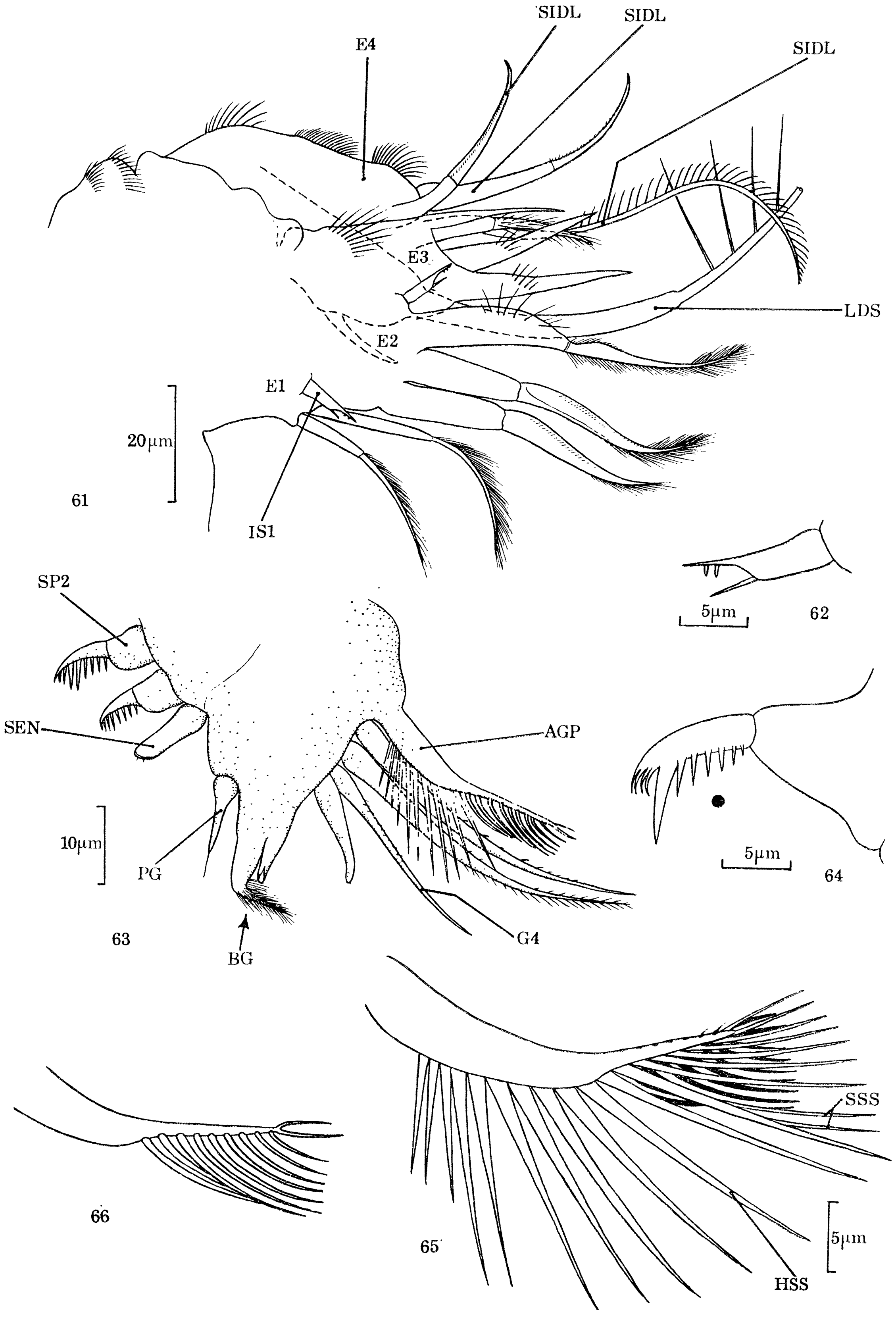
FIGURE 62. Inner spine of endite 1 of trunk limb 1.

FIGURE 63. Gnathobase and adjoining region of trunk limb 2. The row of hyaline setules of the anteriormost gnathobasic spine (AGP) extends to the tip (see figure 65) but is here shown only proximally so as not to obscure the underlying distal row of spinules.

FIGURE 64. Scraper number 4 of trunk limb 2. The black disk represents a particle 1 μm in diameter.

FIGURE 65. Anteriormost gnathobasic spine of trunk limb 2 seen from inside. Members of the row of hyaline setules (HSS) are so orientated that their distal portions are rising towards the observer.

FIGURE 66. Tip of the anteriormost distal gnathobasic spine of trunk limb 2 with the hyaline setules omitted so as to show the arrangement of the distal spinules that are shown in black in figure 65.



FIGURES 61–66. For descriptions see opposite.

crawlers among the Chydoridae and even of such macrothricids as *Acantholeberis* and *Ophryoxus*). Effective balance depends largely on the use of the elaborate ventral armature, some stout spines of which extend laterally (figures 56, 58 and 59) and enable the animal to rest on flocculent deposits. In this they are assisted by the long ventrally and posteriorly directed setae of the antennal endopods.

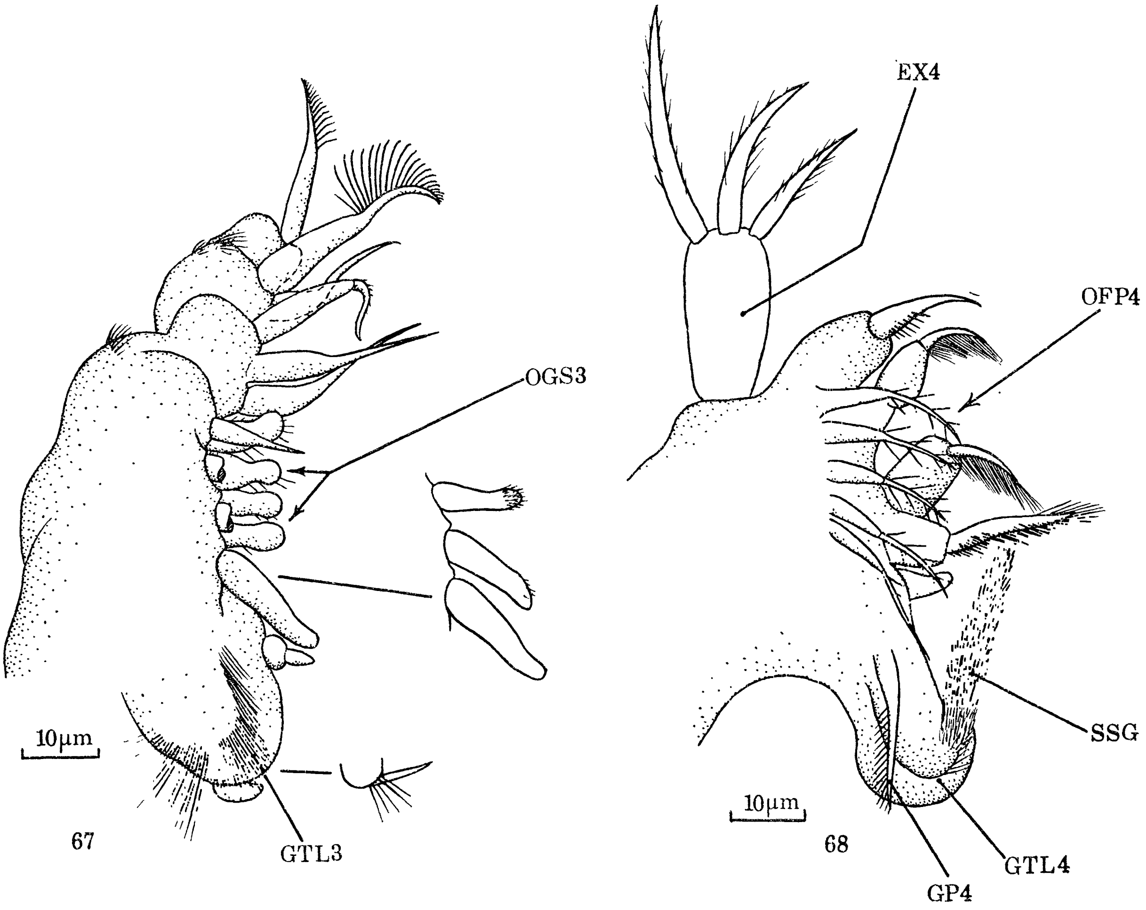
As figures 56–58 show, there are many resemblances to *Acantholeberis* though proportions are considerably different. Similarity extends to the primitively exposed head. There is no real headshield but a duplicature of the cuticle above each antenna, a little better developed than in *Acantholeberis*, indicates its incipient development.

(iii) *The nature of the trunk limbs and the feeding mechanism*

Outstanding features of trunk limb 1 (figures 60 and 61) are the elongate nature, specialized armature and mobility of the seta of the outer distal lobe (LDS). Mobility is described below. That the lobe (ODL) bearing it is slender and elongate (figure 60) is associated with this mobility. The elongate nature and the armature of the setae (SIDL) of the inner distal lobe (E4) are also clearly shown in figures 60 and 61. This lobe, morphologically endite 4, like its outer companion, is mobile and clearly differentiated from the rest of the distal portion of the corm. The rest of the terminal armature of the limb is similar distally to that of *Acantholeberis* but reduced proximally (cf. figures 14 and 61). Endites 2 and 3 bear three and four spines respectively as do their homologues in *Acantholeberis*, and most of these are similar in form in the two animals. More proximally the rest of the major armature is reduced to two setae (four in *Acantholeberis*). As in *Acantholeberis* 'scrapers' (figure 61, IS1) are borne on the inner face of endites 1 and 2, but these are very small and modified by the development of a spinule arising from the distal end of the proximal portion (figure 62).

The two outermost scrapers of trunk limb 2, particularly no. 8, are similarly armed to the setae of the outer distal lobes of trunk limb 1 (figure 60, SP7 and SP8). Their more specialized companions are modified for dragging (figures 63 and 64), no. 4 in particular being highly modified (figure 64). Between the most proximal and the gnathobase is a tubular projection (figure 63, SEN) described by Smirnov (1967) and probably homologous with the most proximal member of the row of sensory setae present on this limb in certain anomopods. *M. propinqua* Sars has a sensory seta in this position (Sars 1909). Two minute setule-like structures can be made out in some, but not all, preparations, otherwise the structure is naked and appears to be completely enclosed, the cuticle of its tip being somewhat thicker than the rest. It thus differs somewhat from other known anomopod sensillae and its occurrence in this position on trunk limb 2 is unique. The adjacent gnathobasic seta (figure 63, PG) terminates in an exceedingly fine bristle and may also be in part sensory. Of the highly modified gnathobasic armature the most specialized of the reduced number of brushing elements of the gnathobasic plate is the anteriormost (figures 63 (AGP), 65 and 66). Distally this bears a row of stiff, curved spinules (figure 66) overlying which, on the inside, is a row of long hyaline setules (figure 65, HSS), extremely difficult to see, and which appear to be flattened or oval in section. These fan out and extend as a complete row over the two adjacent spiniform setae of the gnathobase and somewhat medially (figure 63). Two similar setules (figure 65, SSS) lie beneath them but, being equally hyaline, their insertion has not been made out. The fourth element of the gnathobasic plate (figure 63, G 4) is spiniform and not rigidly inserted but capable of some movement.

The third trunk limbs (figures 60 and 67) resemble those of *Drepanothrix* in most respects. The setae of the grid equivalent to the outer filter plate (OGS3) are stumpy and almost spatulate but nevertheless armed with a few setules on each side. As in *Drepanothrix* the gnathobase is bluntly rounded, setose, and lacks a grid of gnathobasic setae (cf. figure 53). Here, as in *Drepanothrix*, there is an inwardly directed setose brush adjacent to which are two rounded papillae, one small, the other minute. The exopod, omitted from figure 67, is somewhat reduced in comparison with that of many current-producing species but is armed with a fringe of cleaning setules and a long cleaning seta (figure 60, CEX3) with which to brush the inner wall of the carapace. Distal to this are two combs of long cleaning setules (CLC).



Figures 67 and 68. *Macrothrix laticornis.*

Figure 67. Trunk limb 3 as seen *in situ* from the inside. The exopod is omitted. The upper inset shows some of the endite armature that overlies the outer grid of setae (OGS3) and which has been cut short in the figure. The lower inset shows the gnathobasic brush (not visible in the view of the limb illustrated) as seen from the outside and sketched from another individual, and not to exactly the same scale.

Figure 68. Trunk limb 4 seen more or less from behind after dissection and slightly flattened.

The fourth trunk limbs (figures 60 and 68) follow the basic plan but have a specialized gnathobase whose salient feature is an erect seta (SSG) so setose as to have a 'furry' appearance. There is no grid of gnathobasic setae directed into the food groove but a single seta (GP4) is present in what, for such a structure, is a very posterior and ventral position. The grid of outer setae (OFP4) is clearly non-filtratory. In contrast to the enormous flap of current-producing species the exopod (EX4) is much reduced. The corm bears a cleaning lobe (figure 60, CL4) adjacent to the cleaning seta of limb 3.

The fifth trunk limbs are dominated by an enormous epipodite (figure 60, EP5). Each has a flap and two vertically standing sealing setae as in many genera, one of which (VS) is very long and can be seen rising above the epipodite in figure 60. There is no trace of any gnathobasic armature directed into the food groove and the gnathobase itself is ill-defined and setose. Two setae arising from a tiny flap represent the remnants of an exopod whose reduction is one of the noteworthy characteristics of the limb.

Although all details of the feeding mechanism have not been investigated in detail, the salient features are clear. Food is collected largely by the first trunk limbs of whose armature the elongate and specialized seta of the outer distal lobe is particularly important in this respect. This seta has great mobility. Not only can it reach backward and outward (it is seen protruding beyond the limits of the carapace in figure 56) but can swing through a wide arc to extend forward. This mobility is shared in part by the armature of the inner distal lobe. Such apparatus can rake through finely particulate detritus, collecting from it larger particles – cf. the homologous structures in the chydorid *Leydigia leydigii* (figure 144 in Fryer (1968)) – and also whisk fine particles towards the sorting chamber. There they are assisted by 'scrapers' 7 and 8 of trunk limb 2 which are very finely armed (figure 60, SP7, 8) and which should theoretically be able to sweep up an isolated particle less than 1 μm in diameter. Whether the distal elements of the armature of trunk limb 3 also contribute to food collection has not been ascertained but it is probable that they do.

Material is forced into the sorting chamber in the usual manner, there being here no assistance from water currents. Equipment for dealing with both very fine and larger particles is available. That scraper no. 4 of trunk limb 2 (figure 64) is specialized for dragging large particles or accumulations of material is readily apparent, but that it can also handle smaller items is made clear by the black disk which represents a particle only 1 μm in diameter. Other elements of the complex are well suited to whisking very fine particles towards the food groove, this being especially so in the case of the endite armature of trunk limb 4 which is clothed with very fine brush-like setules (figure 68). The tips of the stout spines of endite 2 of trunk limb 1 are also brush-like (figure 61), as are those of endite 1, a specialization which suggests that they at times help to whisk material towards the food groove, but this has not been observed.

On neither trunk limbs 3 nor 4 is the outer grid of setae equipped to retain fine particles (figures 67 and 68). As no currents flow between them and as fine particles are driven directly towards the food groove, their role in respect of such particles would inevitably be slight however they were armed. As it is they possibly retain an occasional larger particle.

Only trunk limb 2 is equipped to deal with large particles that have accumulated in the foreshortened food groove, which indicates clearly that, as in other non-filtering species, such particles are carried there and thence pushed forward by this limb alone. Otherwise all the apparatus in the vicinity of the food groove is specialized for sweeping fine particles. The setose gnathobase of trunk limb 3, and the gnathobasic brush of trunk limb 2 (figure 63, BG) serve this function. As the anterior gnathobasic armature of trunk limb 2 swings forward the stouter elements lead the way and inevitably push forward any large particles that may have accumulated, thereby protecting the delicate setules that follow. The central channel of the food groove is spanned by the fanned-out setules of the anteriormost spine (figures 63, AGP and

65) which are highly specialized for sweeping fine particles, and material is passed in the usual manner, via the maxillules, to the mandibles, whose masticatory surfaces resemble a fine file.

The production of labral gland secretions is not proven. In several longitudinally sectioned individuals food is clearly and neatly lodged in the food groove, but no secretions (usually revealed by blue staining) are to be seen. Food entering the oesophagus becomes moulded into a more discrete, and perhaps more compact, strand which maintains its integrity until discharged into the mid-gut where it quickly disintegrates. Thus secretions may be used, perhaps in small quantities, anteriorly. How they could pass backward without the assistance of a current is difficult to envisage though return movements of trunk limb 2 could perhaps help. It seems, however, that the various setose structures employed are sufficient to pack fine particles neatly into the food groove unaided by secretions, though the presence of such from undetected sources cannot be ruled out.

A morphological and functional study thus suggests that *M. laticornis* is specialized for the collection of fine particles and that the presence of such in the gut is a reflexion of preferences and specializations rather than an inevitable consequence of the situation and food supply in the single locality from which material has been obtained.

(iv) *Conclusions*

Macrothrix laticornis is a benthic species probably associated with muddy or floc-covered bottoms or regions where a thin layer of such material overlies sand, but further ecological data are desirable. There is no respiratory-feeding current and food is collected and manipulated by purely mechanical means, many of the specializations of the apparatus involved being related to the manipulation of very fine particles.

VIII. Observations on the functional morphology of *Macrothrix triserialis* Brady, a successful tropical species

(i) *Ecology and habits*

Macrothrix triserialis (length to *ca.* 1 mm), often referred to in the literature as *M. chevreuxi*, has a pan-tropical distribution and occurs also in the warm subtropics. Here it is often very common. That it is tolerant of a wide range of environmental conditions is indicated by the literature and was confirmed by personal experience in tropical Africa where I found it many times (Fryer 1957*a* and unpublished records). While particularly frequent among submerged vegetation in water bodies of various kinds, including sluggish rivers, it occurs also among marginal grasses and sparse emergent vegetation such as sedges. Habits were not studied in Africa but more recently it was possible to collect and observe living animals in Argentina. While differing from *Acantholeberis curvirostris* in many ways, *M. triserialis* shows a striking overall similarity to that species in its general facies and in certain aspects of its behaviour. Like *Acantholeberis* it has a wide ventral gape bounded on each carapace margin by an array of spines which, while different in form and arrangement, exhibit certain basic similarities (cf. figures 5 and 69). Its carapace, however, has a dorsal ridge akin to that of *M. laticornis*. Like *Acantholeberis*, *M. triserialis* 'leaps' through the water, possibly somewhat less violently, but is the more effective of the two at alighting on its carapace margins. It also has an accomplishment possessed neither by *Acantholeberis* nor, save in a rudimentary form, by any other studied macrothricid, including the congeneric *M. laticornis*. This is the ability to grip certain objects by means of hooks on the first trunk limb and, by means of these, to work its way along with great agility much as do many chydorids. Although *Onchobunops* grips with such hooks it does not use them for locomotion. *Ophryoxus* (§IV) displays the same ability as *M. triserialis*, but in a more rudimentary form and cannot move with such agility. *Iheringula paulensis* G. O. Sars exhibits similar behaviour, but evidently to a less degree than *M. triserialis*. Sars (1900) describes *Iheringula* as a bottom form and 'by no means an active animal' which clings to plants and is sometimes 'seen slowly advancing along the stalks or leaves...without ever moving its antennae'. Although this action is attributed to the first two pairs of trunk limbs it is clearly the first pair only that is involved. These are provided with hooks, somewhat less powerful than those of *Ophryoxus* and much less so than those of *M. triserialis*. It may be to its specialized achievement that the undoubted success of *M. triserialis* is in large part due. By virtue of this

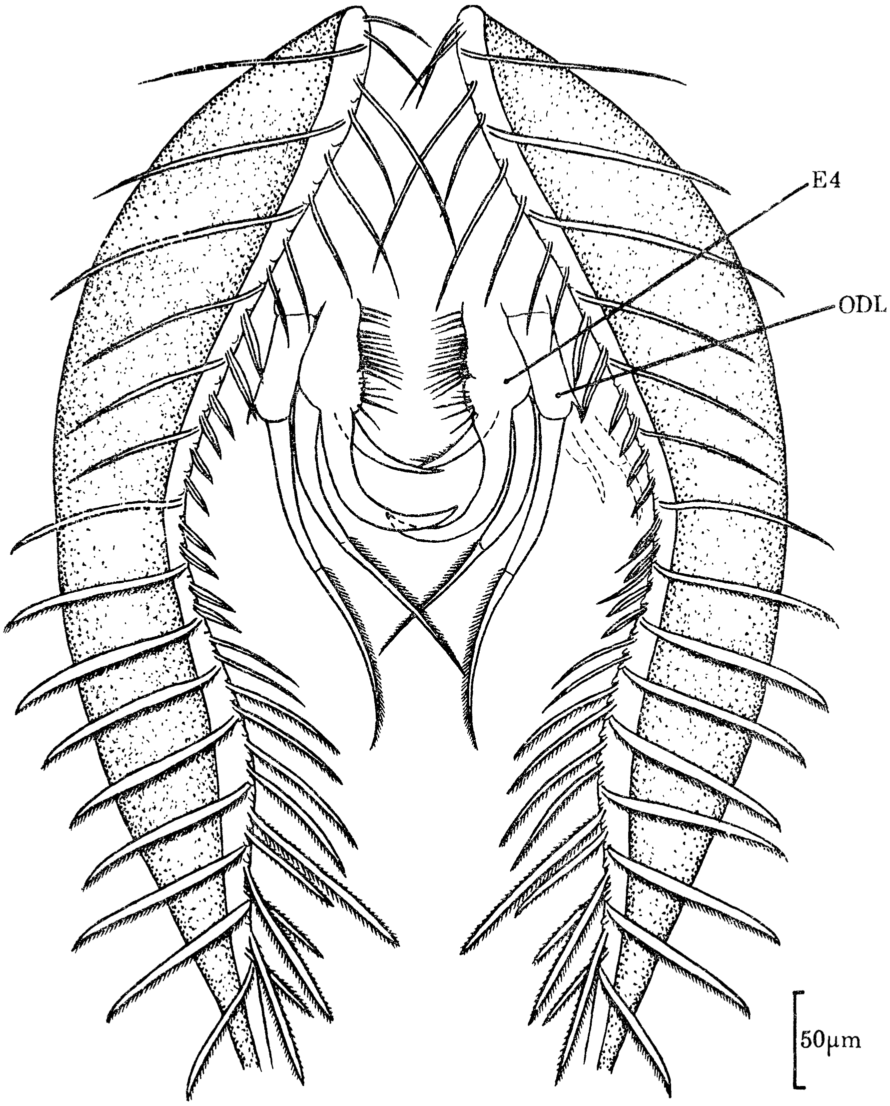
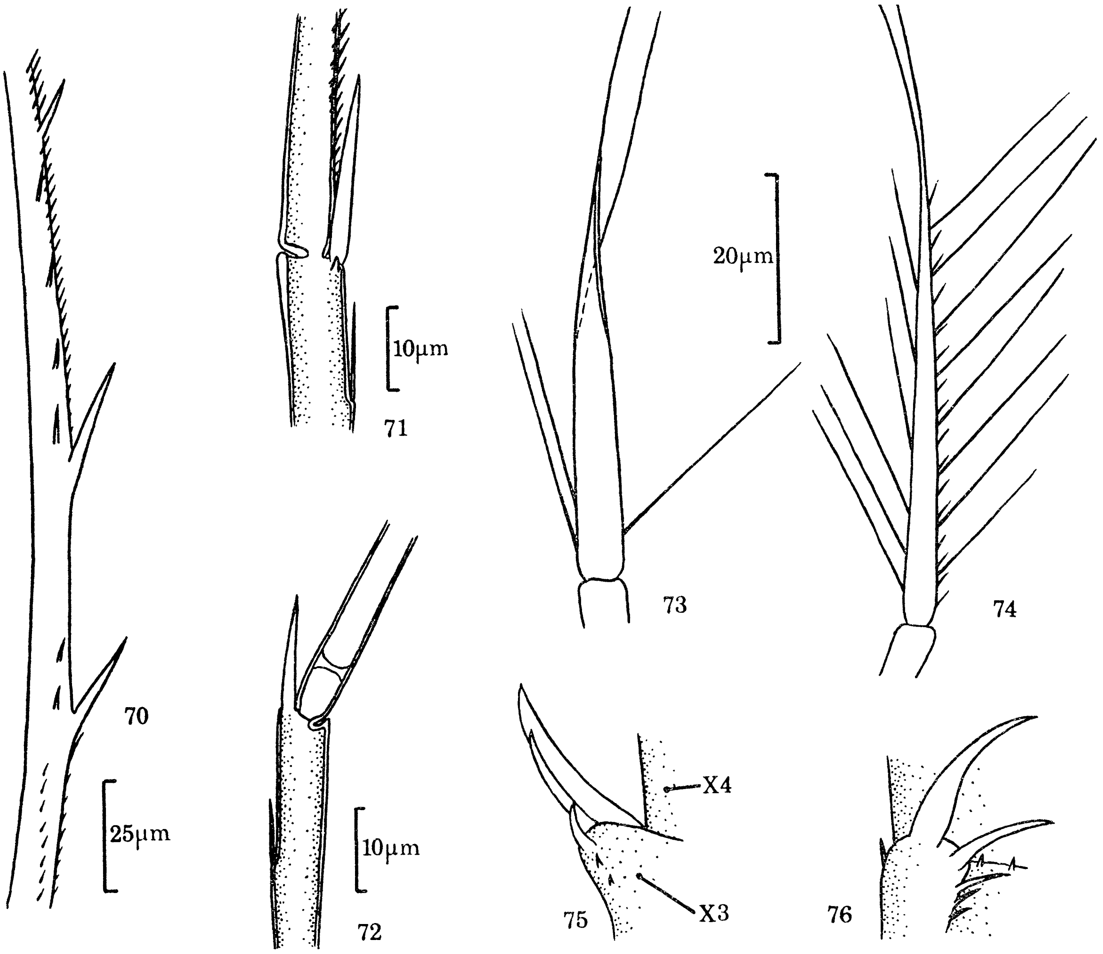


FIGURE 69. *Macrothrix triserialis*. Ventral view of the carapace to show the arrangement of the marginal armature (of which two additional trios of spines complete the complement posterior to the region illustrated) and the grasping, hook-like, distal armature of the first trunk limbs. Other appendages omitted, save that the position of the scrapers of trunk limb two is indicated on one side.

it can match many crawling chydorids at their own game while yet possessing its own advantages of other kinds.

The stout antennae are basically similar to those of *Acantholeberis* and *M. laticornis* and bear setae or spines in the same positions as do the latter (cf. figure 56) and *Streblocerus*. The basal endopod segment bears a stout propping spine whose orientation is similar to that shown for *Acantholeberis* in figures 1, 3 and 5 and for *M. laticornis* in figure 56, but which is stouter than in its homologue in either. In the material studied this shows no trace of a median joint and is armed with spinules, some of them robust (figure 70). Its counterpart on segment 2 of the endopod is two-segmented, stout and spiniform, and has a conspicuous spinule at the distal end of the proximal segment (figure 71) which is exposed by flexure. A similar spinule is borne by the seta of segment 3 of the exopod, by the longest of the three terminal endopod setae, and by two of the three terminal exopod setae (figure 72).



Figures 70–76. *Macrothrix triserialis*. Details of antennal armature.

Figure 70. A portion of the massive spine of the basal endopod segment.

Figure 71. Joint region of the seta of endopod segment 2 to show the sharp spinule.

Figure 72. Joint region of the longest terminal seta of exopod segment 4 to show how, as a result of flexure, the sharp spinule is exposed.

Figures 73 and 74. Distal endopod setae to show the strap-like nature of the distal portion as revealed by torsion.

Figures 75 and 76. Two views of the armature of hook-like spines at the distal extremity of exopod segment 3.

It may be predicted with some confidence that these spinules are used for levering against the substratum but they have not yet been observed in action. Their presence – an important specialization – is related to, and their obvious function facilitated by, the specialized nature of the distal portion of each terminal seta and of the seta of exopod segment 3 which is not cylindrical but strap-like (figures 73 and 74), except at its extreme base where a cylindrical condition is necessary to permit efficient articulation.

Terminally, segments 1, 2 and 3 of the exopod bear an arc of spines (figures 75 and 76), hitherto inadequately illustrated, which, with the spine of the terminal segment, inevitably serve for defence, but whose prime function is probably to facilitate scrambling through vegetation. In this respect *M. triserialis* is more specialized than *M. laticornis* which uses its antennae for propulsion through detritus (§VII). These appendages are not involved in crawling, nor does the post-abdomen push.

While further observations are desirable the post-abdomen is not apparently swung when the animal defecates, and faeces are probably simply left behind as it moves forward. As in *M. laticornis*, and in striking contrast to *Acantholeberis*, there is no respiratory current. Such a lack is perhaps typical of the genus but details of the posterior trunk limbs of most species are not available. As in *M. laticornis* the fifth trunk limbs have an enormous epipodite, but here it is curved and elongate much as in *Lathonura* (§X). The development of large epipodites is apparently a device that helps to compensate for the absence of respiratory currents. What may be a further such device is a thin-walled thimble-shaped projection from the trunk into the brood pouch through which circulates blood from the haemocoele.

In addition to the usual finely particulate organic detritus, the gut contents of Argentinian specimens contained inorganic particles – a reflexion of the fact that food is collected by scraping rather than by dragging in flocculent detritus (see below).

(ii) *Observations on the feeding mechanism and associated structures*

The feeding mechanism has not been studied in detail but certain features are apparent. The indications are that food can be collected either as the animal is gripping or moving by means of trunk limb 1 (though this has not been conclusively established) or when it is lying free (which has been clearly seen). There is no apparent reason why, when the first trunk limbs are in use for locomotion, the second pair should not collect food by essentially the same movements as they use when the first pair are gripping a food mass as described here, and this is almost certainly possible.

An individual not progressing in this way collects food by means of trunk limb 1 whose distal lobes, and particularly the outer, display great mobility and often swing so that their spines reach out and return while the rest of the corm remains stationary. This they do with great vigour. When, as is sometimes the case, large food masses are secured, these are gripped by the first trunk limbs – the hooks of whose inner distal lobes are as well suited to this as to gripping during crawling – and pulled against the ventral carapace armature. From the mass trunk limb 2 scrapes material and passes it into the sorting chamber in the typical manner. In the latter function at least it is assisted by trunk limb 3. The lunging movements of trunk limb 2 include the ramming component of the gnathobasic region common to many species.

Secretions are produced in the labrum and stored in a pair of enormous reservoirs (figure 77, RLG) which are not confined to this structure but extend forward into the head (ER). In this *M. triserialis* is unique among studied species of both the Macrothricidae and Chydoridae.

In *Onchobunops* (§IX) large reservoirs are developed but are confined to the labrum. The gland cells (GCL) are difficult to homologize with those of other anomopods as they have been displaced from their primitive position by the enormous development of the reservoirs. One group lies dorsally between the reservoirs and the oesophagus, others lie against the sides of the reservoirs well inside the head. One suspects that secretions may be discharged in part by contraction of the dorso-ventral muscles of the labrum as this action must inevitably exert pressure on the reservoirs. Copious amounts of secreted material are sometimes to be seen passing up the oesophagus (figure 77, SO).

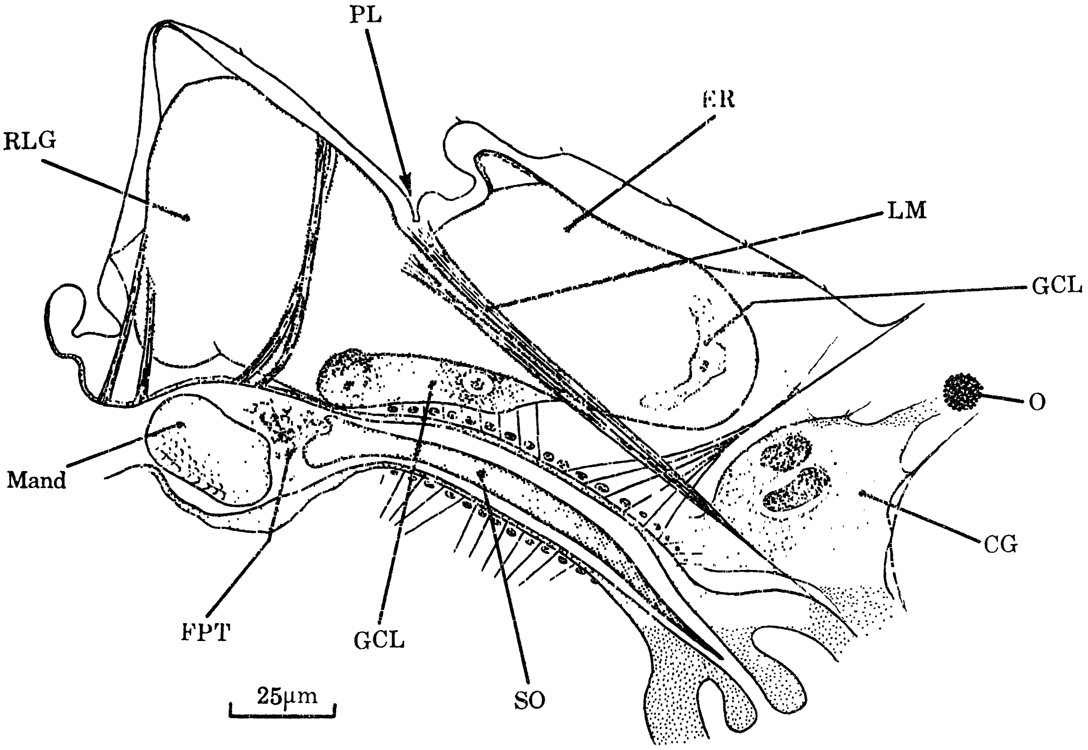


Figure 77. *Macrothrix triserialis*. Longitudinal section through the labrum and ventral part of the head to show one of the two enormous, secretion-filled reservoirs of the labrum (RLG) which lie side by side and extend anteriorly (ER) into the ventral haemocoelic space of the head. Note also the mass of secretion (SO) in the lumen of the oesophagus. The anterior of the two groups of gland cells labelled GCL is not in fact visible at the level at which the rest of the figure is drawn but comes into view as the observer focuses upward.

(iii) *Conclusions*

M. triserialis, a common and widely distributed tropical species, uses the distal armature of trunk limb 1 for grasping and, more important, for propulsion by 'hand over hand' crawling as do many chydorids. To this its undoubted success may well be attributed in part. The incompletely studied feeding mechanism is clearly similar in many respects to that of several other non-filtering species. Secretions of the labral glands are stored in enormous reservoirs that are not confined to the labrum but extend into the head.

IX. ONCHOBUNOPS TUBERCULATUS FRYER & PAGGI, A SPECIES WITH DUAL SPECIALIZATIONS

(i) *Ecology and habits*

Onchobunops tuberculatus (length to 1.1 mm: figures 78 and 79) is a recently described species for which the erection of a separate genus was deemed necessary (Fryer & Paggi 1972). To date it is known only from a single locality in Argentina and is probably a genuinely rare species. It was found only in very shallow water beneath a floating mat of *Azolla* and *Salvinia* which had accumulated in the region of inundation of a large lagoon. The animals were evidently living among the rootlets of these ferns and were not found on the bottom.

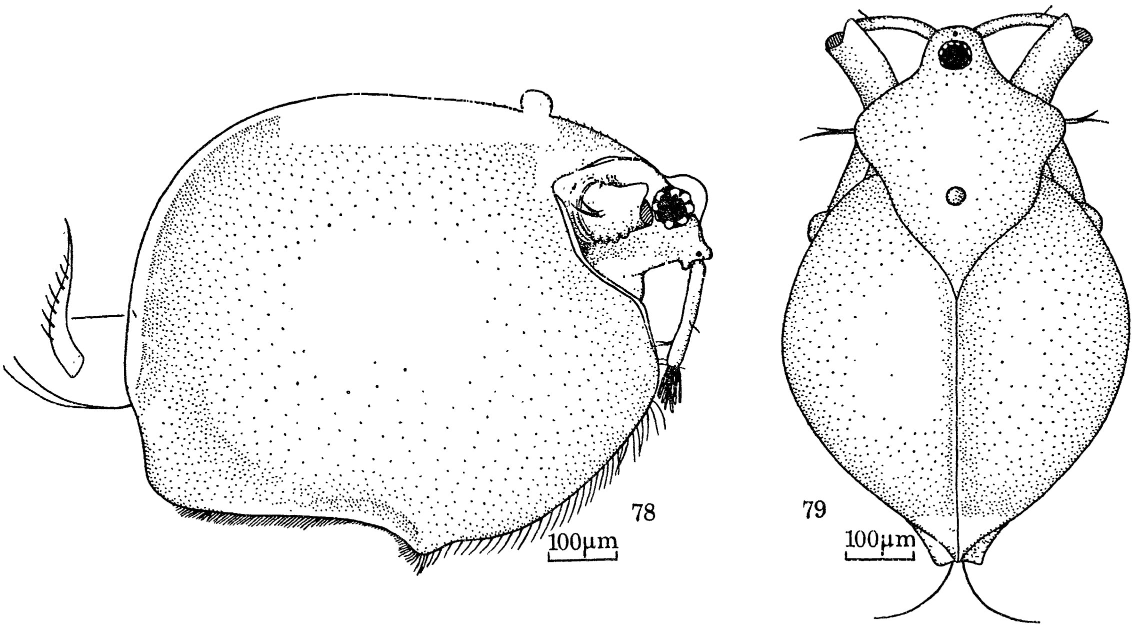
While some of its outstanding specializations are associated with grasping vegetation, *Onchobunops* can also swim steadily, but slowly, and its slender antennae (figure 9 of Fryer & Paggi 1972), which are similar in basic features to those of *Ophryoxus* (figures 19 and 20), save that they have a flexed protopod, are specialized for this and are obviously never used for levering, for which purpose they are totally unsuited. A swimming individual moves slowly through the water but follows a straight, only slightly wavering course if more than a few antennal beats are involved. To judge from the hops made by settled individuals each antennal beat carries the animal forward for about one body length or rather less. Of the complex of movements involved in antennal beat a backward swing in a more or less horizontal plane is the most conspicuous component. A striking attribute, which it shares with *Drepanothrix*, is an ability to swim inverted. The advantages of this to an animal living beneath a floating mat of vegetation are obvious.

Unlike most macrothricids, but like many chydorids, *Onchobunops* habitually frequents and attaches itself to discrete surfaces, in this case vascular plants, as does its relative *Bunops* (Dejdar 1927). For this it has a suite of specializations involving particularly the carapace and first trunk limbs (§(ii)). In its relation to the substratum an attached individual recalls *Lathonura* (§X) and, shape apart, figure 91 gives a good impression of the way in which *Onchobunops* rests on the surface of a leaf. The antennules do not reach the substratum. Attachment – by means of powerful hooks (§(iii)) – is very firm and individuals are loth to release their grasp even when a leaf to which they are attached is moved. Attachment is not confined to flat surfaces, but is practised also on the edges of leaves and other objects. In dishes, lumps of detritus were gripped occasionally: in nature leaves and rootlets of *Azolla* and *Salvinia* must be often grasped. The prime function of the hook-like claws of the first trunk limbs is clearly to grip and it appears that they are seldom used to move the animal forward. Such movement, in small hops, is accomplished by swimming strokes of the antennae.

Unlike most macrothricids *Onchobunops* at times pushes with its post-abdomen. This action may occasionally help it forward and is presumably used should extrication from confined situations be necessary. Such conditions may be involuntarily imposed in nature if wind or waves disturb the floating mat. Thrusting is, however, less vigorous than that observed in *Grimaldina* (§XIV). Individuals move but little when established under congenial conditions and much collecting of food takes place when the animal is stationary.

The food has not been investigated in detail but certainly consists of detrital material scraped from substrates. Particles observed in the gut were in general much coarser than those ingested by most macrothricids. Whether this indicates a distinct preference or is an inevitable reflexion of the habitat in question is not known.

Defecation, which takes place at frequent intervals in a feeding individual, involves but a slight swing of the post-abdomen – a large swing being in any event often precluded by the substratum unless the carapace be lifted. A short faecal ribbon is ejected which is carried away by the current set up by the apparently incessantly beating exopods of trunk limbs 4 and 5. A short ribbon is adaptive. It is easily carried away: a larger ribbon may present disposal problems.



FIGURES 78 AND 79. *Onchobunops tuberculatus.*

FIGURE 78. Adult female, lateral.

FIGURE 79. The same, dorsal.

In each case the antennae are cut near their bases. (From Fryer & Paggi 1972.)

(ii) *Gross morphology and the nature of the labrum*

Of general form (figures 78 and 79) rotundity is one of the most striking features. The broad headshield and specialized cornea-like dome over the compound eye are also noteworthy. Mallory-stained sections show the cuticle of the dome to be similar to the adjoining cuticle and to consist of a very thin outer layer of unstained and a thicker, inner, blue-staining and unsclerotized layer. The ventral carapace margins (figure 80) are highly specialized in relation to a way of life more characteristic of chydorids than macrothricids, though the flanges, so conspicuous a feature of these areas, do not form a continuous level rim as they do in many forms that are associated with surfaces. On each margin are broad anterior (AF) and posterior (PF) flanges, both of which, and particularly the posterior, are profusely setose. Setal insertion on the anterior part of the latter is shown in figure 81. The embayment is wide but of restricted extent, and permits great freedom of action by the first trunk limbs and grants to the second ready access to the substratum.

The labrum is unique among anomopods in having two anterior spikes lying side by side (Fryer & Paggi 1972, figure 10: see also figure 83, AVS). These lie anterior to the first trunk limbs and appear to guard the anterior entrance to the carapace chamber. Notwithstanding the close association with substrata there is a wide gap between the labrum and the surface on

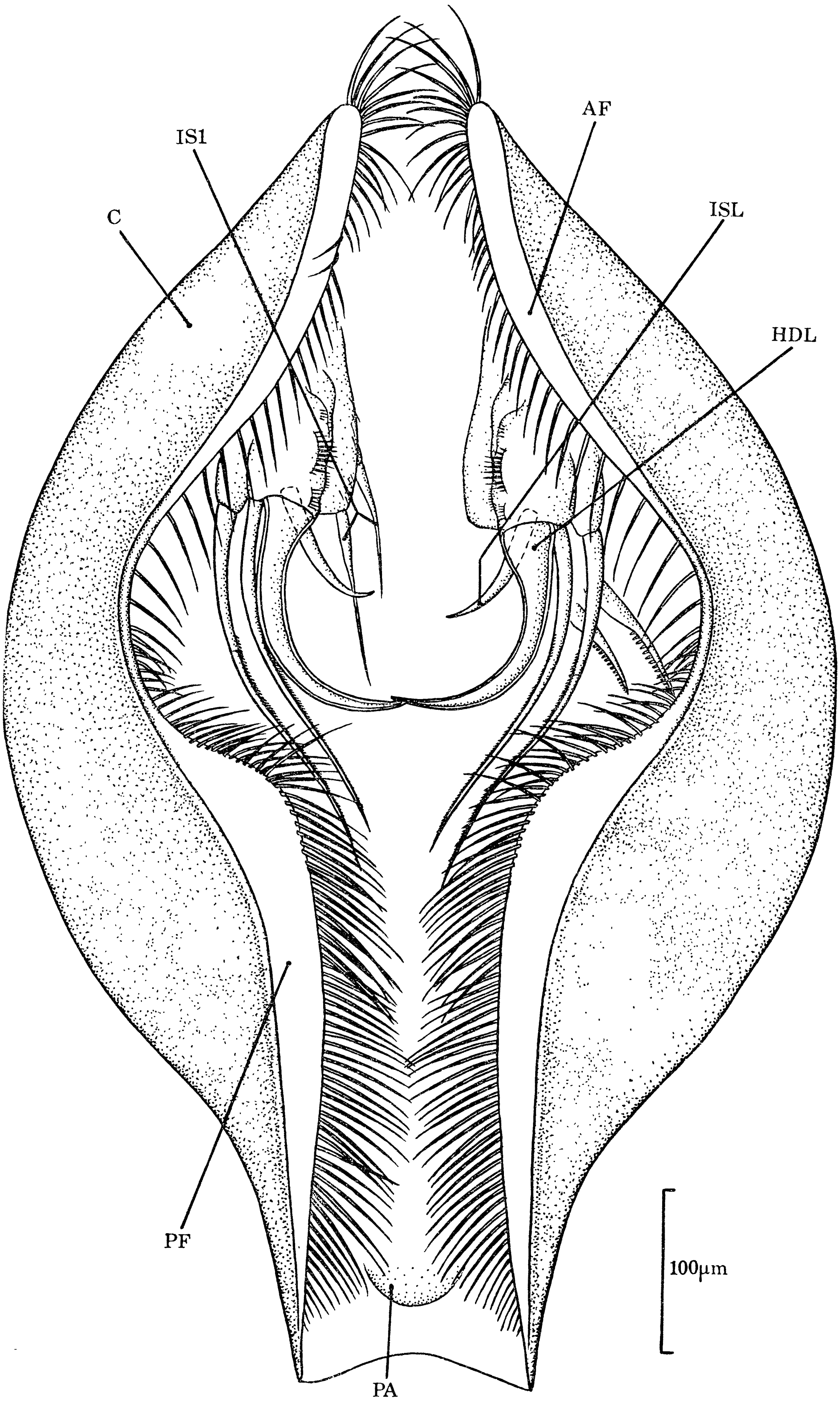
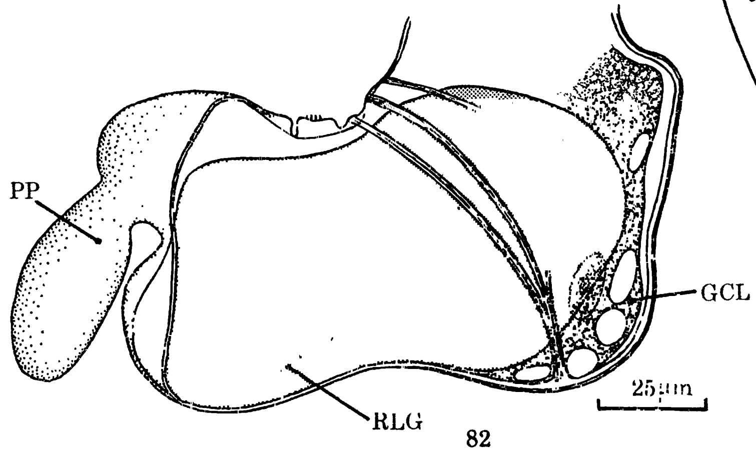


FIGURE 80. *Onchobunops tuberculatus.* Ventral aspect of the trunk region to show the wide embayment bordered by the seta-fringed flanges of the ventral carapace margins and the massive grasping spines of trunk limb 1. On one side scrapers 4 and 5 of trunk limb 2 are shown to reveal their topographic relation to trunk limb 1; otherwise appendages other than trunk limb 1 are omitted.



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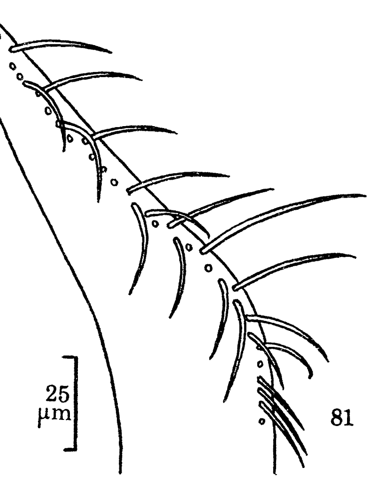

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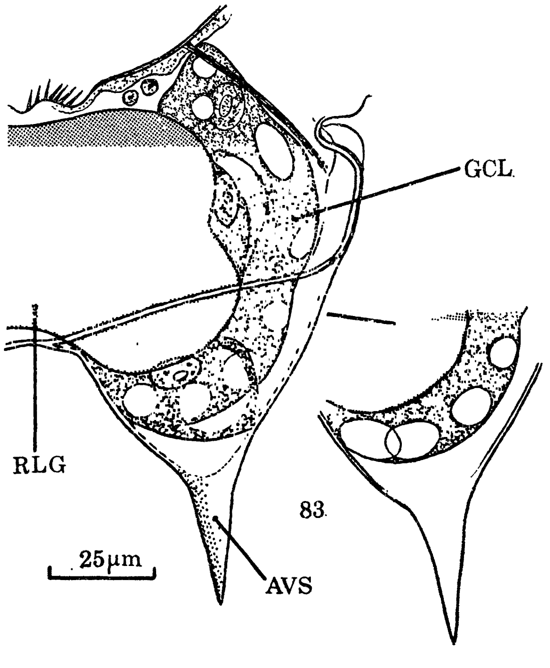

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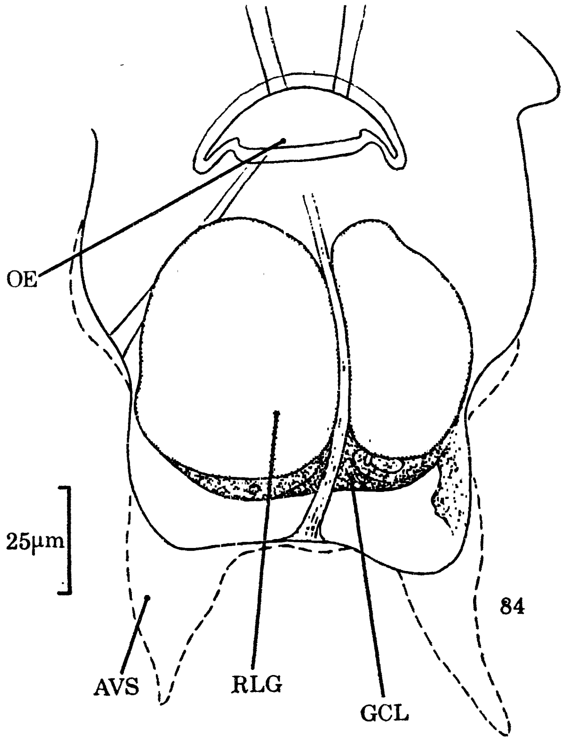

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Figures 81–84. *Onchobunops tuberculatus.*

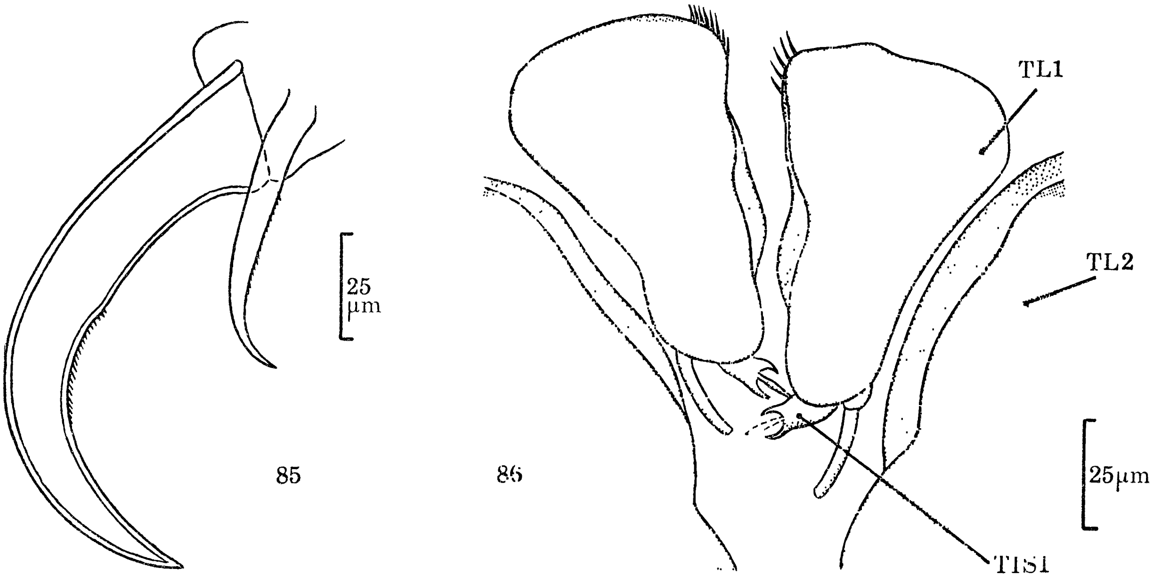
Figure 81. Anterior portion of posterior ventral carapace flange, viewed somewhat obliquely to show the arrangement of the setae, whose point of insertion only is shown in some cases.

Figure 82. Longitudinal section through the labrum to show the extent of the reservoirs and the papillate posterior extremity. For purposes of showing the posterior limits of the reservoir the overlying region has been treated as if transparent. The anterior ventral spikes are not visible in this section, which lies between them.

Figure 83. Longitudinal section through the anterior end of the labrum showing one of the bulky secretion-containing reservoirs (RLG), the mass of anterior gland cells (GCL) and one of the ventral spikes (AVS). The ventral portion is drawn as if transparent to show the cells revealed in a thick section. The inset shows the vacuolated cytoplasm of the gland cells as seen in optical section.

Figure 84. Transverse section through the anterior end of the labrum to show the two reservoirs. The location of the two ventral spikes is indicated from an adjacent section by a dashed line. Other structures are indicated in outline only for topographic purposes.

which the animal rests; this being in contrast to the condition in chydorids with such habits, where a ventral labral keel is regularly present. Posteriorly a papillose projection (figure 82, PP) covered with thin cuticle extends to the level to which the second trunk limbs swing. The labrum contains gland cells (figures 82–84, GCL) presumably homologous with those whose location and histology are admirably described by Cannon (1922) for the daphnid *Simocephalus*.



Figures 85 and 86. *Onchobunops tuberculatus*.

Figure 85. The major grasping spines of trunk limb 1, as seen from beneath, to show the spinules on the inner face of the curve which are not visible in figure 80.

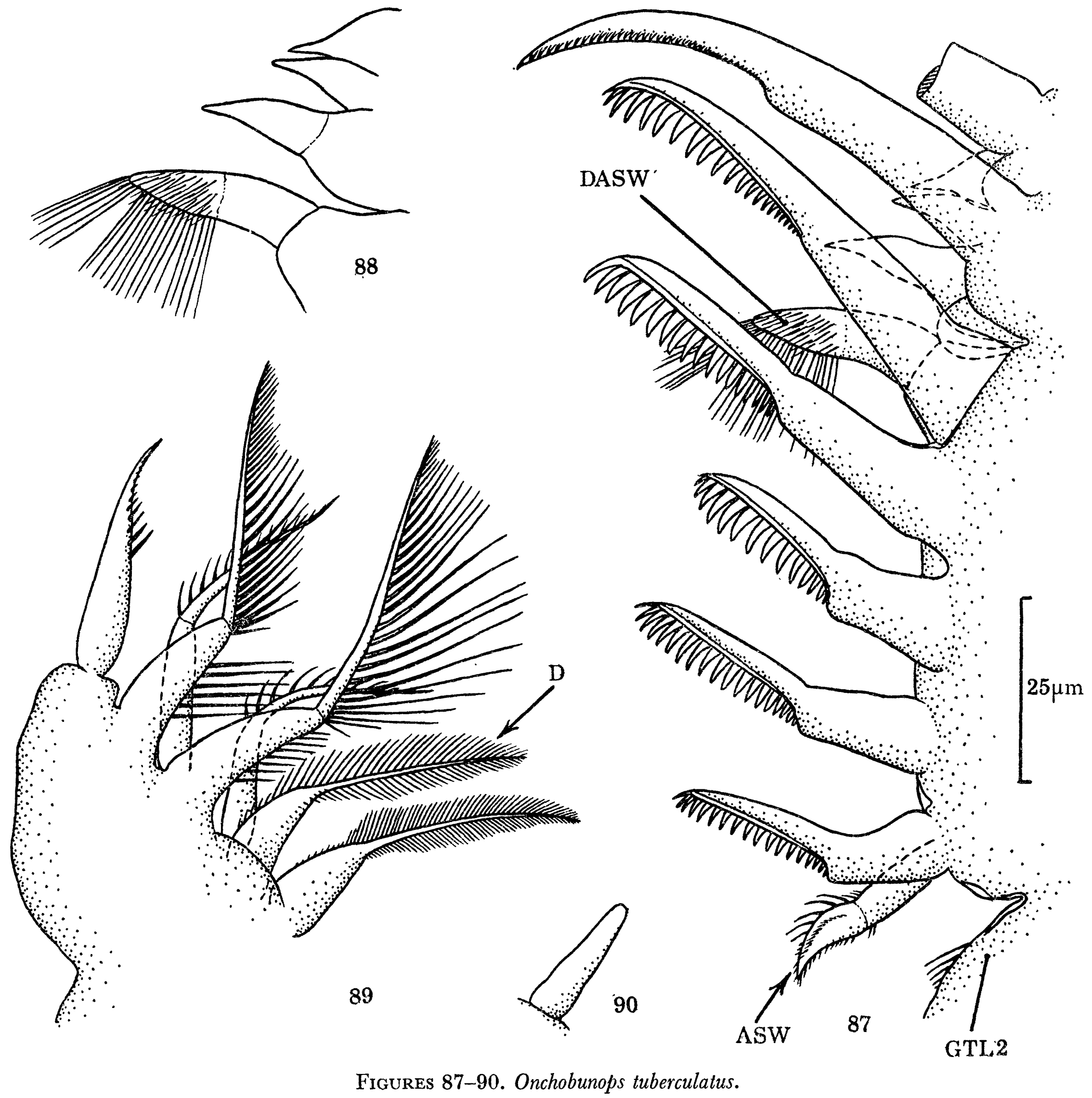
Figure 86. Transverse section through the first trunk limbs, from in front, to show the location and orientation of the trident spines (TIS1). These are directed obliquely posteriorly and here appear considerably foreshortened. In one case the position of the median element – not visible in the thick section – is indicated by dashed lines.

However, these homologies are not easy to confirm for, as in *Macrothrix triserialis* much of the labrum is occupied by two enormous reservoirs (figures 82–84, RLG) whose bulk is such that the gland cells are pushed for the most part into a restricted region anteriorly. These reservoirs probably represent a vast expansion of those which, in several other anomopods, are represented merely by a widened intracellular slit. Adjacent gland cells appear generally to become confluent. Whether the conspicuous cytoplasmic vacuoles of these cells (figures 82 and 83) contain the secretion that finds its way into the reservoirs appears doubtful as these vacuoles are unstained. The secretion in the reservoirs appears more granular and stains more red with Mallory than is the case in other secretion-containing reservoirs so far studied in the Anomopoda, where blue-staining is usual (see especially Fryer 1963) but the amount of material of *Onchobunops* examined is limited. Ducts from the reservoirs have not been traced with certainty nor have liberated secretions that can positively be identified as emanating therefrom been observed, though traces of a blue-staining secretion have been seen near the oesophageal entrance in one preparation.

Other anatomical features, including the antennules, antennae and post-abdomen, are illustrated by Fryer & Paggi (1972).

(iii) *Trunk limb morphology and the feeding mechanism*

The most striking feature of the first trunk limbs is the modification of the spines of the two distal lobes for grasping and not, as in most macrothricids, for food collection. The inner distal lobe (endite 4) bears an extremely stout hook (figure 80, HDL), a smaller hook (ISL), and a long grasping spine armed over much of its length with minute hooklets: the outer distal lobe a long hooklet-armed grasping spine. The tips of the two hook-like spines of the inner distal lobe are used for gripping, and have been seen grasping not only flat surfaces but also a clump of detritus. It is evident that their inner surfaces are also used for this purpose, for here minute



FIGURES 87–90. *Onchobunops tuberculatus.*

FIGURE 87. Scrapers 1–6 of trunk limb 2 and adjacent structures. Note the accessory sweepers (ASW and DASW). The setae of the most proximal sweeper are seen end on and appear much foreshortened.

FIGURE 88. The distal posterior armature.

FIGURE 89. Distal portion of trunk limb 3. Note the difference in coarseness of the filter setae shown.

FIGURE 90. Sensilla, located distal to the gnathobase of trunk limb 3.

spinules, visible only from certain vantage points, are present (figure 85). These must facilitate gripping of the rootlets of the floating ferns among which *Onchobunops* lives.

Every element of the armature of the first trunk limb of *Acantholeberis* (figure 14) has its counterpart in *Onchobunops* and the armature of endites 1–3 is basically the same in each. In *Onchobunops* the inner scrapers of endites 2 and 3 are blade-like (figure 80, IS1), that of endite 1 is the curious, trident-like structure illustrated by Fryer & Paggi (1972, figure 6) whose elaborate form speaks of a specialized but as yet unknown function. These tridents are directed somewhat medially as well as posteriorly (figure 86, TIS1) and, as they lie close together, are presumably more effective than simple spines in preventing any of the large particles scraped by trunk limb 2 from slipping forward between the first trunk limbs. The inner lobe is reduced to a papillose, somewhat setose, projection on which only one soft seta has been detected. Ejector hooks are present.

Trunk limb 2 is a typical raking, sweeping, dragging and pushing appendage which displays certain specializations. External to the scrapers, of which the proximal six are shown in figure 87, are four structures in the vicinity of scrapers 5 and 6 perhaps derived from the primitive row of sensory setae found both in macrothricids (*Acantholeberis*, figure 8) and chydorids (*Eurycercus*, Fryer 1963, figure 25). The most proximal of these (figure 87, DASW) is brush-like, the other three unarmed and possibly sensory (figure 88). Adjacent to the first scraper is a brush-like seta (ASW) which, like the two accessory sweepers in *Lathonura* (figure 98, ASW) clearly helps to bridge the gap between the scrapers of the corm and the gnathobasic armature (cf. also *Guernella*, § XI). This would appear to be the homologue of the guard seta of *Acantholeberis* (figure 8, GDS), and is here referred to as the accessory sweeper. The distal brush-like seta (DASW) is referred to as the distal accessory sweeper but its operation as such has not been observed. The heavy gnathobasic armature is similar to that of many other macrothricids. The anterior gnathobasic setae, of which that adjacent to the food groove is very short, are only five in number, lie more or less at right angles to the corm, and are modified for pushing. Their tips are spiniform and, except for the shortest, finely setose only on that side which faces the food groove (as in *Acantholeberis*, figure 8, and others). The shortest has two rows of fine setules, both of which lie adjacent to the food groove.

Trunk limb 3, the distal portion of whose corm is shown in figure 89, is specialized both for filtering and for moving particles by mechanical means. The gnathobase and outer filter plate each bear six filter setae. In the outer filter plate the most distal seta (D) is much the coarsest; the others are progressively finer, the innermost so fine that its setules are detectable only at high powers. A sensilla (figure 90) is present on what presumably represents the second endite, adjacent to the gnathobase, and a smaller sensilla lies adjacent to seta 3 of the outer filter plate.

Trunk limb 4 is basically similar to that of the likewise filtering *Acantholeberis* (figure 8) though its gnathobasic filter plate is reduced to five setae, the same number as in the outer filter plate.

Trunk limb 5 has a corm similar in essentials to that of *Acantholeberis* (figure 8). It differs markedly, however, in that its gnathobase is devoid of setae (cf. *Grimaldina*, § XIV). As in *Grimaldina* the exopod bears only a single seta but this is large, reaching back to the post-abdomen, is curved, and bears on each side a row of setules that convert it into an efficient paddle. The limb is thus very similar to its homologue in the Daphniidae.

The feeding mechanism has not been studied in detail but the habit, unusual among macrothricids, of gripping with the first trunk limbs while food is collected by scraping with the second pair has been clearly observed, and the principles involved in food manipulation are readily apparent. It is unlikely that active food collection is practised by the third trunk limbs but, as figure 89 reveals, their distal armature is well suited to assisting the transport of material towards the food groove when necessary. Certainly, however, the second pair alone is often capable of the transfer. The filter chamber, similar to that of *Acantholeberis* but much shorter and made up of elements from the third and fourth trunk limbs only, is U-shaped in horizontal section and filters small particles brought against its filters by the respiratory-feeding stream which enters the carapace chamber anteriorly. Labral gland secretions are presumably employed (§(ii)) but this is unproven. All the principles used are clearly the same as in other macrothricids and chydorids with similar apparatus but confirmation by direct observation has not been possible in all cases.

(iv) *Conclusions*

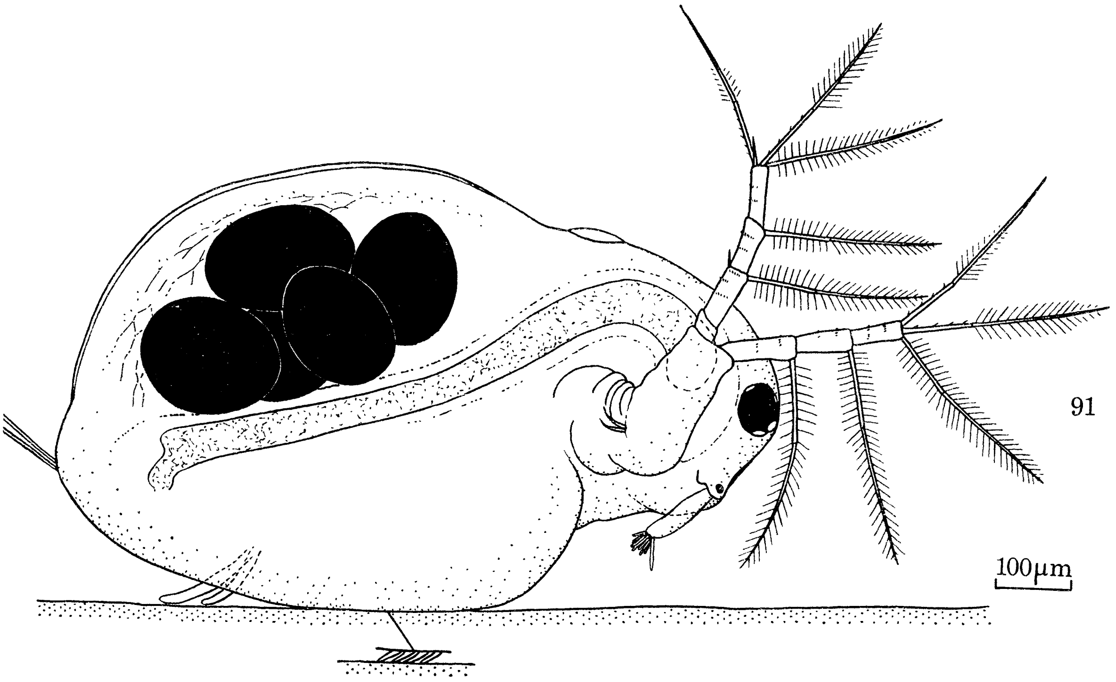
Onchobunops tuberculatus is specialized both for steady swimming, in which it can indulge while inverted, and for intimate association with substrata. Attachment is by means of enormous hooks borne on the first trunk limbs. With this habit are associated complex specializations of the ventral carapace margins. The locomotory function of the first trunk limbs, if any, is slight, forward motion of attached individuals being by means of swimming strokes of the antennae. Food is collected by direct scraping with the second trunk limbs, and manipulated by a combination of mechanical handling and filtration similar to that of *Acantholeberis*. Enormous secretion-filled reservoirs are present in the labrum.

X. THE STRUCTURE, HABITS AND FEEDING MECHANISM OF *LATHONURA RECTIROSTRIS* (O. F. MÜLLER), A SPECIALIZED SUBSTRATUM HUGGER

(i) *Ecology and habits and some related structural peculiarities*

Lathonura rectirostris (length to about 1 mm) is rare in Britain and most of the material used came from a single source, Rydal Water, in the English Lake District. Here it occurs in certain parts of the littoral region where there is a sward of *Littorella uniflora* (L.) accompanied by a few plants of *Lobelia dortmanna* L. growing on a somewhat stony bottom but where there are accumulations of organic detritus. Numbers here fluctuate from year to year and are sometimes low. Earlier, living material collected in Knowsley Park, Lancashire, by Mr A. L. Galliford was used, and the species was also collected in a bog pool over limestone in Ireland where the bottom had a covering of organic detritus. Sergeev (1971) has recently given an account of this species and has brought to light certain important features of its functional morphology and habits, some of which are here confirmed and extended. His animals frequented thickets of *Elodea*, a plant which, like those utilized in Rydal Water, presents an abundance of flat surfaces to an animal the size of *Lathonura*. He also refers to it as occurring in relatively open stands of *Sparganium* and *Menyanthes*.

Unlike most macrothricids, *Lathonura* is a substratum hugger (figures 91 and 92), and its extreme specializations are to a large extent related to its habit of resting ventral surface down and applying its trunk limbs to the underlying material. In this it exhibits certain convergent similarities to the chydorid *Graptoleberis testudinaria* but the method of attachment is very different. Unlike most macrothricids it can move slowly forward while so settled, without assistance from the antennae which are held as shown in figure 91. Swimming is employed for moving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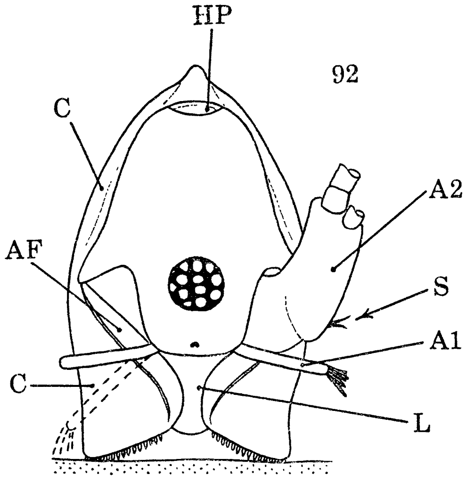
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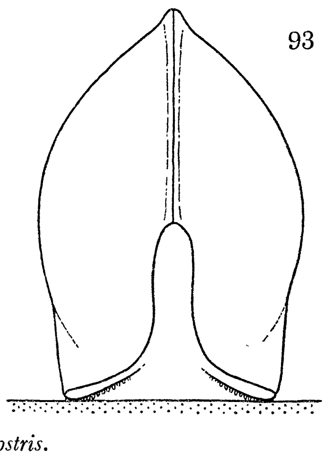
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Figures 91–93. *Lathonura rectirostris.*

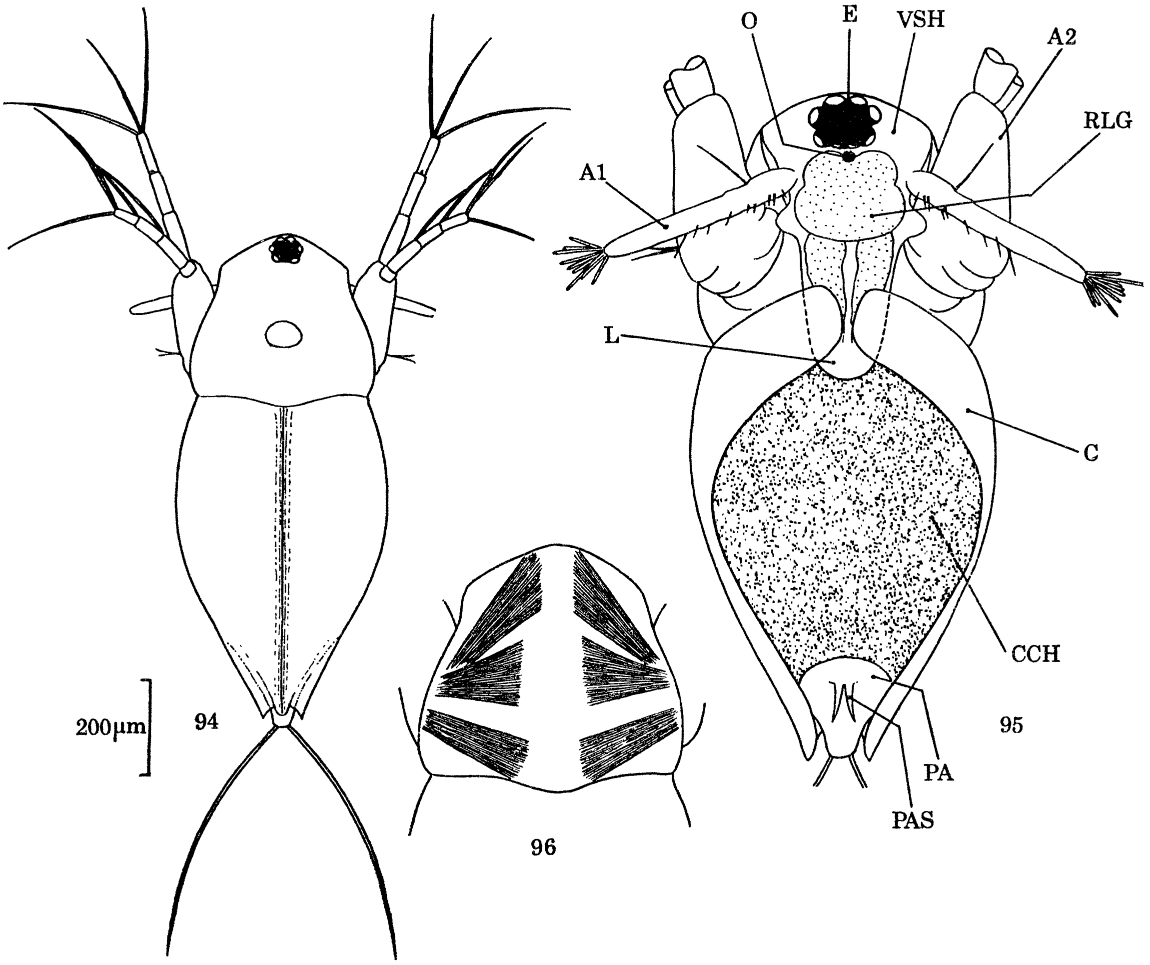
Figure 91. An ephippial female seen from the side as it rests on and moves over a firm substratum. Note the orientation of the antenna, the curvature of whose setae can be appreciated by comparison with figure 94. Because of the angle from which it is seen, the antennule, which is very long (see figure 95), appears much foreshortened. Depending on the angle of view the carapace sometimes, as here, appears to make direct contact with the substratum, at others the setae on which it actually rests can be seen (see inset).

Figure 92. Adult female from in front as it moves over a surface. The right antenna is omitted so that the anterior flange of the carapace is revealed. The antennules, which appear somewhat foreshortened, can be swung so that their sensillae make contact with the substratum as indicated by the right appendage.

Figure 93. Adult female from behind. Post-abdomen omitted.

from place to place. A sudden flick of the antennae causes the animal to hop over the bottom. Antennal movements, which exhibit several specializations, are generally of small amplitude (itself a specialization) and are executed too rapidly to be followed by the human eye. A small amplitude of beat is also shown by the antennae of individuals immersed in a viscous medium, where the motion of the rami is backward, downward and outward. That this is the normal direction of motion is indicated by the arrangement and orientation of the antennal setae and the setules they bear and by the fact that such movements would give the observed forward and upward spring.

In figure 91 most of the antennal setules lie approximately in the plane of the paper or curve somewhat towards the observer and therefore present maximum resistance when the antennae make a backward and outward swing – the movement that propels the animal



Figures 94–96. *Lathonura rectirostris.*

Figure 94. Adult female, dorsal aspect. In brooding females the brood pouch is often more inflated than in this individual.

Figure 95. Adult female, ventral aspect, outline only. Note the enormous ventral gape of the carapace chamber. For details of the carapace margins and the arrangement of the limbs within the carapace chamber see figure 97. Note also the wide lateral span of the antennules, the large labrum extending posteriorly into the carapace chamber beneath the mandibles, and its huge gland cells and reservoirs here sketched as seen in life. The width is slightly accentuated by the pressure needed to hold the animal in the position shown.

Figure 96. Head, dorsal, showing the arrangement of the dorsal extrinsic antennary muscles.

forward. The dorsalmost seta of each ramus is curved towards the observer and their setules therefore offer maximum resistance to the downward component of antennal movement and are the major contributors to lift as the antennae make their basic movement. Antennal action can, however, be modified both by rotation of the protopod and by independent movements of the rami which must allow the downward component to be accentuated when necessary by altering the angle of attack of the setules of most of the setae to give lift as well as forward motion, but details of these subtle changes require specialized equipment for their elucidation.

In relation to habits the antennal setae differ in form and number from those of most other macrothricids. Clearly related to the lack of a need for props, or for levering, and to the lack of any tendency to burrow, is the striking difference between the setae of the two proximal endopod segments of *Lathonura* and of several other macrothricids. In *Lathonura* these are swimming setae similar to their more distal companions: in several other genera, e.g. *Acantholeberis* (figure 1), *Drepanothrix* (figure 40), *Macrothrix* (figure 56), the most proximal is longer and stouter, its segments are ankylosed, and it is devoid of natatory setules. In *Drepanothrix* and *Streblocerus* both are stout and spiniform.

In bearing a seta on the second exopod segment *Lathonura* is unique among European macrothricids and shares this attribute only with the little-known *Guernella* of the Old World tropics (§XI), and the Australasian *Pseudomoina* (§XII). The antennal exopod of most genera bears either terminal setae only (e.g. *Acantholeberis*, figure 1) or these setae plus a seta on the third segment (e.g. *Macrothrix*, figure 56). The possession of this seta, which probably represents the retention of a primitive feature for functional reasons, is clearly related to the presentation of a large surface area to the natatory setae, yet has been lost not only by the most persistent swimmers among the Macrothricidae (*Ophryoxus*, *Bunops* and *Onchobunops*) but also by the predominantly swimming daphnids. *Lathonura* is not a persistent swimmer but probably has to expend more energy over a given distance than a specialized swimmer, and certainly requires a powerful 'heave' to overcome initial inertia (and perhaps to facilitate escape from predators). Such requirements may be better met by the setal arrangement present than by that which, as shown by the daphnids, has been selected as most efficient for persistent swimming.

Cessation of antennal beat by a swimming individual is quickly followed by sinking, during which the trunk rapidly shifts from a horizontal to a vertical position, the antennae serving as parachutes. On touching the bottom an animal may either lie completely inert, often on its side, for some time (for confusion of predators?) or quickly settle ventral surface downwards.

The antennae are not restricted to the ventral and backward sweep that propels the swimming animal and, notwithstanding their flexed protopods, can be swung back so as to wipe the outer surface of the carapace.

In spite of its specializations for swimming, *Lathonura* is reluctant to leave a suitable surface on which it is feeding and often remains there for many hours without using the antennae. On one occasion an individual attached to a leaf fragment remained attached when the leaf was lifted from the water and transferred to another vessel.

A striking attribute of *Lathonura* is that it can move slowly forward without assistance from the antennae. In this it stands in marked contrast to most other macrothricids. Furthermore it can crawl with ease in an inverted position beneath leaves. In addition to being able to move forward with its ventral carapace margins in contact with the substratum it can clamber over irregular objects without such intimate contact (§(iv)) and can negotiate the edge of a leaf and pass from one surface to another.

The post-abdomen is not used for pushing, nor is it used to help support the creeping animal as Sergeev (1971) suggests. Always there is a distinct gap between it and the substratum. It is not even protruded when the animal defecates. Short, compact faecal ribbons are ejected and lie where they are shed. As there is no respiratory current (§(iv)) and as the ribbon lies out of reach of the food collecting apparatus, there is no danger of contamination or re-ingestion even when the animal is moving vertically downwards and the faecal ribbon momentarily lies even within the posterior end of the carapace chamber.

As in many benthic, detritus-feeding anomopods, the food ingested often defies precise definition. Examined gut contents usually consisted of finely comminuted detritus among which many broken diatom frustules were often present, but the indications are that these were mostly collected in this condition and were of no value as food. By virtue of the situations frequented and the means employed for food collection, however, epiphytic algae might be expected to be a more important source of food than in many macrothricids and Sergeev (1971) lists several species which he found in the gut, some in great abundance. He also reports ingestion of the decomposing epidermis of the plants on which it crawls.

(ii) *Gross morphology*

Lathonura has seldom been illustrated, and never in a way which shows its true relation to the substratum. An ephippial female at rest is shown in lateral view in figure 91. The ephippium subsequently shed by this female has been illustrated elsewhere (Fryer 1972). Parthenogenetic females scarcely differ from this in general form. More informative in certain respects are the dorsal (figure 94), and especially the ventral aspects (figures 95 and 97). Anterior (figure 92) and posterior (figure 93) views further clarify the relation to the substratum.

As in *Acantholeberis* there is no headshield, but a well-marked lateral ridge indicates the region from which a headshield develops in certain macrothricid genera. There are no adaptations for pushing, this habit and the specialized orientation of the antennae being mutually exclusive, and the post-abdomen is incapable of providing any motive force. In section the carapace outline is akin to an ogee arch (figure 93), in which respect it shows marked convergent similarity to that of the chydorid *Graptoleberis*. Ventrally the enormous gape – more expansive than that of any other anomopod – is the most evident feature (figures 95 and 97). The trunk limbs, protected ventrally in most species by the carapace, are here largely exposed, and their intimate relation to the substratum is readily apparent.

The ventral carapace margins include a long straight region (figure 91) whose armature is shown in figure 97. Each bears a single row of somewhat swollen setae (MS), about 60 in number, the longest being located posteriorly. It is on these that the animal rests. Posterior to these a row of small spinules extends up each posterior margin. The anterior margins are expanded to form flanges (figure 92, AF) but are unarmed.

The specialized habits of *Lathonura* scarcely involve the head, which lacks a headshield and is also uninfluenced by such specializations as excessive narrowing or modifications for pushing or burrowing which lead to transformations of shape. Consequently its antennal muscles retain what is probably a primitive arrangement. Those which take their origin on the dorsal surface of the head, and can without prejudice to their functions be referred to as dorso-anterior, dorso-median and dorso-posterior extrinsic antennary muscles, are arranged with almost diagrammatic clarity (figure 96).

Of the conspicuous epipodites of the three posterior limbs (§(iii)), that of trunk limb 5 is

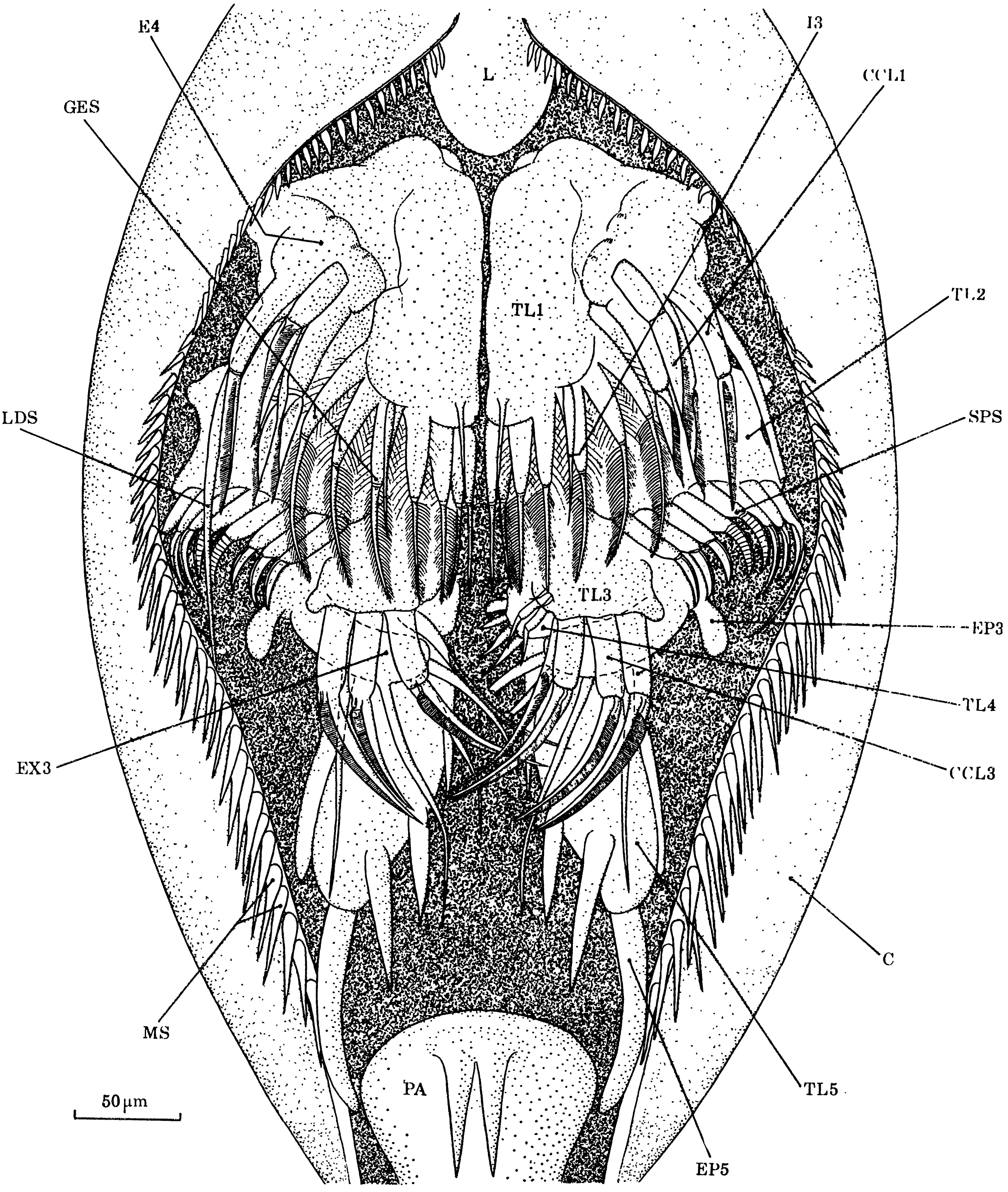


FIGURE 97. *Lathonura rectirostris.* Ventral aspect of the trunk region of an animal lying free. The setae of the ventral margins of the carapace (MS), which in life make contact with the substratum, are here lying free and are directed somewhat towards the observer. In the resting or crawling animal they are directed somewhat more outwardly. The blades of the crawling claws of trunk limb 3 (CCL3) are deliberately shown a little more in face view than they are when the limb is in the position shown. Such a view is usually obtained when the scrapers are swung more laterally. In the position shown the blades lie more at right angles to the observer. Some of the armature of trunk limbs 3 and 4 is omitted on the right-hand limbs, and some setae are cut short for clarity.

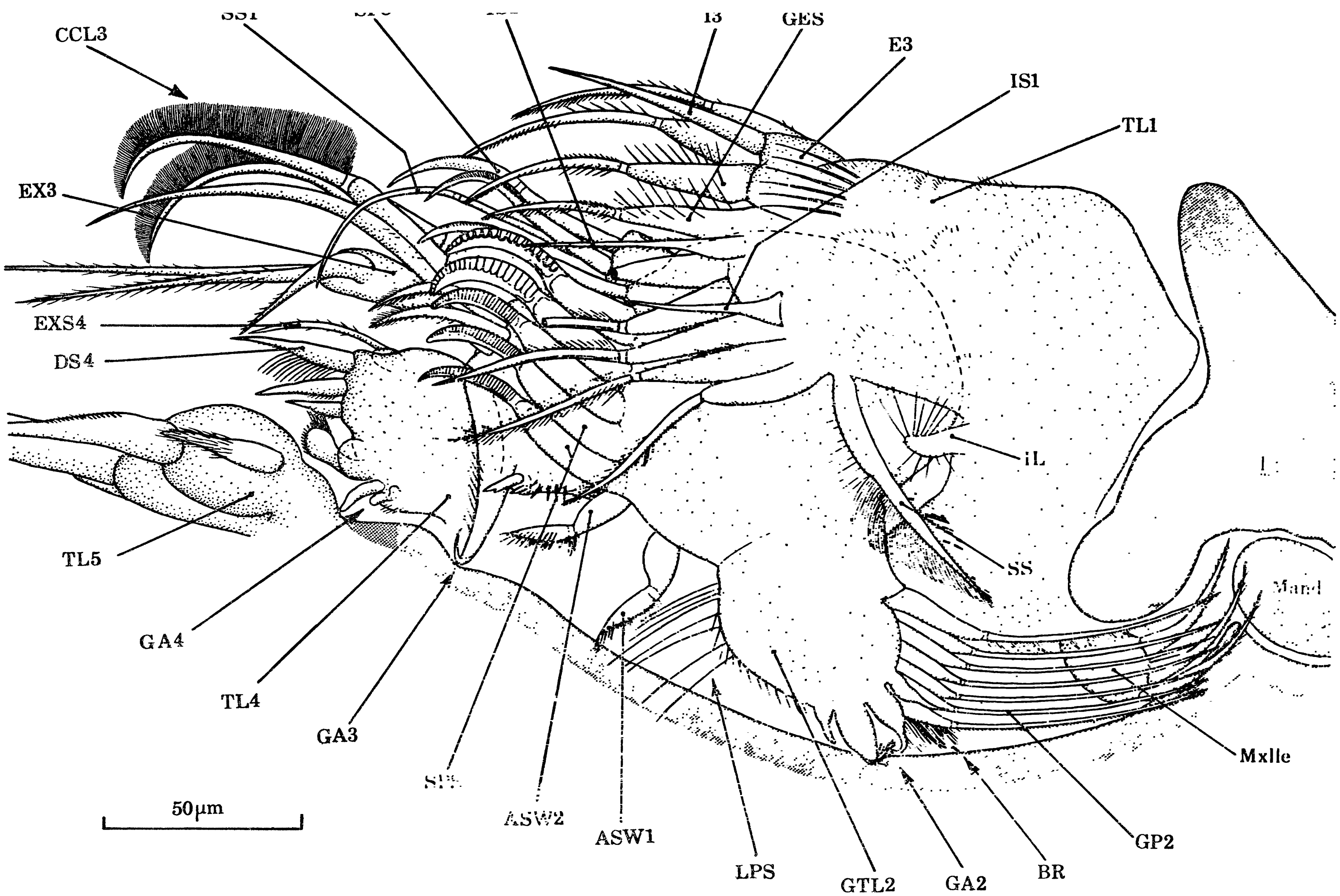
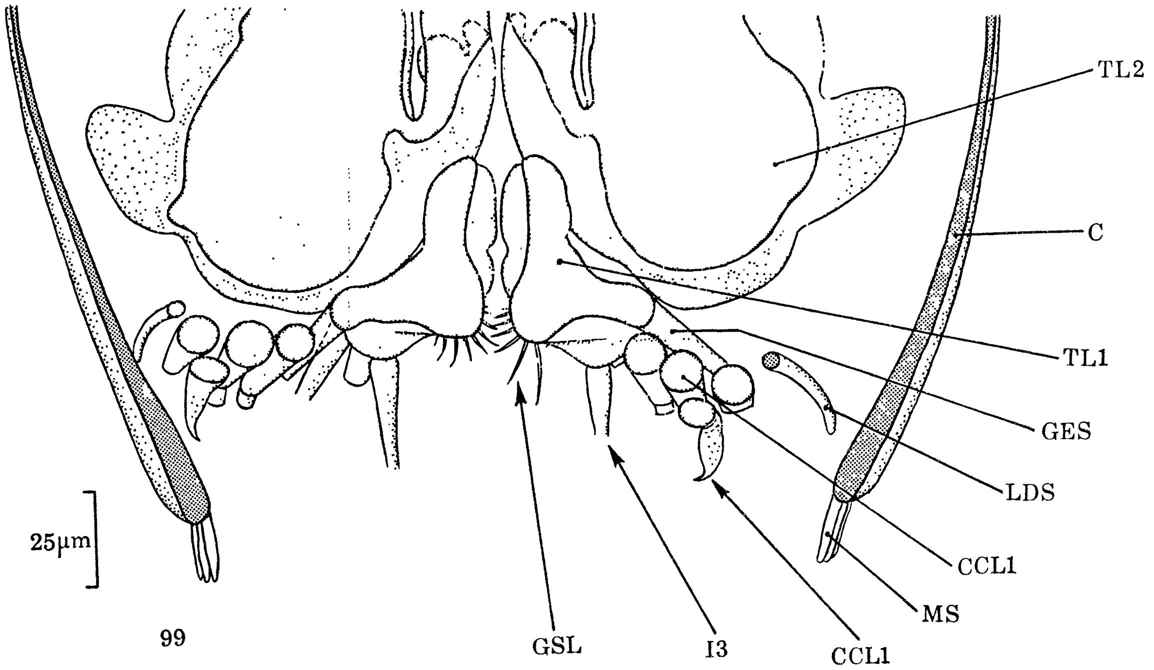
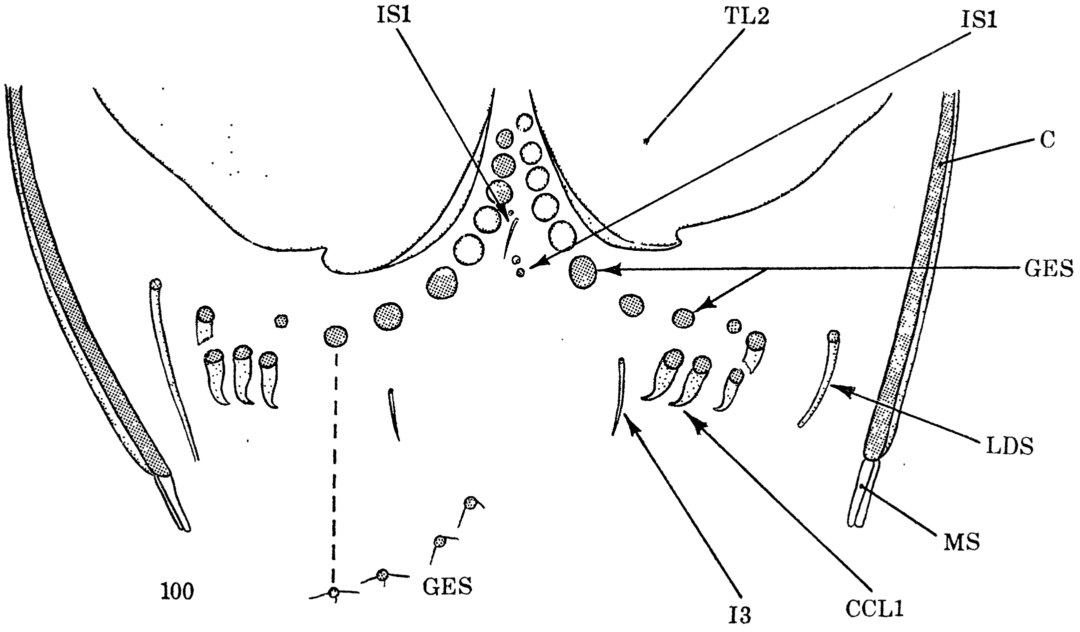


FIGURE 98. *Lathonura rectirostris*. Right appendages viewed from the inner side. The figure is based largely on a dissection, with some details added from sections. In life the posterior trunk limbs are more closely associated than shown here where trunk limb 4 has been swung outwards so that its armature, seen more or less end on, can be more clearly seen. In undisturbed sections it lies so closely adjacent to the scrapers of trunk limb 2 that its nature is difficult to appreciate. Trunk limb 5 has been pulled back and is folded towards the observer so that a ventro-lateral view is obtained. Of the three crawling claws of trunk limb 3 (CCL3) one is omitted for clarity. The crawling claws of trunk limb 1 lie behind the corm of the limb and are not visible in this view (see figure 97). The appearance of most of the ventral elements of the limb armature in lateral and ventral aspects can be readily appreciated by a comparison of this figure and figure 97.





Figures 99 and 100. *Lathonura rectirostris.*

Figure 99. Transverse section through the distal portions of the first and second trunk limbs cutting through the bases of the three dorsalmost crawling claws (CCL1) of trunk limb 1 and viewed from in front.

Figure 100. The same, a little more posteriorly and cutting through the arc of endite spines (GES) of trunk limb 1. (The slice is in fact sufficiently thick for the thickness of these to be revealed in some cases but for clarity this is not indicated.) The inset shows four of these spines more posteriorly.

especially well developed and protrudes from the carapace chamber (figures 91 and 97, EP5). If the epipodites serve a respiratory function, these features are probably related to the lack of a respiratory stream (§(iv)). The enormous head pore (figures 91 and 92, HP) – the largest within the Anomopoda – is probably also respiratory. As sections show, it is spanned by cuticle thinner than that of the surrounding head region and overlies vascular tissue.

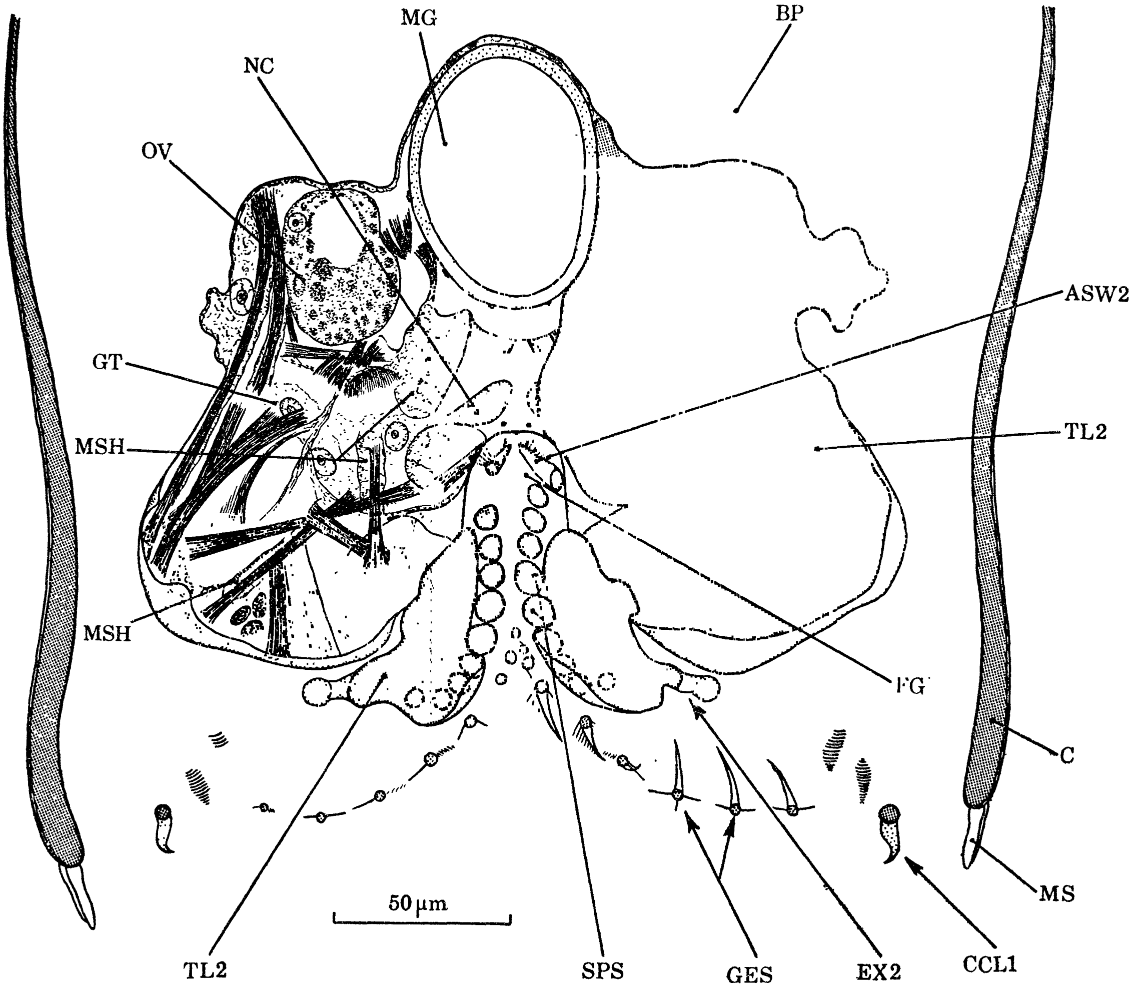


Figure 101. *Lathonura rectirostris*. Transverse section at the level of the scrapers of trunk limb 2, from in front, which shows the arc of guarding endite spines (GES) of trunk limb 1, the distal extremities of some of the crawling claws (CCL1) of trunk limb 1, the location with respect to the food groove (FG) of the posterior accessory sweepers (ASW2) of trunk limb 2, and gives some indication of the internal complexity, especially of the muscular system, of trunk limb 2.

(iii) *Morphology and arrangement of the appendages*

The mandibles exhibit the basic features described in detail for chydorids (Fryer 1963, 1968). The maxillules (figure 98, Mxlle) are typical.

As figure 91 makes clear, the orientation of the trunk, mirrored by the almost straight alimentary canal, is such that its appendages are accommodated in a space, wedge-shaped in longitudinal section. Furthermore the curvature of the food groove (figure 98) is such as to reduce still further the space occupied by the posterior limbs, of which the fourth pair is greatly reduced. The food groove itself is abbreviated posteriorly and, though its limits defy precise definition, terminates at the anterior extremity of the fifth trunk limbs.

While all the trunk limbs are constructed on the basic anomopod plan, several exhibit striking modifications. This is apparent from figure 97. The relations of the trunk limbs to each other and to the substratum, with which all save the fourth make contact, can be visualized by comparison of figures 97–101. An outstanding feature of the first trunk limb is the armature of the inner distal lobe (E4) which lies lateral to the structures visible in figure 98, i.e. below the plane of the paper, and is therefore not to be seen. This is armed with four stout scraper-like spines (CCL1) whose blades lie at right angles to the substratum. Of these, three make up a distinct trio. The only other investigated anomopod to possess similar structures (but which have a different function) is the chydorid *Graptoleberis* in which species, however, only two of the three spines of this lobe are so modified. *Lathonura* shares the possession of four spines by the female with only three other macrothricid genera (§XVII). (Four are sometimes present in the male in which this limb is modified for clasping the female.) In the Chydoridae, irrespective of their function, there are usually three spines, though the number may be reduced for functional reasons, as in *Anchistropus* where only one enormous hook is necessary for gripping its hydrid host. Three spines are also typical in the Macrothricidae. It is the fourth, ventralmost, scraper which is the addition to the regularly occurring trio.

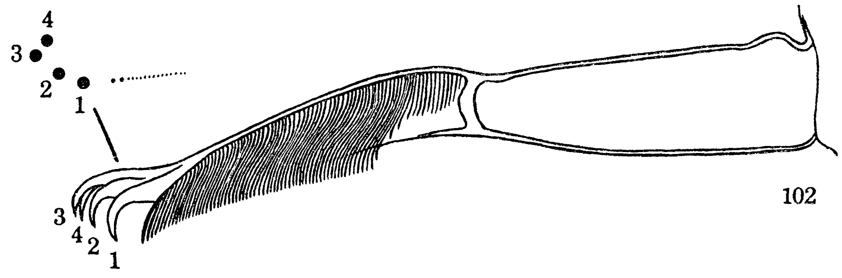
Although scraper-like in appearance, these spines are specialized for a very different function – grasping as the animal is pulled forward – and are here referred to as crawling claws. They also differ somewhat among themselves (figures 102–104). Each bears distally a close-set row of flattened plates that, set transverse to the shaft, makes up the blade (BPT), each individual plate (PT) being shaped as indicated in figures 99–101 and 104, and each having a specialized tip. The tips form a line of minute grasping hooklets (figures 102–105).

All, and especially the innermost of the trio of crawling claws, have specialized tips. The tip of the innermost is expanded into four minute hooks which are spread in an arc in the same plane as the plates of the blade (figure 102). The two distalmost blades are also somewhat modified. The adjacent claws have less elaborate distal specializations (figures 103–104).

The arrangement of the stout backwardly directed spines of the three proximal endites of trunk limb 1 is unique. Nevertheless it is easy to homologize each, and each element of the accompanying armature, with its counterpart in *Acantholeberis* (figure 14) and to assign each to its respective endite. Although in many anomopods the major spines of the proximal endites are arranged in an arc and extend back over the second trunk limb, in no investigated species is this so obvious, or the arc so regular, as in *Lathonura*. This, and the nature of the spines, here called guarding endite spines (GES), is clear from figures 97, 100, 101 and, to some extent, 98. The five outermost (most ventral), which belong to endites 2 and 3, are provided with stout spinules distally (figure 98, and especially figure 97). The arrangement of these spinules is also made clear by figure 100, inset, GES. Passing proximally, the next two spines lie deeper in the carapace chamber. Each has a stiff distal portion provided with a thick cuticle; thus contrasting markedly with the distal portion of the two most proximal spines which are thin walled throughout and brush-like (figure 98). A distinctively armed screening seta (figure 98, SS) is present, as are inner scrapers (IS1) of endites 1 and 2. That of endite 1 is located too deep in the median chamber to be visible in figure 97. That of endite 2 is sparsely setose. Their homologue on endite 3 (I3) is a simple spine.

The inner lobe (IL) is exceedingly delicate and very difficult to locate, being much less easy to observe in dissections than figure 98 suggests. Although carefully sought, no ejector hooks have been found. For the lack of these, a condition shared only by *Neothrix* among investigated anomopods, a functional explanation is suggested in § (iv).

Typically eight scrapers are present on trunk limb 2; here to the outside of the usual series an additional, very long seta (figures 97 and 98, SST) is present. This attribute too is shared with *Neothrix*. In contrast to the generally prevailing situation in which scraper no. 1 is located near to the gnathobase, there is in *Lathonura* a wide gap (figure 98). Arising from the outer face of the corm in this region are two spines, here designated accessory sweepers (figure 98, ASW1 and 2), of which a functional counterpart is known only in *Guernella* (§ XI) and in *Onchobunops*



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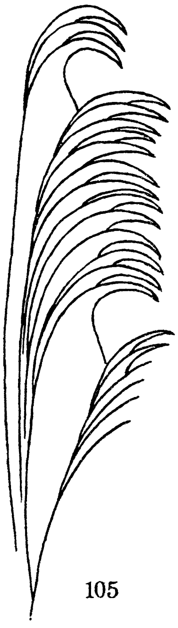

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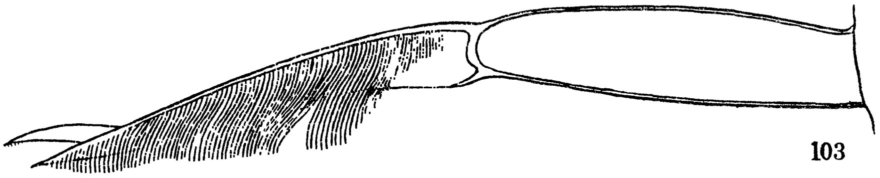

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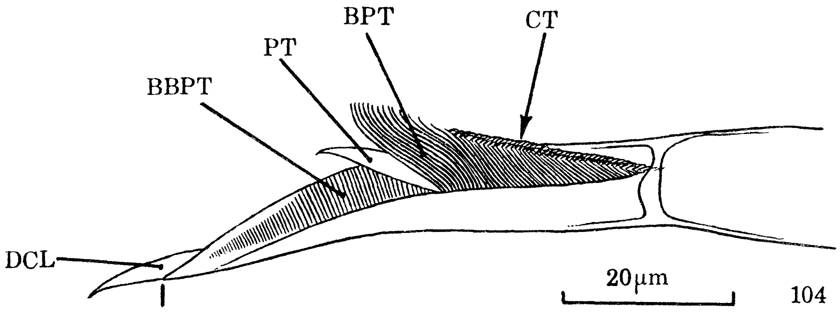

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FIGURES 102–105. *Lathonura rectirostris*.

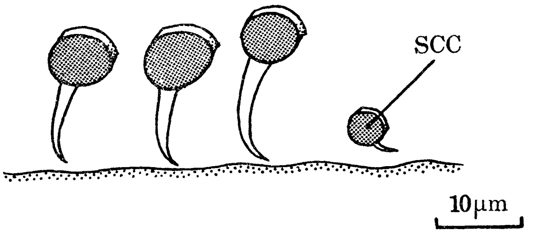
FIGURE 102. Innermost of the trio of crawling claws on the inner distal lobe of trunk limb 1, seen from the side so that the plates of the blade are seen more or less edge on. Note the distal claws. The adjacent dots show diagrammatically in plan view the arrangement of these claws and the grasping tips of the plates in relation to the substratum.

FIGURE 103. Middle claw of the trio, seen from the side. The 'parting' in the blade is a result of mounting.

FIGURE 104. Ventralmost claw; not one of the trio, more or less ventral. The plates of the blade are shown only in the proximal region where they are rising and their tips curving towards the observer. Their width cannot be seen. The most distal plate shown (PT) is displaced and reveals its flattened form. Beyond it no plates are shown but the lines represent the insertion of their bases as revealed by careful focusing. The end of the spine proper is indicated by a vertical line. That part lying distal to this (DCL) is a distal claw.

FIGURE 105. Tips of about a score of adjacent plates of the distal portion of a blade of a crawling claw of trunk limb 1, prepared from a photograph obtained with the scanning electron microscope. The plates are rising obliquely towards the observer.

(§IX) where only one is present. Whether these represent modifications of the sensory setae present to the outside of the scrapers of some species or of the guard seta, or both (see *Acantholeberis*, figure 8, for location), is not clear. Salient features of the gnathobase (GTL2) are shown in figure 98. The spines of the gnathobasic plate (GP2) lie close together and very near to their partners on the opposite limb. Although each of the anterior six is finely setose (shown only on the anteriormost in figure 98) the setules are exceedingly fine and easy to overlook.



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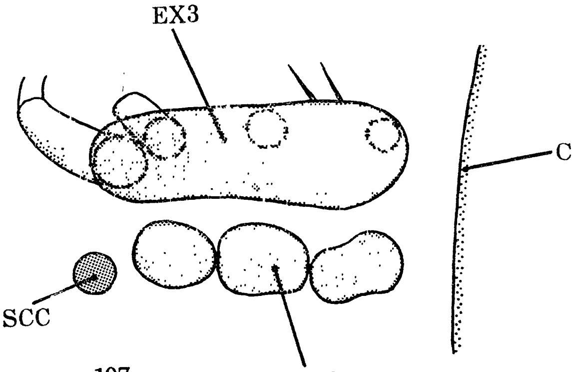

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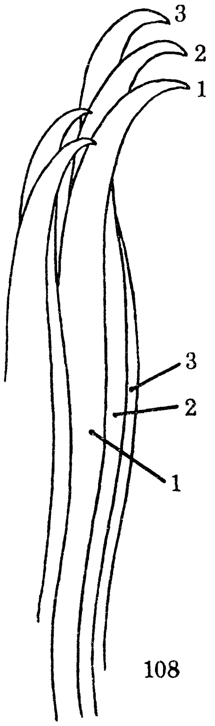

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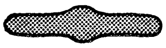


FIGURES 106–109. *Lathonura rectirostris.*

FIGURE 106. Transverse section through the distal portions of the crawling claws of the right trunk limb 3 seen from in front. Slightly simplified. Orientation is dorsal surface uppermost. The surface to be grasped has been indicated diagrammatically.

FIGURE 107. The same, but of the left limb, further forward, cutting through the proximal portions of the crawling claws and also through the exopod (cf. figure 97 for orientation).

FIGURE 108. A group of the individual spinules that make up the blade of the crawling claws of trunk limb 3, based on a photograph obtained with the scanning electron microscope. The spinules are here rising obliquely towards the observer.

FIGURE 109. Diagrammatic transverse section through the basal region of a single spinule (not to scale) to show the strengthening rib revealed in some spinules by the scanning electron microscope.

Those of the posteriormost, which lies nearest to the food groove, are shorter and stouter than those of the rest. All have minute spiniform setules near the tip. The basal portion of the posteriormost is provided on its outer side with long, slender, soft setules which make up a brush (BR) that inevitably sweeps along the median, and particularly the lateral, wall of the food groove as the gnathobase swings forwards. Part of the heavy gnathobasic armature (GA2) also includes a brush (larger than apparent in figure 98 as it is there curved away from the observer). On the posterior face of the gnathobase are several long, presumably sensory, setules (LPS). Sections indicate that these press against the floor of the food groove and presumably convey information to the central nervous system concerning the location of the limb with respect to the food groove.

The third trunk limbs (figures 97 and 98) are greatly reduced proximally and highly specialized distally. The almost complete disappearance of the gnathobasic plate is the outstanding feature of the proximal region (figure 98). Minute setae, detectable only with great difficulty, and which can scarcely be functional, are all that remain to indicate the position of the former gnathobasic plate. The development of enormous broad-bladed crawling claws (CCL3) is the dominant feature distally (figures 97 and 98). These claws, while superficially similar to those of the first trunk limbs, and fulfilling a similar function, differ considerably in detail. They lie approximately parallel to, and the blades which they bear, at right angles to, the substratum with which they are in no way impeded from making contact by the well-developed exopods (EX3) which curve towards the mid-line and lie deeper within the carapace chamber than the blades (figures 97, 98 and 107).

Each blade is made up of numerous elongate spinules (figure 108), flattened, especially proximally, but less broad than the plates that are their equivalents on the first trunk limb. Each spinule has a hook-like tip whose orientation with respect to the substratum is evident from figure 106. In some cases the spinules are strengthened by a rib (figure 109), revealed by the scanning electron microscope, which runs from the base and peters out towards the tip. A spine that arises internal and dorsal to this trio of claws (figures 97, 98, 106 and 107, SCC) also bears spinules whose orientation is such as to permit them also to grasp the substratum (figure 106).

(iv) *Crawling and feeding*

The wide gape, extensive straight regions of the ventral margins, and specialized marginal setae permit effortless balance on any reasonably flat surface provided the slope is not excessive, and the first two features at least presumably represent early specializations to the present way of life. These could not of themselves, however, permit what amounts almost to gliding over surfaces while inclined at various angles or inverted beneath suitable objects. Such an ability demands an efficient means of attachment such as is provided by suction in the chydorids *Alonella exigua* and *Graptoleberis testudinaria*. *Lathonura* lacks the means of providing and maintaining such suction and, as Sergeev (1971) has shown, attaches itself by purely mechanical devices. What superficially resemble scraping blades borne by the crawling claws of the inner distal lobe of trunk limb 1 are in fact close-set rows of minute hooks whose arrangement (§ (iii)) permits hundreds of which to grip the material on which the animal is resting. Further, the blades are so arranged that the pull of the hooks is in part towards the mid-line and each set thus pulls towards that of the opposite limb. The effectiveness of the grip of these claws is clearly revealed by comparison of individuals resting on a leaf and on a glass surface. Scraping by the second trunk limbs does not affect the stability of animals attached to a leaf: individuals resting on glass, which cannot be effectively gripped, wobble considerably as scraping takes place. Whether the blades of the crawling claws of trunk limb 3, which assist in locomotion, are important for attachment when the animal is moving over flat surfaces is uncertain though they grip the substratum when it negotiates the edge of a thin flat object (see below).

Forward progression is achieved by a pull exerted by the first trunk limbs and by pressure exerted by the third – a form of quadrupedal gait unique within the Anomopoda. In exerting a forward pull the first trunk limbs behave as they do in many chydorids, but the amplitude of movement here is very small; so small as to be almost imperceptible at times. Forward movement of the limb, which takes place after the animal has been dragged forward for a very short distance, is also accomplished with great rapidity. The conspicuous forward reach seen in many chydorids is not practised. Similarly the amplitude of movement of the third trunk limbs is very small. Here the three crawling claws are spread so that the edges of their blades are in contact with the substratum (figure 106) against which, because of their orientation, they push rather than pull. In this they are assisted by the supplementary claw (SCC). There is no regular sequence of movement of trunk limbs 1 and 3 though on an even surface such a sequence may be established for several successive 'steps', and usually the forward movement of one pair of appendages is matched, after a momentary pause, by that of the other. This moves the animal forward in many small increments, each of which probably does not as a rule exceed 3 or 4 % of the animal's length and is sometimes less than this, but precise measurements have not been made. The rate of forward movement varies considerably according to the nature of the surface and the amount of food present but is seldom faster than one body length per minute in adults. Sergeev (1971) gives rates of from 0.14 to 0.65 mm/min at about 20 °C and notes that animals may remain stationary for several minutes.

Such locomotion can be practised as the animal clings, inverted, to the underside of a leaf, the mechanism being precisely the same as that used by a tree creeper (*Certhea familiaris*) as it creeps along the undersurface of a horizontal branch. In each case claws grip the substratum while a counterthrust is provided, in the bird by the stiff tail feathers, in *Lathonura* by the carapace. Even if, as seems possible, the claws of the third trunk limbs are not particularly effective in gripping, momentary release of the grip of the first trunk limbs by *Lathonura* need have no serious consequences as its density is but little greater than that of water. Unlike a tree creeper, which rarely moves down a tree trunk, *Lathonura* can move vertically downwards with ease.

The long seta of the outer distal lobe of trunk limb 1 is not involved in locomotion, but appears to explore the substratum. At times it protrudes laterally, passing between or beneath the carapace setae in order to do so – thereby illustrating the mobility of the cushion which these form between carapace and substratum. The long exopod setae of trunk limb 3 curve ventrally and their tips make contact with the substratum. The large swollen distal setae of trunk limb 5 also touch the substratum and perhaps grant some degree of stability, and the large epipodites of these limbs also make contact but are too soft to fulfil a similar role.

While progression is usually as described, individuals at times crawl to the edge of a leaf fragment so that as much as half those portions of the carapace margins that normally make contact with the substratum protrude. At such times the crawling claws of the first trunk limbs may protrude ventrally and only their tips grip the substratum – the efficacy of the minute distal hooks being thereby demonstrated. Even under these circumstances the long external seta is not employed for grasping. At such times the crawling claws of trunk limb 3 certainly grip, and exhibit greater mobility than is called for during normal locomotion. According to Sergeev (1971), if *Lathonura* crawls along a stem whose diameter is small relative to itself, the carapace margins are drawn somewhat towards each other.

By virtue of its widespread antennae (figures 91 and 94) *Lathonura* is not adapted for penetrating gaps among vegetation, as are several crawling chydorids, which either use the antennae for scrambling in such situations, fold them back alongside the carapace, or tuck them inside the carapace chamber (Fryer 1968). Sergeev (1971), impressed by the moderate bilateral compression of the body, implied that it is so adapted but acknowledges that bilateral compression is much less than in many chydorids. Equally it lacks the means of exerting force against obstacles by levering with the post-abdomen. The antennae encounter some obstacles before the antennules, the reverse of the situation in crawling chydorids. Exploration ahead by the antennules would demand excessively long appendages even if they were sited at the anterior extremity of the head. Instead they extend laterally and are largely protected by the antennae. While mobile they are often held at such an angle that their sensillae do not make contact with the substratum (figures 91 and 92). An earlier warning of the approach of a predator from behind is given by the post-abdominal setae than in chydorids with similar habits (cf. the long setae shown in figure 94 with the shorter setae of *Peracantha truncata*, *Alonella exigua* and *Graptoleberis testudinaria* in figures 35, 50 and 63 respectively in Fryer 1968).

As Sergeev (1971) has shown, no currents pass through the carapace chamber, and food is collected and manipulated by purely mechanical means. It is collected by vigorous scraping movements of the second trunk limbs which swing at rates of up to 200 cycles/min in juveniles but usually little more than half this rate in adults, the rate varying according to circumstances. Material coming within the field of operation of the scraping spines of these limbs has already passed beneath the arc of backwardly directed guarding endite spines (figures 97, 100 and 101, GES) of each first trunk limb. These form a protective grid which prevents food material from entering the median inter-limb chamber anterior to the scrapers of the second trunk limbs, where its presence would be an embarrassment. The development of this screen can be correlated, perhaps directly, with the absence of any means of removing material from the space between the first trunk limbs, and with the restrictions placed on the freedom of movement of these limbs by the methods of attachment and locomotion. Attachment necessitates almost constant gripping and prohibits such movements of the first trunk limbs as are available both to crawling chydorids and macrothricids and to macrothricids that collect food by outreach of the distal lobes of these limbs – though it does not restrict independent movement of the corm entirely. This appears to have led even to the loss of ejector hooks (a condition otherwise known only in *Neothrix*). As the post-abdominal claws cannot be used to clear the inter-limb space, and as no currents are available for hydraulic scouring, it is imperative that food material be excluded, and it is suggested that this is the major function of the arc of guarding endite spines. Confirmation of the importance of excluding particles is provided by the careful guarding of the median gap between the antero-ventral portion of each corm, which lies near the substratum, by an arc of long guard setules (figure 99, GSL).

Because of its proximity to the scrapers of trunk limb 2, the arc of guarding endite spines of trunk limb 1 must in general also prevent the scrapers from encountering large 'awkward' objects, the scraping of which could more easily lead to dislodgement than in species gripping with powerful claws, and which are no embarrassment to species that feed while lying free. This does not mean that clumps of food are not dealt with at times.

Because the lobe (endite) of trunk limb 1 that bears the scrapers can move independently of the rest of the limb it is possible for the animal to grip the substratum and still move the corm of the limb to some extent. This ability was once seen to be utilized to enable the first trunk limbs to turn around an encountered clump of material. The ventralmost inner spines (figure 98, IS1), and perhaps the inner spine of endite 3 (I3), were probably the main tools used but this could not be seen clearly.

Scraping by the second trunk limbs is performed with the usual complex anomopod movement that includes a transverse and dorsal swing of wide amplitude. Superimposed on this are additional dorsal and forward components of motion, the whole limb being dragged towards the trunk with an almost snatch-like movement, which at the same time rams the gnathobase forward. Some indication of the complexity of the muscular system involved is gained from figure 101, which shows only part of the whole.

Notwithstanding the enormous swing of trunk limb 2 (figure 97 shows the scrapers before the working stroke begins; figures 98 and 101 near its end) the gap between the scrapers and the gnathobasic armature (greater than in any other studied species) is such that an efficient bridging is accomplished only by virtue of the accessory sweepers (figure 98, ASW1, 2). The way in which these sweep along the food groove is clearly seen here and in figure 101. Anteriorly the gnathobasic armature carries food forward to the maxillules and mandibles in the usual way by purely mechanical means.

Usually the second trunk limbs alone scrape the substratum, and indeed scraping and forwarding of the collected food sometimes takes place without apparent movements of other limbs. Very occasionally, however, the conspicuous scraper-like crawling claws of trunk limb 3 swing in an arc towards the mid-line in a manner suggestive of scraping. As the surface swept is flat this is essentially a two-dimensional movement. Such sweeping, though rarely observed, may take place with great vigour and with swings of wide amplitude. Although impressive when seen, it is extremely doubtful whether this activity contributes to food collection and, even if it does, it is certainly not a regular component of this process. Except when the animal first settles, the ground over which trunk limb 3 sweeps during such swings has already been effectively scraped by trunk limb 2 and little or nothing will remain to be collected. Further, it is extremely doubtful whether, unless they operated considerably out of phase, which they have never been seen to do, these scrapers could carry material sufficiently far forward to come within the orbit of trunk limb 2 – the only effective means of transporting it further. Finally the scraper-like spines have a well-defined role which they could not fulfil if they served to collect food material. The purpose of the large, rarely observed swings, remains unknown but is perhaps connected with grooming, possibly of the deeper lying portions of the limbs.

The more proximal parts of trunk limb 3 play a very minor role in food manipulation but the reduced gnathobasic armature probably makes a very small contribution to the anterior movement of material along the food groove at times. According to Sergeev (1971) the exopods of the third trunk limbs play a part in ejecting unwanted material beyond the limits of the carapace, but this I have not observed.

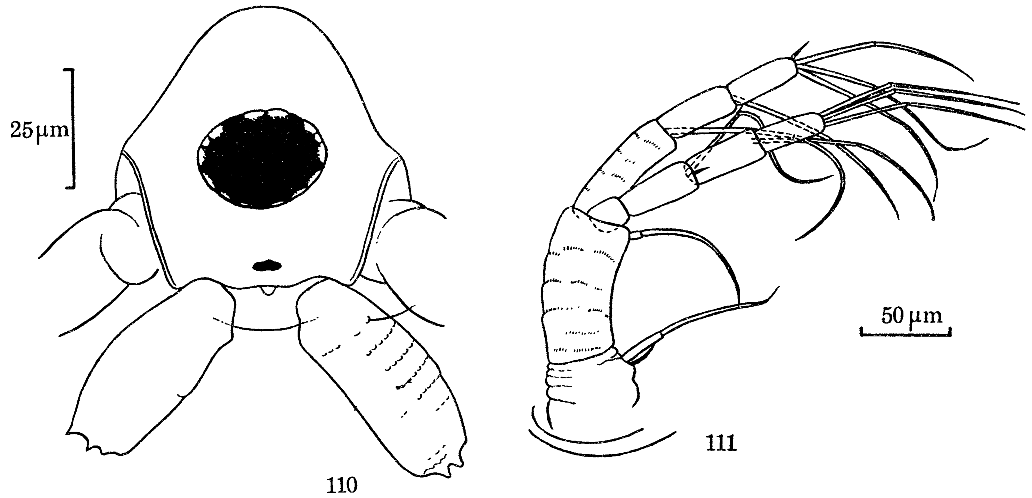
Although trunk limb 4 is by no means always involved, it from time to time swings so that its armature moves essentially towards the mid-line and food groove as in other chydorids and macrothricids. As very little food material ever seems to lie posterior to trunk limb 3 its role is slight and it is not equipped to push large accumulations along the food groove.

From the point of view of the feeding mechanism the fifth trunk limbs are passive barriers at the posterior end of the food groove in the vicinity of which, and at a deeper level than can be seen in figure 97, their swollen basal portions meet in the mid-line.

Although labral gland secretions are produced and there is a large reservoir for their storage (figure 95) these cannot escape from the anterior end of the food groove. Thus, in contrast to chydorids such as *Eurycercus* (Fryer 1962, 1963) and *Alonopsis* (Fryer 1968), where filtration is employed and secretions are used to entangle particulate matter at the posterior end of the food groove, food is passed without such assistance almost to the mouthparts.

(v) *Conclusions*

Lathonura rectirostris is highly specialized for creeping over and removing food from surfaces, and can do so while inverted provided the surface can be gripped by the numerous hooklets with which unique crawling claws of the first trunk limbs are provided. These operate in conjunction with the highly specialized ventral margins of the carapace, and, perhaps always, with scraper-like crawling claws of trunk limb 3 the edges of whose blades also grip the substratum. The ventral gape is the widest of any macrothricid. Crawling and feeding are intimately related and feeding is almost certainly impossible if attachment to a suitable substratum cannot be achieved. Forward movement is effected by dragging with the first and pushing with the third trunk limbs. Such quadrupedal locomotion is unique within the Anomopoda. Individual increments of movement are very small. The antennae play no part in crawling but are more specialized for swimming than those of many macrothricids. There is no feeding-respiratory current. The second trunk limbs are used for food collection and are the prime agents in its subsequent manipulation.



FIGURES 110 AND 111. *Guernella raphaelis.*

FIGURE 110. Head and antennules as seen from in front. The sensillae of the antennules are omitted.

FIGURE 111. Antenna. Some of the setae bear long setules but many appear to have broken off in the available material and their exact arrangement is unknown.

XI. A NOTE ON *GUERNELLA RAPHAELIS* RICHARD

The minute *Guernella raphaelis* (length to *ca.* 0.4 mm), of which according to Thomas (1961) *G. ceylonica* Daday is a synonym, is known only from a few localities in tropical Africa, India, Ceylon and New Guinea. Nothing is recorded about its habits and little about its ecology save that Thomas (1961) found it in shallow swampy situations in Uganda and that this appears to be in keeping with one of the situations from which Daday (1898) obtained material. Mr Thomas kindly presented me with the few preserved specimens in his possession. Information gleaned from these suggests that *Guernella* swims, probably in hops, over the bottom. The head (figure 110) is broader than might be suspected from available illustrations of the lateral view and is provided with a distinct headshield whose thickened rim does not, however, extend very far laterally. There are no anatomical features to suggest that it rows into deposits; indeed the reverse is the case, and the post-abdomen is minute and certainly not used for pushing (cf. *Neothrix* §XIII). Apart from a few minute setae posteriorly, the ventral carapace margins are unarmed – an unusual condition which perhaps suggests that it frequents areas where the bottom is covered with decaying vegetation rather than fine particles. There are wide flanges along the anterior margins.

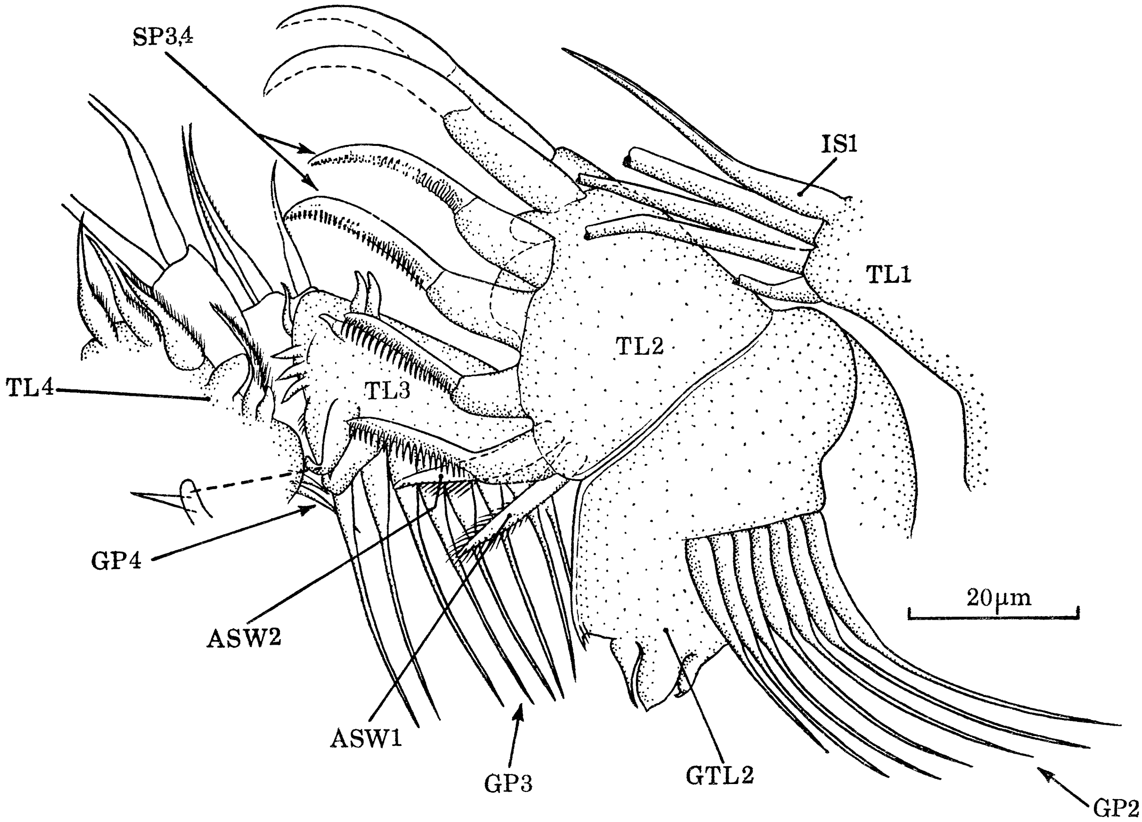


FIGURE 112. *Guernella raphaelis*. Details of those parts of trunk limbs 2, 3 and 4 that border the median chamber, as seen from the inside after dissection. The spatial relations of trunk limbs 2 and 3 and the orientation of the distal and lateral parts of trunk limb 3 have been somewhat disturbed during dissection but the important relation of the accessory sweepers of trunk limb 2 (ASW1, 2) to the gnathobasic plate (GP3) of trunk limb 3 shows little, if any, distortion. The inset shows the tip of one of the heavy gnathobasic spines of trunk limb 3 as seen from a different angle.

The antennae (figure 111) are provided with the same complement of swimming setae as *Lathonura* and *Pseudomoina*. That this is possibly of phyletic significance is supported by the fact that, as in these genera, there are four spines on the inner distal lobe (endite 4) of trunk limb 1, these being similar to those of *Pseudomoina* (§XII). There is also a conspicuous dorsal organ (head pore) as in *Lathonura*.

The nature of the median chamber is shown in figure 112, which also reveals salient features of the trunk limbs. Reduction of the posterior limbs is apparent. Whether trunk limb 5 participates is not clear but it retains a long vertical seta such as helps to seal the chamber posteriorly in some species. The gnathobasic plate of trunk limb 4 (GP4) is reduced to two minute setae. Trunk limb 3, on the other hand, has a well-developed gnathobasic plate (GP3) which evidently acts as a chute to guide particles towards the food groove. Associated with this, and clearly used for brushing such particles, are two accessory sweepers (ASW1, 2) on trunk limb 2, remarkably similar to those of *Lathonura* to whose median chamber that of *Guernella* bears a general overall resemblance save that the gnathobasic plate of trunk limb 3, so well developed in *Guernella*, is virtually absent in *Lathonura* (cf. figures 98 and 112).

A striking feature of trunk limb 1 is the massive development of the ejector hooks which are, relatively, the best developed of any macrothricid. Only observations on the living animal can reveal the significance of their great size, though their function is clear. Whether, as seems likely, *Guernella* grips material with the armature of the outer lobe of trunk limb 1 remains to be ascertained, but food particles are obviously whisked into the median chamber by trunk limb 2, perhaps with assistance from the inner spines of trunk limb 1, which are well developed (figure 112, IS1), and passed forward by mechanical means.

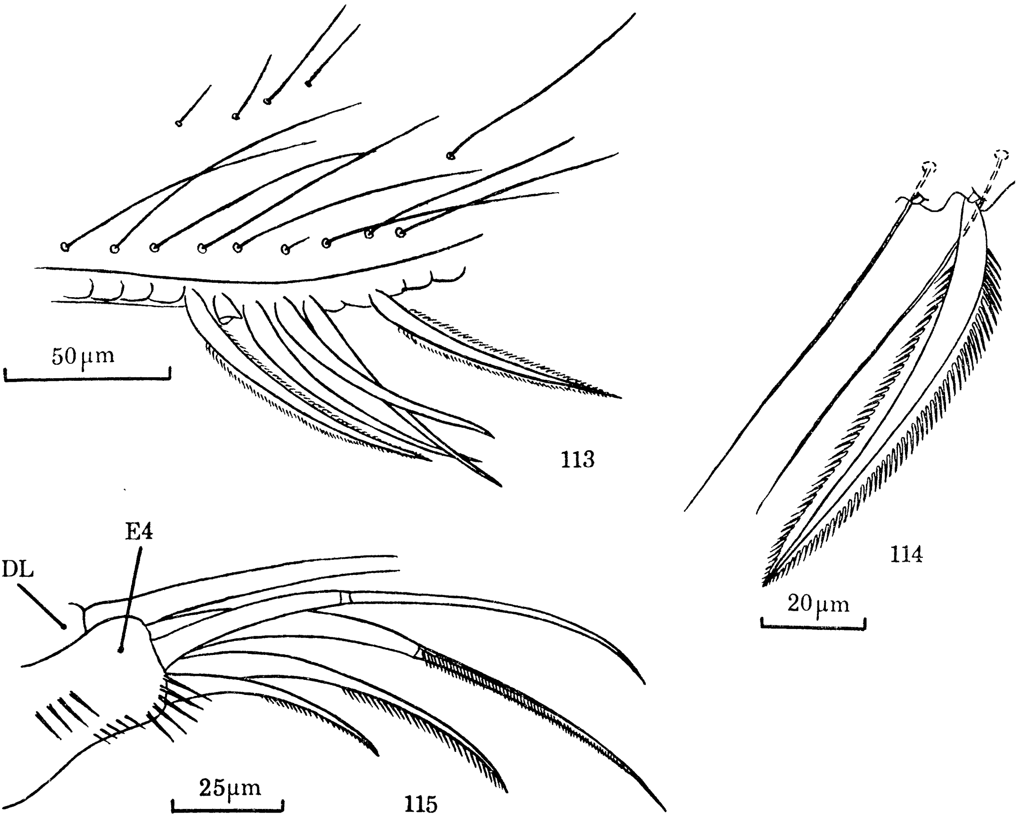
Other data on *Guernella* are presented in table 1 (p. 262) and its possible affinities are discussed in §XVII.

XII. A NOTE ON *PSEUDOMOINA LEMNAE* (KING)

This species, which attains a length of 1.2 mm and appears to be restricted to Eastern Australia and New Zealand, was originally described as a daphnid under the name *Moina lemnae* by King (1853), but was shown to be a macrothricid by Sars (1912) who made clear many of the salient features of its anatomy. A re-description has recently been given by Petkovski (1973). The information given by these authors and that gleaned from some preserved material given to me by Dr N. N. Smirnov enables certain features of the genus to be assessed in an evolutionary context, but information on habits is as yet almost entirely wanting. Ecology and habits are mentioned only by King (1853), who merely records that it was found among *Lemna* and that its 'habits are rather sluggish'. Petkovski's material came from a swamp. King's remarks about the first pair of trunk limbs being replaced by an organ 'apparently adapted for clasping' were based on his confusion of the rather hook-like labral keel with these limbs (Sars 1912).

As Sars observed, while 'some points of agreement are found to exist between it and the genus *Lathonura*', the antennae and antennules being strikingly similar, there are also conspicuous differences. The overall superficial appearance is, however, much like that of *Lathonura*, and certain similarities between the two genera, not noted by Sars, indicate possible phyletic affinity. *Pseudomoina* has a wide embayment fringed by specialized setae referred to by Sars as stout and 'somewhat spiniform', but not illustrated, and by Petkovski as 'befiederte Stacheln' and shown as rather spiniform. These (figures 113 and 114) are in fact not spiniform but have a double fringe of setules whose proximal portions fuse to form a continuous membrane. Their arrangement is similar to that of the swollen setae of *Lathonura*, to which they also exhibit some general, but not striking, resemblance. They are very easily detached and many are missing in the material available. Petkovski reports likewise. To the outside of these is a row of very long, extremely slender (sensory?) setules (figures 113 and 114), and similar, but shorter, setules are strewn over the ventral parts of the carapace. The inference is that the ventral setae are used to support the resting animal, as they are in *Lathonura* and certain chydorids, but observations on the living animal are needed to establish this. The first trunk limbs are probably used for gripping, and locomotion by means of the antennae is almost certainly similar to that of *Lathonura*.

The trunk limbs (see figures in Sars (1912) and Petkovski (1973)) are specialized in an entirely different manner from those of *Lathonura*, for *Pseudomoina* is a filter feeder. While these limbs display many individual attributes their function can be readily appreciated in the light of other filter feeders. The lack of gnathobasic armature on trunk limb 5 is noteworthy. In this respect the limb thus approaches the daphnid condition, but to a less striking extent than in *Grimaldina* (§XIV). Two features shared with *Lathonura* call for comment. The inner distal lobe of trunk limb 1 bears four spines (figure 115). Among investigated macrothricids this feature is shared only with *Lathonura*, *Guernella* and *Neothrix:* in others three spines or claws are present. The gnathobasic plate of trunk limb 2 also resembles that of *Lathonura* in its arrangement but is directed more towards the food groove than anteriorly. Here seven spiniform setae are present as shown by Petkovski (only six are shown by Sars) of which, as in *Lathonura*, the anteriormost is partially hidden behind the second when seen in face view. In other features, however, the limb, like its fellows, is specialized in a very different manner from that of *Lathonura* in connexion with an entirely different method of food collection. The possible phyletic affinities of *Pseudomoina* are discussed in §XVII.



FIGURES 113–115. *Pseudomoina lemnae.*

FIGURE 113. Part of ventral region of carapace showing the marginal setae (membrane omitted in some) and the long slender setules of the carapace surface, of which those in the ventral row are rising towards the observer.

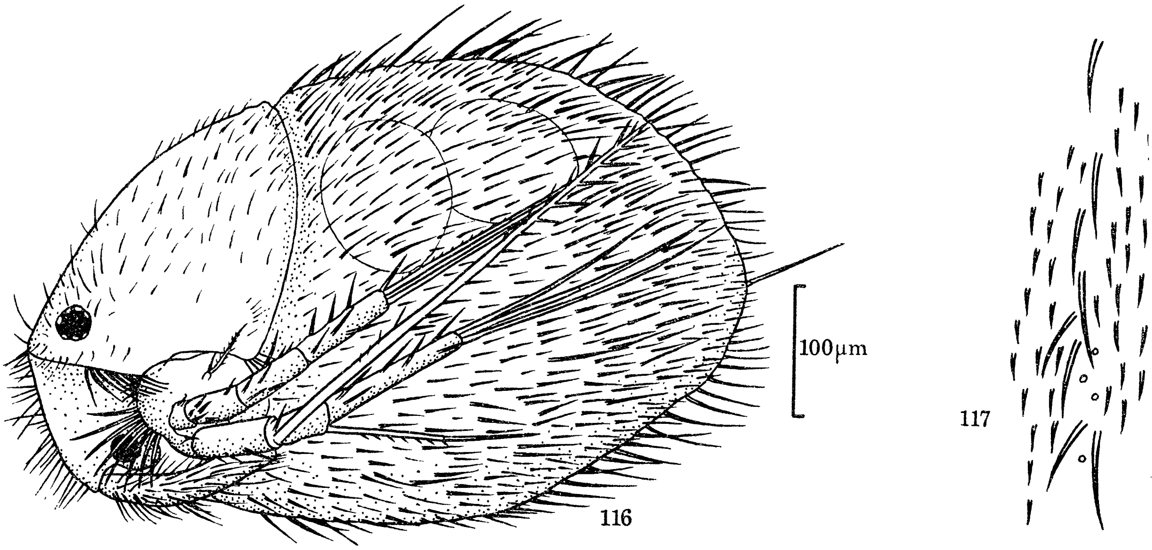
FIGURE 114. Details of a marginal seta, from the inside.

FIGURE 115. The inner distal lobe of trunk limb 1.

XIII. Observations on *Neothrix armata* Gurney, a benthic specialist

(i) *Ecology and habits and associated anatomical features*

Since being briefly described from individuals which Gurney (1927) reared from dried mud obtained from Queensland, Australia, *Neothrix armata* (figure 116: length to *ca.* 0.54 mm) appears to have been unreported in the literature. Thanks to Dr Ann Chapman I have had for examination a few preserved specimens obtained by her in Lake Rotoiti, New Zealand, a eutrophic to mesotrophic lake where *Neothrix* lives on the bottom and can be found only by sifting deposits which are here composed of fine mud. The material examined came from 42 m, a greater depth than that frequented by most macrothricids other than *Ilyocryptus* spp.



Figures 116 and 117. *Neothrix armata.*

Figure 116. Adult female, lateral, from a preserved specimen. The antennae, from which one distal spine of the exopod is omitted for clarity, are probably lying in an unnatural position.

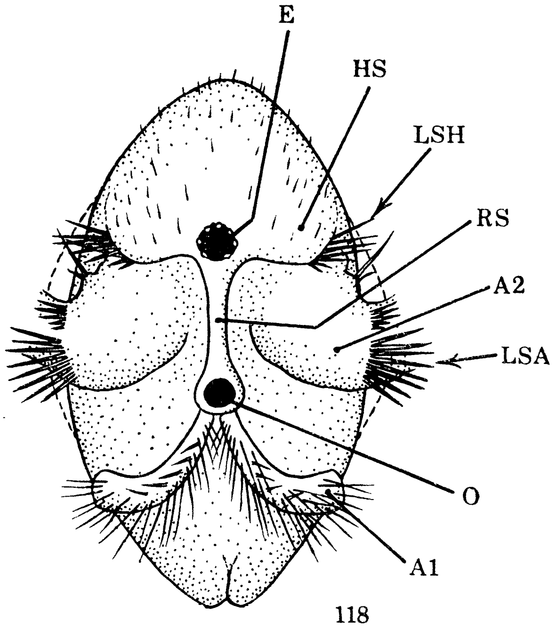
Figure 117. Some of the spinules of the mid-dorsal region of the carapace.

The adaptations of *Neothrix* are clearly those of an animal that ploughs through bottom deposits and burrows into them. Dr Chapman does not remember seeing it swim and is 'sure that it did not hop or bounce around'. She describes it as trundling slowly through detritus at what she refers to as 'definitely a slow scuffle'.

In contrast to *Ilyocryptus* it is always clean. An outstanding feature is the array of stiff spinules with which those surfaces that would otherwise make contact with the substratum are provided. While these insulate the cuticle from potentially clogging deposits, a more important function is probably to reduce friction as the animal moves through soft material, just as runners reduce friction on a sledge. Along the mid-dorsal line is a double row of spinules stouter than those of the general armature (figure 117), probably serving a similar function to the dorsal tooth of *Drepanothrix.* The head has a headshield, more or less triangular in horizontal section, much as in *Drepanothrix* but more sharply pointed, which must facilitate penetration of, or pushing through, deposits. Ventrally, below the compound eye, it is extremely narrow and forms a distinct rostrum (figure 118, RS) but widens posteriorly where it gives rise to the labrum.

As in other burrowers the eye is small, being here particularly so and only a little larger than the ocellus. A fringe of long spinules at the lateral margins of the headshield (figures 116, 118, LSH) is particularly noteworthy. There is a single large head pore (dorsal organ) recalling that of *Lathonura* and *Guernella*.

Anteriorly the carapace has a distinct flange which continues some way along the ventral



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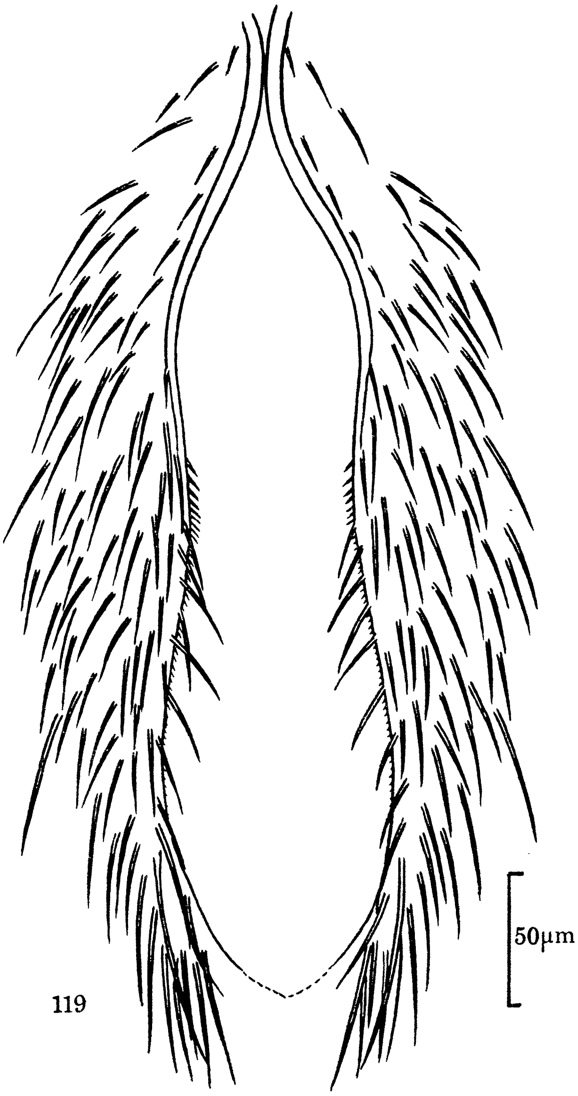

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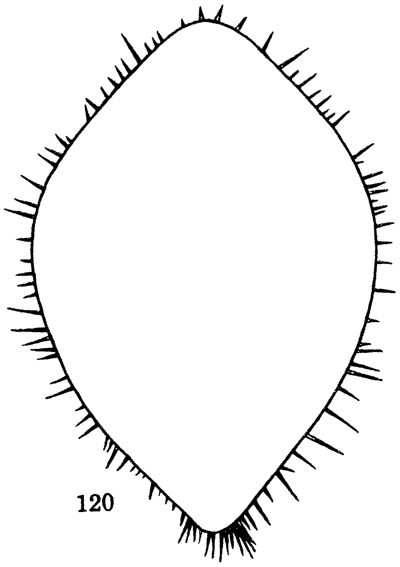

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Figures 118–120. *Neothrix armata*.

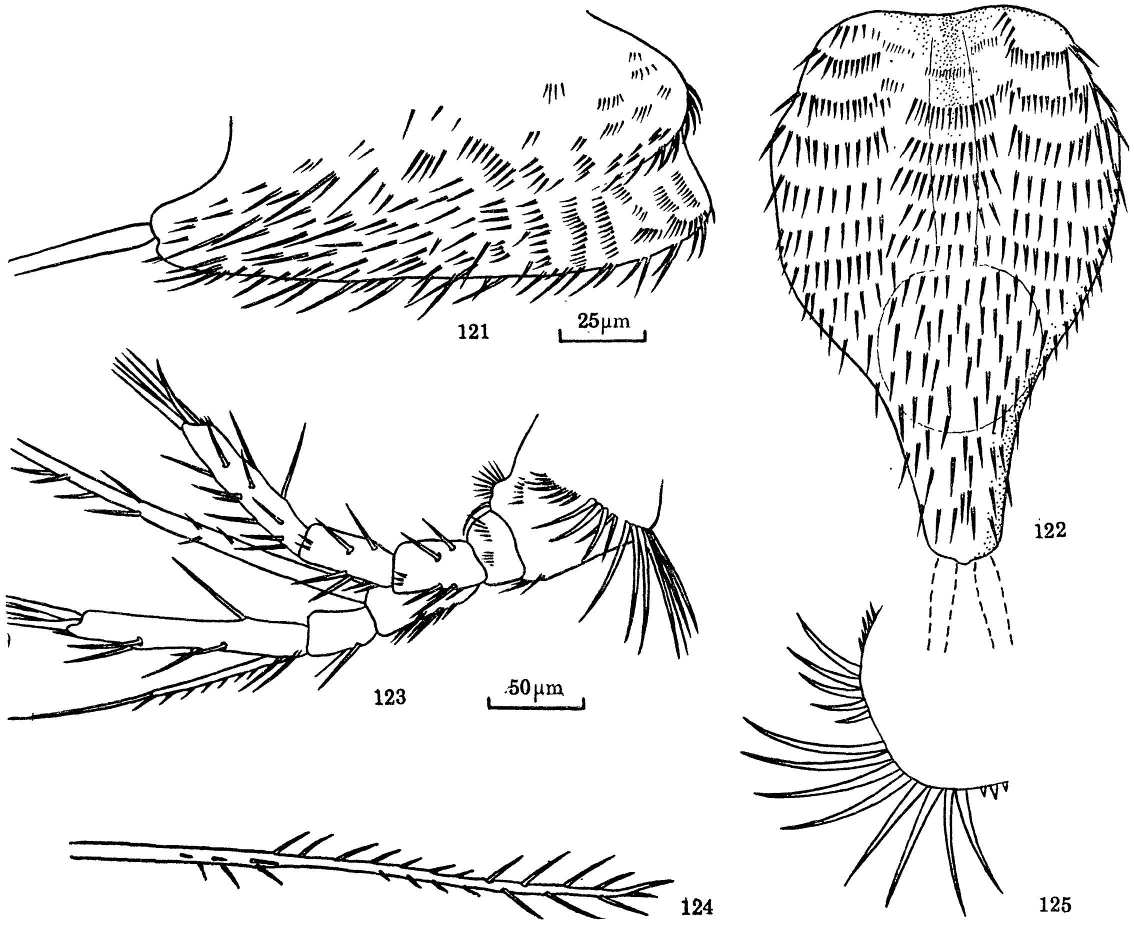
Figure 118. Anterior view, somewhat simplified, to show the extreme narrowness of the anterior ventral part of the head and the location of the two ventral series of levering spines of the antennal protopod.

Figure 119. Embayment region.

Figure 120. Optical transverse section, based on a photograph, about half way along the carapace, to indicate the shape of the body in a specimen in which the ventral embayment is largely closed after preservation.

margin (figure 119) and peters out as the embayment reaches its widest point at the level of the anterior trunk limbs. This region is unarmed, but posteriorly, where the ventral margins lack a flange, arise a few spines scarcely to be distinguished from those covering the general surface of the cuticle. The embayment appears to be about as wide as that of *Drepanothrix* and similar in shape, but the available material is subject to considerable distortion. In some specimens the ventral aperture is virtually closed as a result of preservation, but whether this feat can be performed in life is doubtful. Certainly, however, the aperture is well guarded – anteriorly by the labrum, whose long keel (figure 126) is setose, and the first trunk limbs; posteriorly by the post-abdomen (figures 121 and 122) whose morphologically ventral face is extremely wide and armed with an array of spinules. As Gurney (1927) noted, it lacks claws – a condition unique in the Anomopoda. Its structure suggests that it is incapable of independent movement but its position can presumably be shifted somewhat by the small movements of which the trunk is doubtless capable.

The alimentary canal is not coiled and the mid-gut terminates in a swelling adjacent to the rectum, presumably the functional equivalent of the diverticulum of certain genera.



FIGURES 121–125. *Neothrix armata.*

FIGURE 121. Post-abdomen, lateral. Note the absence of distal claws.
FIGURE 122. Post-abdomen, ventral.
FIGURE 123. Antenna, lateral.
FIGURE 124. The distal spine of the proximal endopod segment of the antenna.
FIGURE 125. Levering spines of antennal protopod, seen from behind.

The most striking feature of the antennules (figure 116 and 118, A1) is their armature of spinules, again presumably facilitating the penetration of deposits. Likewise the rami of the antennae (figure 123) are provided with spinules in addition to the locomotory armature which, on the exopod, is restricted to three distal setae, of which, for clarity, only two are shown in figure 116. The spine of the basal endopod segment is highly specialized (figures 116, 123 and 124), clearly for levering. In soft material its numerous spinules will facilitate purchase. On the protopod are three arcs of spines of which all are seen in figures 123 and 125, only the two ventralmost in figures 116 and 118, LSA. The component spines of the ventralmost are long and curved. The obvious inference is that these are employed for granting purchase or for sweeping aside detritus during forward progression, but their location is less distal than that of the burrowing spine of *Drepanothrix*, which suggests somewhat different antennal action. This can only be ascertained by observation of the living animal.

The trunk limbs, of which certain attributes are listed in table 1 (p. 262), reveal that *Neothrix* handles particles mechanically and does not use filtration. Trunk limb 1 has the same basic form as that of *Acantholeberis* but is foreshortened and lacks both an inner lobe and ejector hooks. The latter feature is shared only with *Lathonura* among investigated anomopods. Inner spines are also lacking. Both the inner and flat ventral surface of the limb are armed with numerous rows of setules and spinules. The long seta of the outer distal lobe is armed with numerous hooklets and closely resembles the outer seta of the inner distal lobe of *Macrothrix laticornis* shown in figure 61. The inner distal lobe bears four spines, a feature shared by few genera (table 1).

In general form trunk limb 2 is typical of macrothricids and chydorids but exhibits a striking feature clearly related to mud-frequenting habits that is unique within the Macrothricidae but has a parallel in the mud-frequenting chydorids *Leydigia* and *Monospilus* (Fryer 1968), namely a carpet of exceedingly fine setules on the posterior, and particularly the outer, face of the gnathobase (figure 127, CS). These lie adjacent to, and ensure the cleanliness of, the lateral walls of the food groove. One of the dorsal elements of the gnathobasic armature is a long setose seta (BG), whose function also is clearly to sweep along the bottom of the food groove. This is not homologous with the sweeping seta of *Leydigia* which is a modified element of the gnathobasic plate, but fulfils a similar function. *Neothrix* shares with *Lathonura* the distinction of having an armature of not eight but nine elements on trunk limb 2. As in *Lathonura* the outermost (no. 9) is long and slender. Six orally directed gnathobasic spines are present.

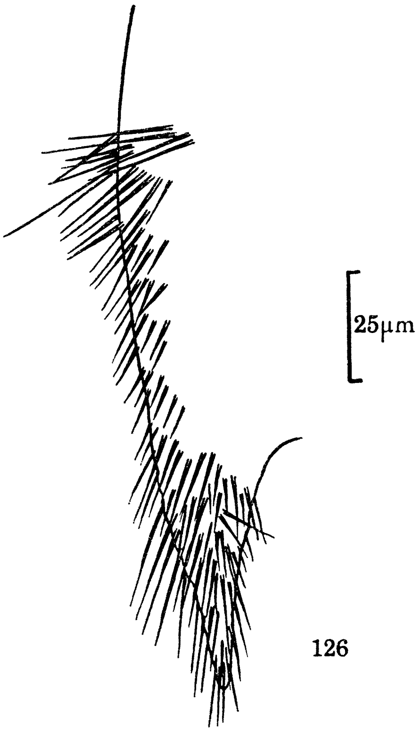
Although trunk limb 3 is reduced and non-filtratory, two setae homologous with those of an outer filter plate are present, as in *Streblocerus* and *Drepanothrix*, and presumably have a screening function. A long reflexed gnathobasic seta is present.

The fourth trunk limb is reduced, having no gnathobasic plate or outer plate of setae. Typical vertical-standing spines are present and are provided with exceedingly fine setules that fan out to form a carpet-like array. The exopod is a simple flap armed with two setae that may help to prevent the ingress of detritus.

The fifth trunk limb is much reduced and has a simple flap-like exopod.

Perhaps the most intriguing feature of *Neothrix* is the apparent lack of any means of removing excess food from the food groove, neither ejector hooks of the first trunk limbs nor post-abdominal claws being present. This suggests both efficient screening of the entrances to the carapace chamber – of which there is clear morphological evidence – and a means of food collection that does not drag in excess material. Food is almost certainly collected by the first trunk limbs – which can have no grasping function in the habitat frequented – and the indications, both from gut contents and the nature of the limbs, is that fine particles are collected. Flocculent masses, such as are dragged in by *Acantholeberis* and *Drepanothrix*, would probably be unmanageable, and on the basis of what is known it is predicted that *Neothrix* will prove to be rather rigorously restricted to bottoms covered with finely particulate detritus.

As Gurney (1927) remarked, the post-abdomen, while 'quite unlike that of any other genus', bears most resemblance to that of *Lathonura* but thought that to this genus *Neothrix* 'has otherwise little relationship'. There are, however, other similarities – an otherwise unique absence of ejector hooks (perhaps for unrelated functional reasons), a conspicuous dorsal



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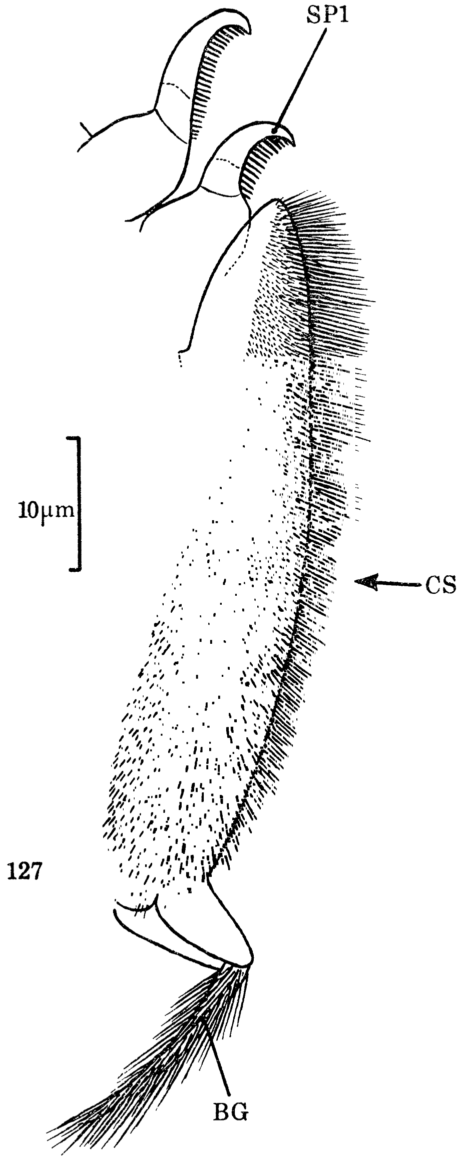

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FIGURES 126 AND 127. *Neothrix armata*.

FIGURE 126. Labral keel.

FIGURE 127. Gnathobase and the two most proximal scrapers of trunk limb 2 orientated to show the carpet of setules on the outer face of the gnathobase and its proximal sweeping seta.

organ, and the presence of four spines on the inner distal lobe of trunk limb 1. The possible phyletic significance of these features is discussed in §XVII.

(ii) *Conclusions*

Neothrix armata is a benthic and probably burrowing species whose morphological attributes suggest mud-frequenting habits. Its antennae are highly specialized, probably for levering in soft mud, and the spiny armature of the carapace and headshield probably facilitate movement in muddy situations. The trunk limbs are specialized for the mechanical handling of food particles: filtration is not used. The second has a setose gnathobase, unique within the Macrothricidae, and a brush-like seta which serve to clean the food groove and which reflect mud-frequenting habits.

XIV. Observations on the functional morphology of *Grimaldina brazzai* Richard

(i) *Ecology, habits and associated morphological features*

Grimaldina brazzai (length to *ca.* 0.9 mm) has a wide distribution in tropical Africa and South America, extends northwards to the southern part of the U.S.A. and has been found also in New Guinea. Most records are for marshy pools, and Thomas (1961), who studied the Cladocera of swamps in Uganda, regards it as characteristic of such habitats. Here it lives among vegetation and bottom debris. Sars (1901), who reared individuals in an aquarium, showed it to be 'a very pronounced bottom form'. I found it four times in Africa (Fryer 1957*a* and unpublished records) either among vegetation, not always the same kind, or debris, which in one case consisted of dead leaves on the bottom of pools in a Zambian swamp forest. Habits were not then investigated but more recently I was able to observe a few living animals collected at the swampy margin of a lagoon in Argentina. These revealed certain unreported features.

Although of benthic habits, for which it has evolved a specialization found in few macrothricids, *Grimaldina* appears not to be a burrower. Its antennae, although having a flexed protopod, are adapted for swimming and not for levering. All their setae are of the natatory type and their complement includes a seta on segment 3 of the exopod such as is not present even in *Ophryoxus*. Disturbed individuals move with the typical macrothricid 'hop' but this is less violent than the escape reaction of either *Macrothrix triserialis*, with which comparison was possible, or of *Acantholeberis*. These are presumably the 'rather slow' movements 'effected in a pronouncedly jumping manner' described by Sars (1901). It can also swim steadily and smoothly, but slowly, though like most macrothricids it evidently leaves the bottom with reluctance as Sars has already reported. When escaping a sucking pipette it continues to swim steadily, as do most chydorids, rather than 'leaping', which is probably restricted largely to rapid take-off.

Unlike most macrothricids it thrusts powerfully with its post-abdomen – a striking specialization. Related to this is the great depth, the bilateral compression and the powerful distal armature of the post-abdomen (figures 128 and 129) (cf. the broad, immobile post-abdomen of many macrothricids). The great, functionally ventral, expansion proximal to the anus (PAL) is almost plate-like and has a sclerotized edge, and the distal region is also narrow, but provided with widely splayed spines. The principles involved are the same as in such chydorids as *Eurycercus*, which exploits compression for strength (Fryer 1963), and *Leydigia*, which employs compression and splayed-out spines for purchase (Fryer 1968). *Grimaldina* appears to be equipped to push against both firm and soft substrata but more observations are needed.

As in *Onchobunops* (§IX) the fifth trunk limb is daphnid-like in general form. Its gnathobase lacks setae and it has a single, large, curved, exopod seta. Beating of the exopods of limbs 4 and 5 is best described as vibration, for movements are extremely rapid and of very small amplitude and contrast strongly with the more leisurely beating of wide amplitude exhibited by many anomopods. The result achieved is, however, the same in each case – the setting up of feeding-respiratory currents.

Scanty observations on food in the gut revealed greenish material including tiny algae and detritus but – save in the absence of any inorganic bottom debris – gave no indications as to its exact source.

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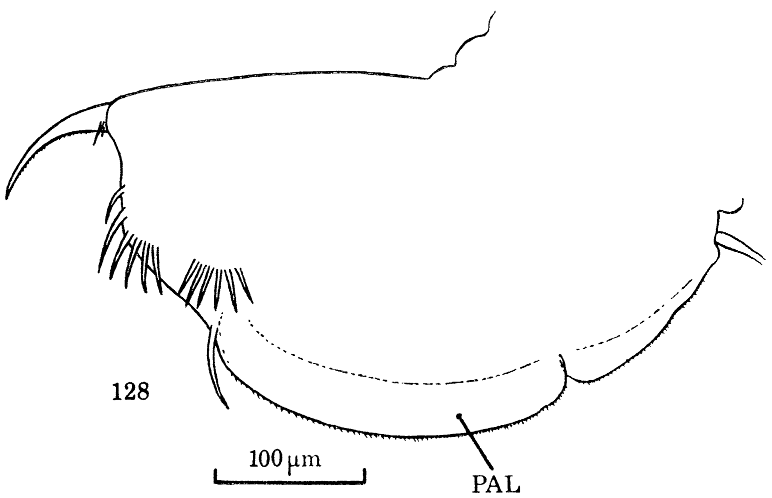

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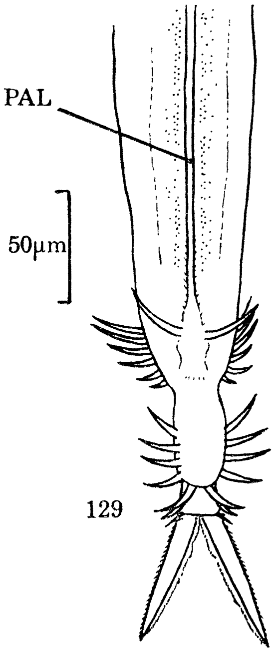


Figures 128 and 129. *Grimaldina brazzai.*

Figure 128. Post-abdomen, lateral. Note the broad lamella (PAL) on the pushing edge.

Figure 129. Distal portion of post-abdomen, seen from the topographically ventral (morphologically dorsal) aspect. Note the splayed out distal spines.

(ii) *Notes on functional morphology*

General form is illustrated by several authors, the most readily accessible figure being that of Birge, in Brooks (1959), the most recent that of Rey & Saint-Jean (1968). There is a distinct headshield which, while less developed than for example in *Onchobunops*, extends laterally to grant some protection to the coxal region of the antennae and represents an advance on the condition in *Acantholeberis*. There is a simple lozenge-shaped embayment. Except for a few stiff setae anteriorly its margins are fringed by relatively short simple setae. This arrangement is more suited to steady swimming (cf. *Ophryoxus*) than an encumbering array (cf. *Acantholeberis*), and may also be related to easy movement over detritus-covered bottoms and between vegetation, but further observations are required.

It has not been possible to study the feeding mechanism but filtration of collected particles is certainly involved. The filter chamber, whose filtering surfaces are composed entirely by trunk limbs 3 and 4, is very well developed and the indications are that fine particles are collected. Thus the denticulation of the scrapers of trunk limb 2 is extremely fine and suggestive of whisking rather than scraping. Its gnathobasic spines are long and slender, the anteriormost being modified for sweeping by a posterior row of fine spinules. Trunk limb 1 is relatively slender, which suggests great mobility, for which its musculature also appears suited, and the distal lobes bear slender claws. The use of these is enigmatic as they appear not to be specialized for dragging flocculent material as they are for example in *Acantholeberis* but are not specialized for grasping. Further observations are required.

(iii) *Conclusions*

Grimaldina brazzai is a bottom-frequenting species which, while not a burrower, is able to push with the post-abdomen which is highly specialized for this purpose, and is also capable of steady swimming. Filter feeding is practised. While details remain to be elucidated it is clear that filtration is restricted to trunk limbs 3 and 4.

XV. Some aspects of the functional morphology and habits of *Parophryoxus tubulatus* Doolittle, a species of uncertain destiny

(i) *Ecology and habits*

Nothing appears to have been recorded of the habits of *Parophryoxus tubulatus* (length to *ca.* 1.15 mm: figure 130), described by Doolittle (1909), who later (Doolittle 1911) gave a competent, illustrated account of its gross anatomy and reported that it occurred rarely in weedy situations at the shallow margins of certain New England lakes. Thanks to Dr Clyde E. Goulden I was able to visit Lake Lacawac, Pennsylvania, where he had, but in very small numbers, found *P. tubulatus*, and here five female specimens were collected and studied alive, two of them being subsequently sectioned. These were found in late August, in shallow water near the margin, among water lilies (*Nymphaea*), over a bottom covered with flocculent material about 60–70 % of which is made up of organic matter (C. E. Goulden, personal communication). In the region where the animals were collected the pH is usually approximately 5.4 and, if only for short periods each day, the temperature may rise to about 30 °C in summer. For information on Lake Lacawac see Goulden (1971).

The habits of *P. tubulatus* prove to be markedly different from those of *Ophryoxus gracilis*, which occurs in the same lake and with which first-hand comparison was therefore possible. The differences could scarcely have been predicted on the basis of available descriptions which, like the generic names, emphasize similarities rather than differences. All individuals of *P. tubulatus* seen alive were 'dirty'. The carapace evidently produces sticky material to which particles of diverse origin adhere in a similar, but less striking, manner to that seen in *Ilyocryptus*. The detrital burden is even less than that carried by *I. agilis* Kurz to whose 'comparative cleanness' Scourfield (1894) refers, and is much less than that of *I. sordidus* (§XVI). *Ophryoxus* is always clean. This dirtiness, perhaps a form of camouflage, reflects association with bottom deposits, for although *Parophryoxus* can swim freely, it does so less strongly than *Ophryoxus*, and moves over the bottom in a different manner. As in other macrothricids it seldom swims save when disturbed and, when it does, usually moves only for a short distance provided material on which it can alight is available. On this it settles ventral-side down, but in its subsequent movements over and among deposits its body may be orientated in almost any direction. An animal installed in a suitable deposit often remains still for many minutes – possibly much longer in nature. Subsequent locomotion among deposits is by means of rowing movements of the antennae, not by the levering action employed by *Streblocerus* and *Drepanothrix* for which it lacks the necessary equipment.

The antennal protopod is straight (§(ii)), which permits movements of an entirely different kind from those practised by *Acantholeberis*. Each antenna can be swung forward and dorsally until its protopod lies more or less parallel to the body and is directed anteriorly. Because the protopod is straight both rami are then directed forward. When the antennae of *Acantholeberis* are in an equivalent position the exopod is directed vertically (figure 1). Beyond the horizontal the protopod can pass no further dorsally as a result of a simple swing but now swings laterally, that is backwards, rising somewhat at first then moving ventrally as it swings posteriorly. This is the working stroke which moves the animal forward. At the end of this phase the protopod may return to a position near the body or, if the animal continues to move, continues forward while still extended laterally so that its tip swings through an essentially circular or elliptical course. Such slow 'whirling' movements resemble those used by *Ilyocryptus* (§XVI) and row the animal through the detritus, the general similarity being particularly close when, as is sometimes the case, forward movement is achieved while the animal lies on its back. The antennal rami are flexible and their position can be adjusted according to circumstances, and the two antennae move independently of each other as required.

Several rowing movements may succeed each other and move the animal slowly over and through detritus, but a settled and feeding individual generally moves only a very short distance before pausing again for several minutes (cf. *Streblocerus* and *Drepanothrix*).

In spite of its benthic habits and the fact that it can swing its post-abdomen much more freely than many macrothricids, *Parophryoxus* appears to make no use of it for pushing, nor is its structure suited to this purpose (§(ii)). Thus, while in some respects specialized for a benthic way of life, this species also displays features perhaps selected to increase efficiency in other ways (swimming) which can scarcely be interpreted as adaptations to life on detritus-covered bottoms. In this apparent conflict may reside a major reason for its limited success, as indicated by its restricted distribution and its rareness in such places as it has colonized.

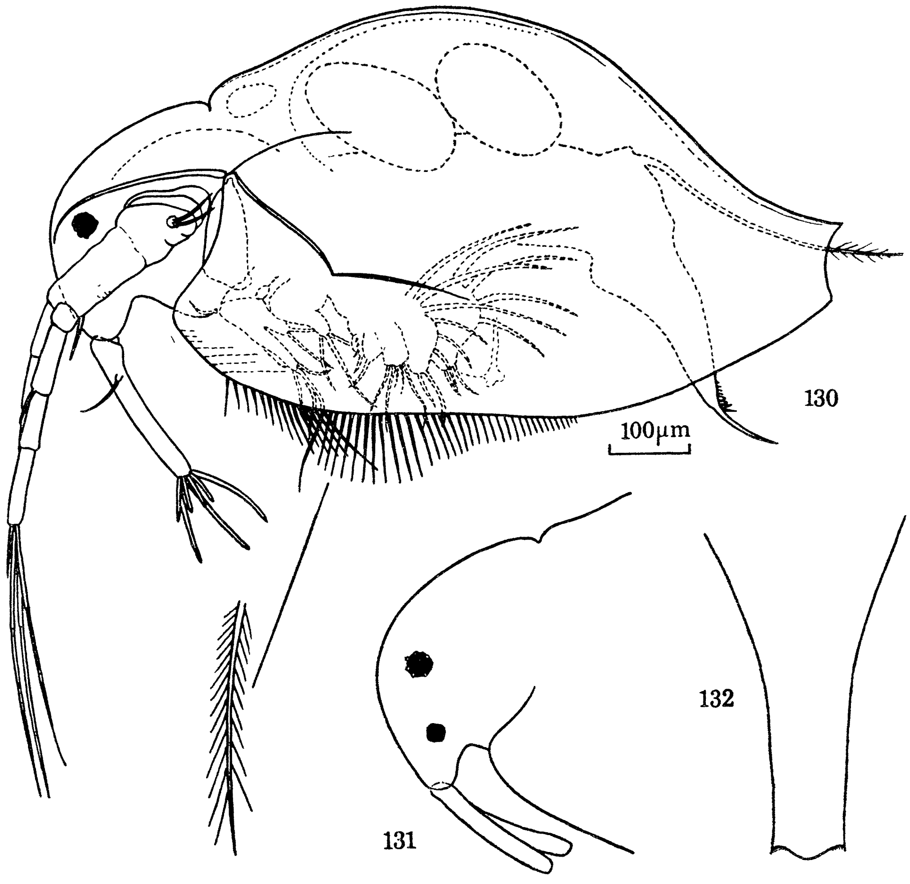
So far as could be ascertained food consists of flocculent, and for the most part finely particulate, detritus. Defecation takes place at frequent intervals; small quantities of material being discharged on each occasion. There is no accumulation of material in the rectal region such as occurs in *Ophryoxus*. Discharge involves no protrusion, or even movement, of the post-abdomen, and the faeces are discharged with considerable force through the posterior 'tube' of the carapace chamber by means of the exhalent respiratory current.

(ii) *Gross morphology*

The general appearance is shown in figures 130 and 131. (See also figures in Doolittle (1911).) The most striking features of the carapace are its prolongation and bilateral compression posteriorly, the close association of its ventral margins in the same region, and the small posterior aperture of the carapace chamber. Geometrically the posterior portion of the chamber is thus a bilaterally compressed cone terminating in a tube (figure 132) through which the exhalent current is discharged with considerable velocity. This removes faeces discharged within the carapace chamber (an unusual feature) and is associated with the discharge of small quantities of material at frequent intervals, but may have other functions. If the respiratory current flows as the animal swims it must, by jet-propulsion, inevitably lend some slight assistance to the antennae.

The otherwise delicate carapace is strengthened by a dorsal ridge and by lateral cuticular ridges which converge and meet the posterior corner of the headshield at the point of mandibular articulation (figure 130) which is thereby granted rigidity as by the legs of a tripod. A light reticulation gives further strength.

The ventral aperture is confined to the region opposite the limbs and is lozenge-shaped, the widest part being opposite the anterior trunk limbs. Its marginal armature is simple in structure and arrangement but functionally specialized. Each margin bears a single row of setae. Near the antero-ventral corner seven slender setae (indicated by dashed lines in figure 130) are



Figures 130–132. *Parophryoxus tubulatus.*

Figure 130. Adult female, lateral. From a preserved specimen. In life the antennae can be directed forward but their rami are never orientated as in *Acantholeberis* (figure 1) and many other macrothricids. Here the antenna is in approximately the position through which it passes shortly after commencing its working stroke in a swimming individual. For clarity the distal setae of the endopod, which arise behind the exopod, are omitted. In life the post-abdomen is generally swung forward and contained entirely within the carapace chamber though it can be, but seldom is, swung back further than shown here. The inset gives details of one of the stiff ventral setae.

Figure 131. Outline of the anterior portion of the body of another individual to show the shape of the head and the size of the very small eye in relation to the ocellus.

Figure 132. Posterior end of the carapace, dorsal, to show how it is bilaterally compressed to form a distorted conical tube.

directed essentially inwards. Adjacent to the anterior trunk limbs some fifteen setae are directed outwards. Behind these is a conspicuous row of about 36 stiff spine-like setae of which the first 11 or 12 are long and are directed inwards and ventrally so that their tips lie not far apart and can make contact or overlap when the carapace lobes are pulled together. Posterior to these the setae diminish rapidly in size. Thus, the ventral aperture is screened against the ingress of extraneous particles save at the anterior end (cf. *Ilyocryptus*, §XVI). Here, of necessity, the unscreened region is more extensive than in *Ilyocryptus* as the first trunk limbs require access to the exterior.

A distinct headshield overhangs the antennal coxa on each side and narrows rapidly anteriorly. Its presence will facilitate shallow burrowing. The compound eye is extremely small, not much bigger than the ocellus, (figure 130). This would appear to be related to burrowing rather than to swimming habits.

The long antennules are shown in figure 130. The antennae are long and slender and have a straight protopod, thus differing markedly from the majority of the Macrothricidae. In the female the only swimming setae are the three that arise at the tip of the distal segment of each ramus. This arrangement, unique within the Anomopoda and reflected by feeble swimming abilities, may have evolved in connexion with substrate-burrowing – but in a manner quite different from that exploited by *Streblocerus* and *Drepanothrix*. Doolittle (1911) showed that in the male there is an additional swimming seta on endopod segments 1 and 2. Such sexual dimorphism is also unique among anomopods and may be related to a need for more active swimming by the male when in search of a mate or to grasping of the female.

The post-abdomen is long and slender and feebly armed on its morphologically dorsal margin. While it can be swung well back (cf. the inability of many macrothricids to do this), its lightness and structure make it of little help in pushing (cf. the massive pushing post-abdomen of the burrowing *Ilyocryptus*, §XVI) and there is no evidence that it is regularly so used. Its lightness is probably associated with swimming (cf. *Ophryoxus* and the Daphniidae).

An egg-bearing female carried two eggs only, and in another only two embryos were present. As these lay side by side and completely filled the brood pouch it seems probable that *Parophryoxus* has stabilized the brood size at two, as have most chydorids.

(iii) *Observations on the trunk limbs and feeding mechanism*

As both time and live material were limited it is not possible to give a detailed account of the feeding mechanism, but certain features of this process and of trunk limb morphology are now apparent. While accurate, the illustration of the first trunk limb given by Doolittle (1911) is drawn in such a way that it does not reveal the essential slenderness, particularly of the distal lobes. These bear long, slender setae that extend well beyond the confines of the carapace chamber (figure 130). The two setae of endite 1 are long and their distal portions lash-like, being similar in form and orientation to, but much longer and more slender than, those of *Macrothrix laticornis* shown in figure 61. These extend into the filter chamber and are able to reach the food groove posterior to the level of trunk limb 2, a perhaps unique specialization that suggests they may help to whisk food particles towards the food groove.

Trunk limb 2 is a typical scraping appendage, the nature of whose individual scrapers suggests the whisking of fine particles rather than the handling of more bulky material. The gnathobasic plate has eight setae (six only are shown by Doolittle) which, apart from curvature at their tips for sweeping, appear to be typical filter setae though in the single set of longitudinal sections available the setules cannot with absolute certainty be distinguished. This filter plate is continuous with gnathobasic filter plates on trunk limbs 3 and 4 which bear eight and seven setae respectively (seven and six according to Doolittle), the general make-up of the filter chamber being much as shown for *Acantholeberis* in figure 8 save that the gnathobasic plate of trunk limb 2 contributes to the continuous filtering area adjacent to the food groove (cf. *Eurycercus* (Fryer 1963, figure 45) and *Peracantha* (Fryer 1968, figure 47)). Adjacent to the food groove the filter chamber is sealed posteriorly by the gnathobasic plate of trunk limb 5 which consists of six obliquely directed setae, more robust than those of the more anterior gnathobases and more coarsely setose.

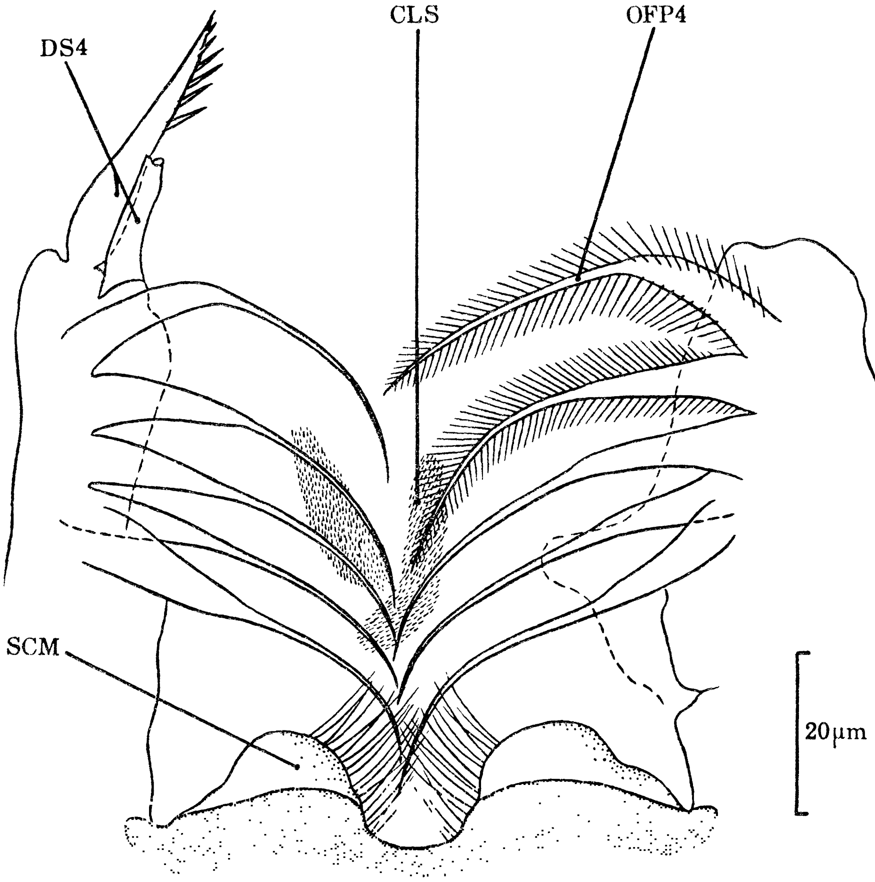


FIGURE 133. *Parophryoxus tubulatus*. Transverse section through the outer filter plate region of trunk limb 4. Filter setules are indicated on only the two ventralmost setae. Part of trunk limb 5 bearing cleaning setules (CLS) is just skimmed in this section. A pseudo-food groove effect is given at this level by the setule-covered mounds. The groove itself is here shallow.

Trunk limbs 3 and 4 each have an outer filter plate arranged much as in *Acantholeberis* (figure 8) but that of trunk limb 3 has more setae – seven certainly and eight if a distal seta is part of the series. The outer filter plate of trunk limb 4 is extremely well developed and foreshadows (though not in a phyletic manner) the situation in *Ilyocryptus* (§XVI). Five setae are present (only four are shown by Doolittle) and these (figure 133) extend in an arc to span the wide gap at the posterior end of the filter chamber. Although in several other species their homologues fulfil a similar function, only in *Ilyocryptus*, in which they are even more extensively developed, are these setae so relatively large and conspicuous (cf. figure 140). The ventralmost has the most widely separated setules, the dorsalmost (nearest the food groove) the finest. On the three most ventral the setules can be discerned only with difficulty even with an oil-immersion lens.

Water is pumped through the carapace and filter chambers by the exopods of the posterior limbs. The main inhalent current enters the carapace chamber in the antero-ventral (unguarded) region (figure 130).

Food is collected by the first trunk limbs which reach out as in *Acantholeberis* and bring in flocculent material. Although observing time was limited, no evidence of direct food collection by trunk limb 2 was obtained, nor would this be expected from the habits. The indications are that the rest of the sequence is similar in principle to that of such filter feeders as *Acantholeberis* and several chydorids. Considerable significance is, however, attached to the fact that, just as do the fourth limbs, the third pair also move in a regular manner. A long, distal spine borne by trunk limb 3 may assist in the inward transport of flocculent material.

(iv) *Conclusions*

The habits of *Parophryoxus* are different from what might have been expected. It swims only feebly and is by preference a burrower into soft deposits which it penetrates by use of the antennae in a manner that foreshadows the mechanism employed by *Ilyocryptus*. Certain morphological features, particularly the great development of the outer filter plate of trunk limb 4, also exhibit similarity to those of *Ilyocryptus* but the two genera are not related to each other in an ancestor-descendant manner.

XVI. The structure, habits and feeding mechanism of *Ilyocryptus sordidus* (Lievin), a mud-frequenting burrower

(i) *Ecology and habits*

That *Ilyocryptus sordidus* (figures 134 and 137: length to about 1 mm) is a truly benthic species with a preference for muddy substrata into which it burrows is well known. For this habit it is so specialized that adults have lost the ability to swim. Related species, *I. agilis* (Kurz) and the non-European *I. spinifer* Herrick, while having similar habits, can still swim, though extremely feebly.

I. sordidus retains the old carapace and headshield at the time of the moult. Among macrothricids this is unique to, but not practised by all members of, the genus *Ilyocryptus*, but carapace retention has evolved independently in the chydorid genera *Alonopsis* and *Monospilus*. The carapace and dorsal surface of the headshield also collect a burden of detritus (figure 137), perhaps helpful as an increaser of density, and excellent camouflage. Retention of old carapaces obviates the need to collect a new load after each moult, increases density, and enables a complex defensive device to be built up (§(ii)). The detritus burden is not, as sometimes suggested, a consequence of the incomplete moult, but is a highly specialized adaptation.

While a mud-frequenter, *I. sordidus* can colonize sandy and stony bottoms provided these are covered by a few millimetres of suitable detritus. This may be of flocculent organic material or true gyttja. Into such material it penetrates freely, sometimes to considerable depths. Thus, while 75% of the individuals collected by Cole (1955) were in the uppermost centimetre of material, one was found 8–10 cm below the surface, and while Chirkova (1970) recorded about 87 % of the population in the upper 2 cm of the mud she found that about 1.5 % had penetrated to depths of 8–10 cm. Such deep penetration may not always be possible because of lack of oxygen. Both vegetation-covered and bare substrata are frequented and it sometimes lives at considerable depths; *ca.* 60 m according to Lilljeborg (1900) who regarded it as a deep water rather than a littoral form. It is, however, sometimes abundant in shallow water, the most convenient source of material for the present study for example being a shallow, swampy seepage with abundant *Sphagnum* where the animals often occurred in only a few centimetres of water. Cole (1955) showed it to be much more abundant in the littoral than in the sub-littoral region of two lakes and to be absent from the deeper waters that became deoxygenated in summer. In such situations, however, the habits of *Ilyocryptus* would make migration into deeper water during the oxygenated period a slow process. Both acidic and calcareous waters are frequented. The situations which it inhabits are often oxygen-poor – it has been found in foul organic mud such as would never be expected to harbour *Drepanothrix* or *Streblocerus* – and a physiological adaptation is the production of sufficient haemoglobin in the blood to make the animal bright red – which in turn has probably favoured selection for the mud-encrusting habit.

Prolonged observations by Chirkova (1972) have recently revealed remarkable and previously unsuspected habits. That adults are very slow moving is well known, but she has shown that in conditions where food is abundant they are essentially sedentary and ensconce themselves in what amounts almost to a 'nest' in the mud, which they vacate with reluctance, e.g. when the water is agitated. More remarkable, such ejected individuals may later return to their 'nest'. Undisturbed females were found to move not more than 1 cm in 24 h. In conditions of food scarcity movement is greater.

Newly emerged young can swim, and those shed at the mud surface can therefore effect some dispersal. Chirkova (1972) found that the duration of swimming varies according to the nature of the bottom, being very brief when food is plentiful; up to 2 or 3 days in uncongenial situations. By contrast, young shed within the mud do not disperse at all and this leads to aggregations whose density may reach 11000/m^2 whereas closely adjacent areas may be uncolonized.

When disturbed *I. sordidus* remains motionless and even the beating of the posterior exopods, otherwise in almost incessant motion, ceases. At such times the coat of detritus renders the animal virtually invisible.

By virtue of the method employed for its collection (§(v)) the food consists either of small particles or light flocculent aggregations of detritus and most of the gut contents appear to be of such material. Occasional diatoms whose length exceeded half the diameter of the mid-gut have, however, been seen among them.

(ii) *Gross morphology*

Although *Ilyocryptus sordidus* is often mentioned in the literature, where levering with the massive post-abdomen is generally noted as related to the way of life, some of its most striking adaptations to life in mud appear to have passed unnoticed. The general form is wedge-shaped in the vertical and bluntly rounded in the horizontal plane, the former characteristic being shared with *Drepanothrix* which also burrows. In striking contrast to many macrothricids, in which the head is long and narrow, that of *Ilyocryptus* is extremely short – as short as is compatible with the housing of the massive coxae of the antennae – and is covered dorsally by a broad headshield (figure 136). Both these features are clearly adaptations to the habit of burrowing. The headshield comprises thick, distinctly sclerotized, cuticle and is strengthened medially and posteriorly by the cuticles of previous instars which become firmly attached to the definitive cuticle.

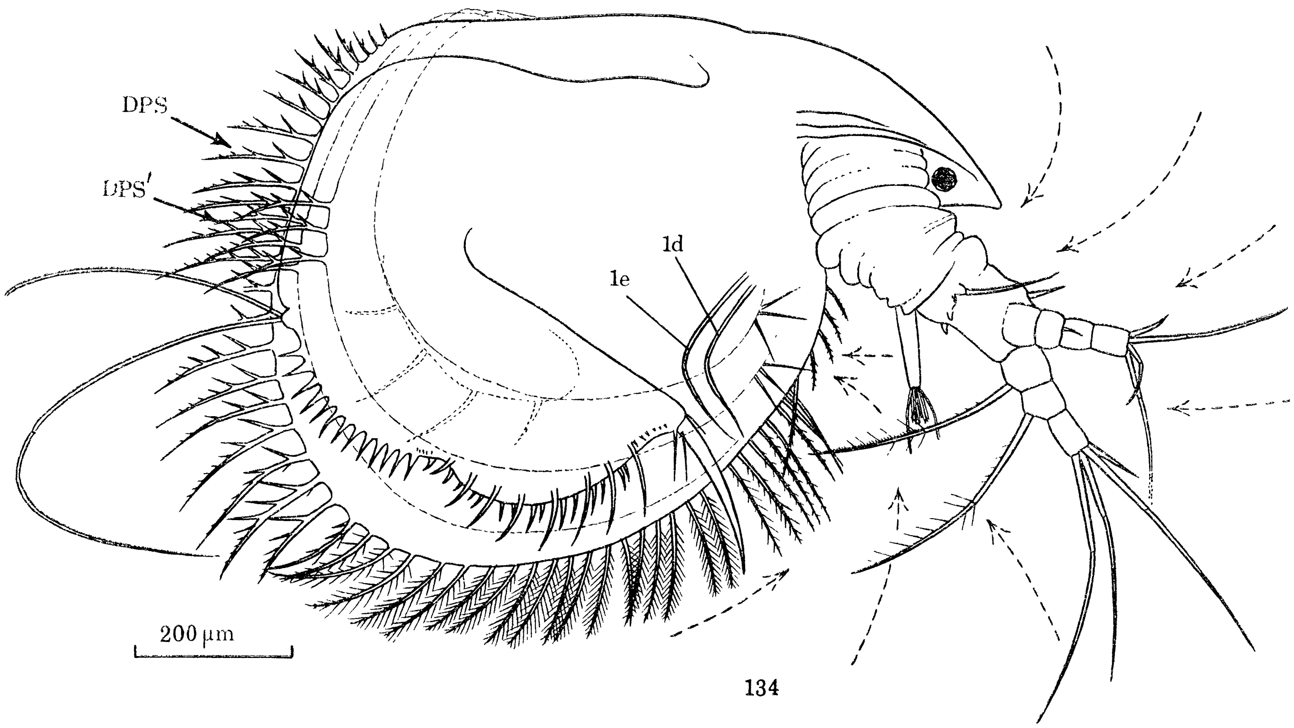
As *Ilyocryptus* lives among amorphous detritus the selective forces operating during the evolution of the carapace margins have been very different from those in forms associated with firm substrata. The end-points include an ability to close the carapace chamber almost completely, the development of screening setae ventrally, and of elaborate defensive spines posteriorly. Effective closure, whose value is self-evident, is readily visualized from figure 137. Ventrally there is a row of 32 or more, slender, relatively simple setae, of which the four anteriormost are directed essentially outwards, the next three as shown in figures 134 and 137, the rest obliquely inwards towards their neighbours on the opposite valve, and outwards. The long posterior margin is armed with a row of elaborate spines (figure 135) whose several sharp-pointed lateral tines are directed in different planes and form a defensive fence. The effectiveness of this device is enormously increased by the habit of retaining old carapaces. The result is a series of more or less concentric rows (at least six in large individuals) of such spines. Those of the old carapaces are of necessity directed outwards by virtue of the ever-increasing size of successive definitive carapaces which widens the inter-valve angle of the older, overlying carapaces. The posterior and dorsal part of the carapace thus becomes protected by a hedgehog-like array of branched spines (figure 134, in which only a sample of such spines (DPS and DPS′) is shown, and figure 137). This is undoubtedly the most specialized such device in the Anomopoda, though a similar end-point may have been reached by different means in the ill-described *Macrothrix cacta* Vavra. This device also facilitates retention of the coat of detritus. The slender ventral setae of old carapaces, particularly the anterior members, may persist for a time but, with the exception of a persistent anterior group of 3 (figure 137, GRS), often break off and play no part in the defence mechanism. The function of the persistent setae is described in § (iii).

Although not readily apparent except in transverse sections there is a small dorsal ridge which grants strength and reduces friction as the animal moves through mud.

Although the carrying of a detrital burden is well known, only Frič & Vávra (1894) have, somewhat fancifully, illustrated this. Otherwise published figures are of cleaned individuals. This deficiency is remedied in figure 137. The layer of detritus covering the headshield is generally thin, presumably because of abrasion during pushing. Neither the adhesion of the detritus nor the means whereby old cuticles are retained is fully understood. A secretion is probably involved in the former. Contrary to the condition in the chydorid *Alonopsis elongata* where old carapaces are readily shed, they are here physically fused to each other, and the same is true of the headshield (figure 136) where adhesion is a prerequisite of retention.

The compound eye is small but has well-defined lenses. The antennules are two-segmented, a primitive feature known in anomopods only in *Ilyocryptus* and an animal mentioned in §XVII. Both this and their considerable length, also primitive, have, however, probably been retained as adaptations; the joint to increase flexibility and the length to facilitate testing of the inflowing food-bearing stream.

Details of the antennae are shown in figures 134, 136 and 137, and certain attributes referred to in § (iii). The contrast between these appendages, here used entirely for rowing through mud, and those of forms such as *Ophryoxus* and *Lathonura* where their main or sole employment is in swimming, strikingly reveals the diversity of function to which basically similar structures



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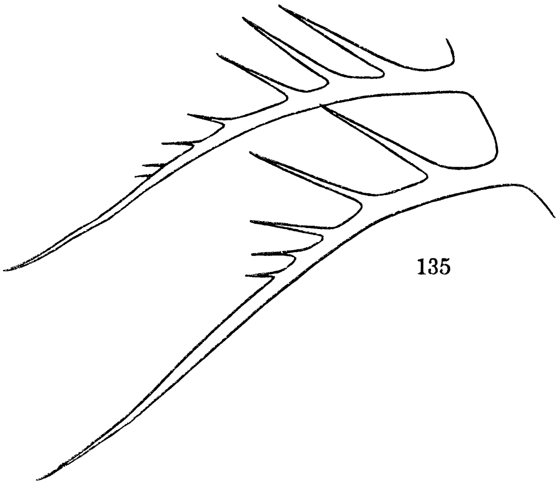

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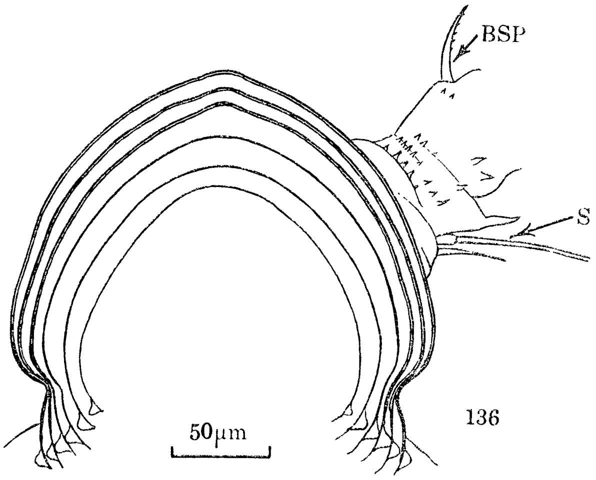

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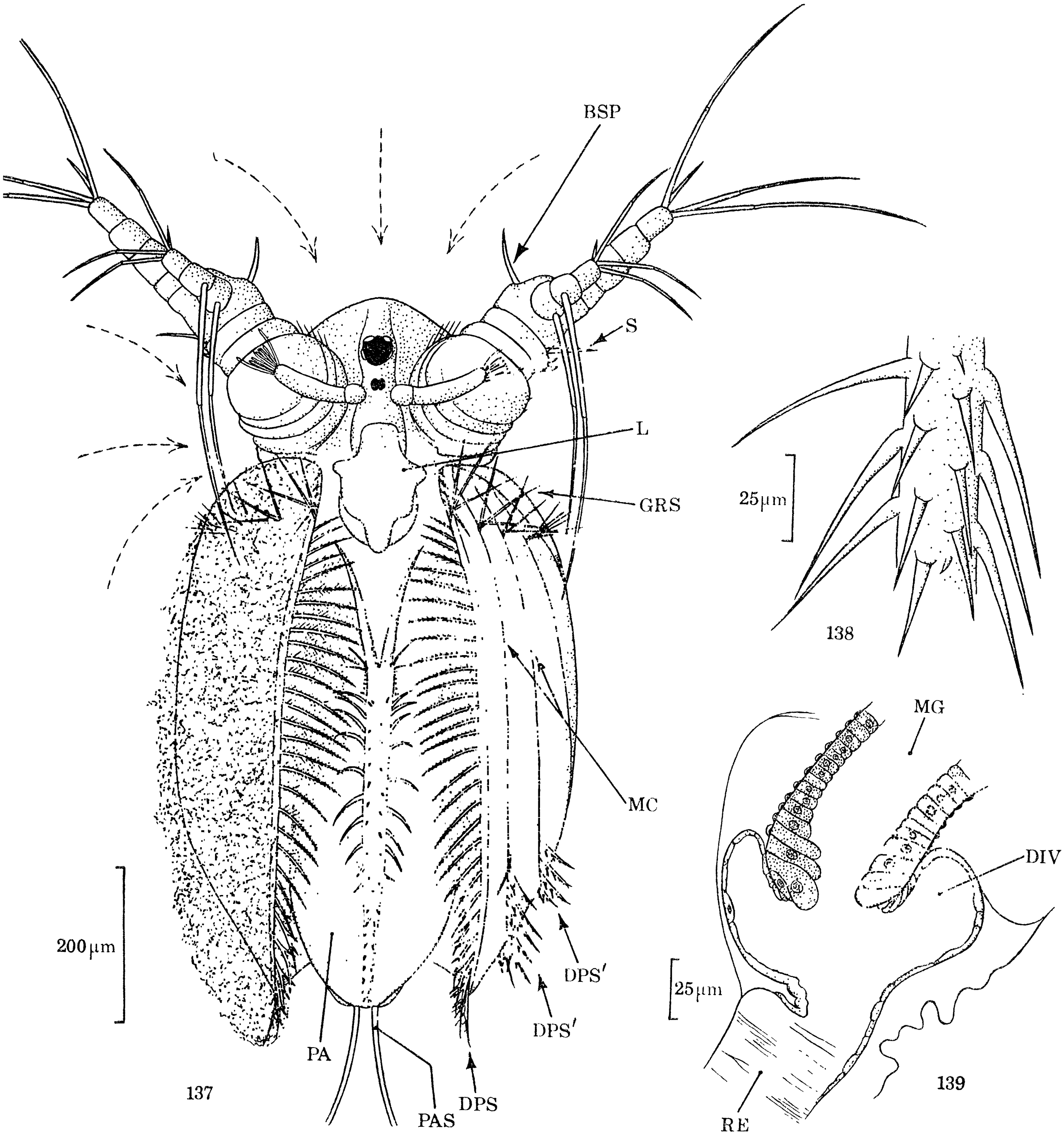
Figures 134–136. *Ilyocryptus sordidus.*

Figure 134. Adult female, lateral. The animal is drawn as though the carapace, normally obscured by detritus, was transparent, in order to show the location and nature of the massive post-abdomen and also the position of the important curved guard setae (1d and 1e) of trunk limb 1. The positions of three of the five old carapaces retained by this individual are indicated, and part of the armature of two of these (DPS′) is shown posteriorly in addition to that of the definitive carapace (DPS). Arrows indicate the approximate course of the main inflow of water into the carapace chamber.

Figure 135. Details of two adjacent defensive spines of the posterior carapace margin.

Figure 136. Headshield, dorsal. Note the successive, firmly fused, cuticles.



Figures 137–139. *Ilyocryptus sordidus.*

Figure 137. Adult female, ventral. The mid-ventral gape of the valves is here wider than is the case when the animal is ploughing through mud. The right valve is shown with its encrustation of detritus, the left after its removal. Note how, while the distal portion of the post-abdomen is narrow in section – as is the topographically ventral part of the proximal portion – the more proximal region is massive. Arrows indicate the direction of inhalent currents. The apparent difference in length of certain setae in the lateral and ventral views reflects the different angles of view.

Figure 138. Part of the distal armature of the distal portion of the post-abdomen, from below but viewed from a different angle from figure 137. Note the mobility of the large marginal denticles, some of which are shown in the extended position.

Figure 139. Longitudinal section through the posterior end of the gut showing the diverticulum.

can be adapted. Of the two sensory setae of the basis one is very long, the other very short (figures 134, 136 and 137, S), an unusual condition among anomopods. The labrum is shown in figures 137 and 146, L.

The gut, which is not coiled, is encircled posteriorly by a cup-shaped reservoir (figure 139, DIV) that, mechanically at least, fulfils the same role as the diverticulum of *Acantholeberis*. Immediately anterior to the rectum the mid-gut discharges into this thin-walled region much as does the oesophagus into the mid-gut, and here material accumulates before discharge via the rectum. Defecation takes place less frequently than in many anomopods.

(iii) *Locomotion*

Ilyocryptus rows through detritus with its antennae and also pushes with the large, highly specialized post-abdomen. Although it lies predominantly with its ventral surface uppermost as it does so, this is by no means invariably the case and it may move through detritus in almost any position according to circumstances. The short, stout, antennae (figures 134, 136 and 137) swing so that their distal portions describe an elliptical course oblique to the longitudinal axis, an action fancifully likened to that of the paddles of a paddle-steamer (Storch 1925) – criticized by Eriksson (1934) – or the propellers of an aeroplane (Hanko 1926). Movement from the resting position (figure 137) is backward with at first dorsal and outward, then inward and ventral components, this being the working stroke. The return movement is forward with at first an inward and ventral, then a forward and outward component. An exactly similar course is not followed each time: the movement can be varied according to circumstances and may even be completely reversed. The antennary setae often cross as they come together ventrally – for mutual cleansing? – and are also regularly wiped across the antero-ventral portion of the carapace. It is here that a group of persistent stout setae remain from the carapaces of earlier instars (figures 134 and 137, GRS) and, as the antennal rami pass inward, ventrally and forward, their setae are wiped by these carapace setae, the wiping being inevitably from base to tip. The functional significance – grooming – of these persistent setae is thus made clear. The antennal setae are more constantly exposed to clogging detritus than those of most anomopods, and grooming is therefore important. Because they lie behind the massive antennae the grooming setae of the carapace scarcely interfere with burrowing. That they yield to pressure can be seen when the antennal armature sweeps along them.

Antennal movements are slow and deliberate ('low-geared'), thereby permitting the development of maximum power and operation at high mechanical efficiencies. Their action, while suited to ploughing through soft mud and detritus, does not lend itself to the development of long, stout antennal props such as are seen in *Acantholeberis* and, in particular, in *Drepanothrix*. A rigid, unjointed, spiniform endopod armature such as that of *Drepanothrix* would be totally unsuited to the antennal action of *Ilyocryptus* though stout setae are obviously desirable for leverage. A compromise situation has evolved in which all the antennal setae are robust proximally but whose flexibility is safeguarded by an effective joint which demarcates the more slender spiniform distal portion from the proximal. The result is a widely spread array of five endopod and three exopod setae that grant purchase during the working part of the cycle but pass easily through the mud during the non-working return. In their leverage they are aided by stout terminal spines on each ramus which are also sufficiently long to grant considerable purchase. A stout burrowing spine (figures 136 and 137, BSP) is present on the protopod as in *Drepanothrix* – a striking example of convergence in animals that otherwise differ in many attributes – and there is a small spine on the second exopod segment. An array of spines, spinules and cuticular elaborations (figure 136) may facilitate burrowing but may equally be concerned with holding mud particles away from the antennary cuticle.

That the well-known habit of pushing with the post-abdomen is an unusual attribute of macrothricids has gone unremarked. The adoption of this habit represents a large evolutionary step, taken more than once during anomopod evolution. The massive post-abdomen is shown in side view in several taxonomic accounts (see also figure 134) but this gives no indication of its width away from the margin and proximally where massive muscles are housed. This is shown in figure 137 (PA) which also reveals the array of divergent marginal spines which grant purchase. Of these the longer members are mobile (figure 138) and can be widely spread when used for levering yet 'fold' during the non-working stroke. The narrowness of the ventral (morphologically dorsal) edge region allows edge-on pushing without bending as in *Eurycercus* (Fryer 1963) and *Leydigia* (Fryer 1968). As with antennal movements, swings of the post-abdomen are slow, for the same mechanical reasons.

(iv) *The trunk limbs*

While recognizably derived from the basic anomopod plan, the trunk limbs of *Ilyocryptus* show divergent specialization to a striking degree, and some of the anterior limbs in particular are less similar to those of other macrothricids than are those of most chydorids. The arrangement of the limbs is shown in figure 140, understanding of which is facilitated by consideration of outline figures of some of the individual appendages (figures 141–145) and of horizontal slices through them and the mouthparts (figures 146–149). Code letters are used for descriptive purposes only and do not necessarily imply homology from limb to limb.

Each first trunk limb (figure 141) has a slender corm on which it is difficult to recognize endites. Homology with structures in other genera is uncertain but the distal armature is borne on two lobes presumably homologous with endite 4 and the outer distal lobe of *Acantholeberis* (figure 14). All the proximal armature may belong to one endite homologous with endite 1 of *Acantholeberis*, intervening endites having become completely confluent and their armature having been lost. Of the distal armature, seta 1a is of enormous length (figure 141), armed with many long, precisely arranged setules (figure 140), and reaches back over the entrance of the filter chamber (figures 140 and 146). The more proximal setae are also highly specialized, 1d and 1e especially being of enormous length, having a distinctive curvature of great functional significance, and being armed distally with long setules. These setae, with their companions on the opposite limb, make up a sieve which guards the entrance to the filter chamber – here for descriptive convenience at times referred to as the filtering basket. Seta 1g is a screening seta similar to that found in certain other genera but with longer posterior setules than in any other studied anomopod. Ejector hooks (EH) are present distally. Trunk limb 1 plays an important but largely passive role during the process of feeding. Its movements consist essentially of a backward and forward swing of the corm. Other movements enable the ejector hooks to be used. When these are in action the limb displays a high degree of manoeuvrability never revealed during food collection.

Of the attributes of trunk limb 2 (figure 142) the most striking is that while the gnathobase is well developed and similar in many respects to that of many other macrothricids and chydorids, the distal part is small, and specialized in an entirely different manner from that of other members of these families. Here, instead of scrapers used in food collection, are

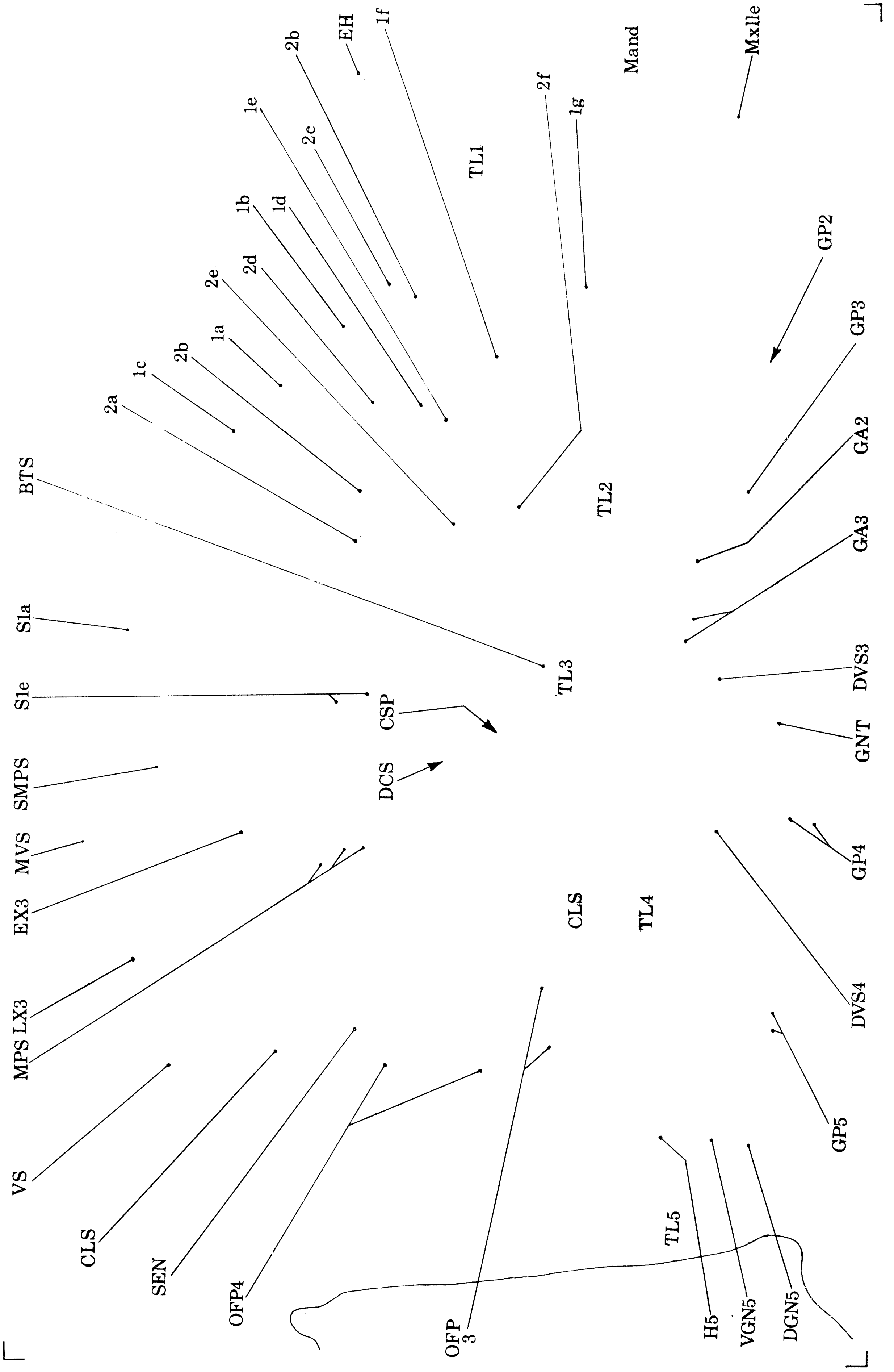


FIGURE 140. Overlay.

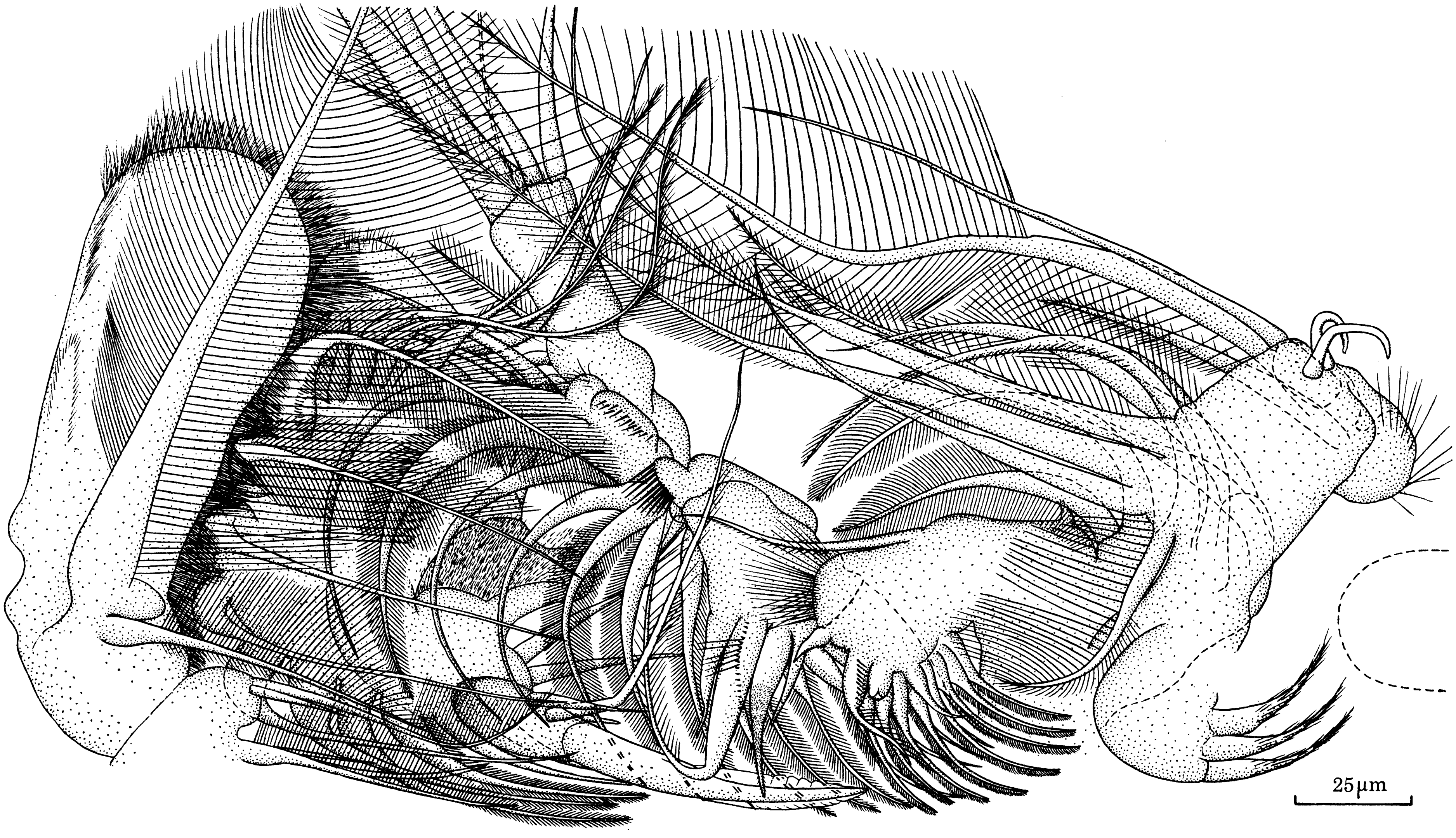


Figure 140. *Ilyocryptus sordidus*. The filter chamber and associated structures as revealed by dissection. As indicated by the overlay the sixth trunk limb lies nearer to the observer than do the filtering setae of trunk limb 4 and helps to seal the filter chamber (filtering basket) posteriorly. The position of the masticatory region of the mandible, dislodged during dissection, and indicated by a dotted outline, is added from a longitudinal section. To avoid unnecessary confusion the filtratory setules of many filter setae are omitted. The labrum has been removed and the distal portion of seta 2c is omitted. The limits of individual appendages are most easily appreciated by reference to figures 141–145. Of the distal setae of the first trunk limb, 1a, 1d and 1e are the major contributors to the screening sieve across the entrance to the filtering basket. 1f is the posterior ejector seta. In life setae 1d and 1e are both curved as shown for seta 1d (see also figure 141). As a result of dissection in a viscous medium, seta 1e has here straightened distally – which enables its full length to be shown. Its true course is indicated by dashed lines.

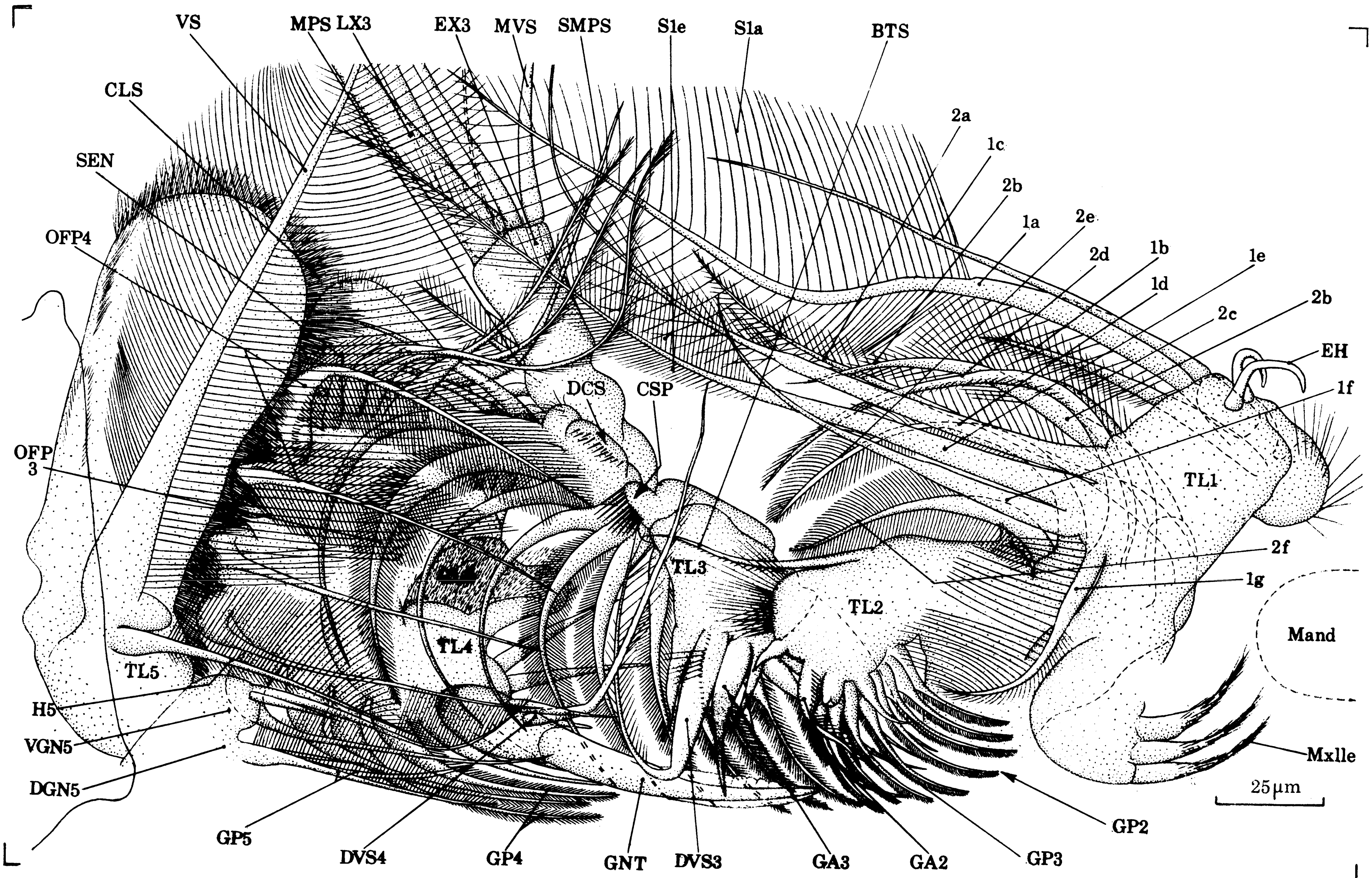
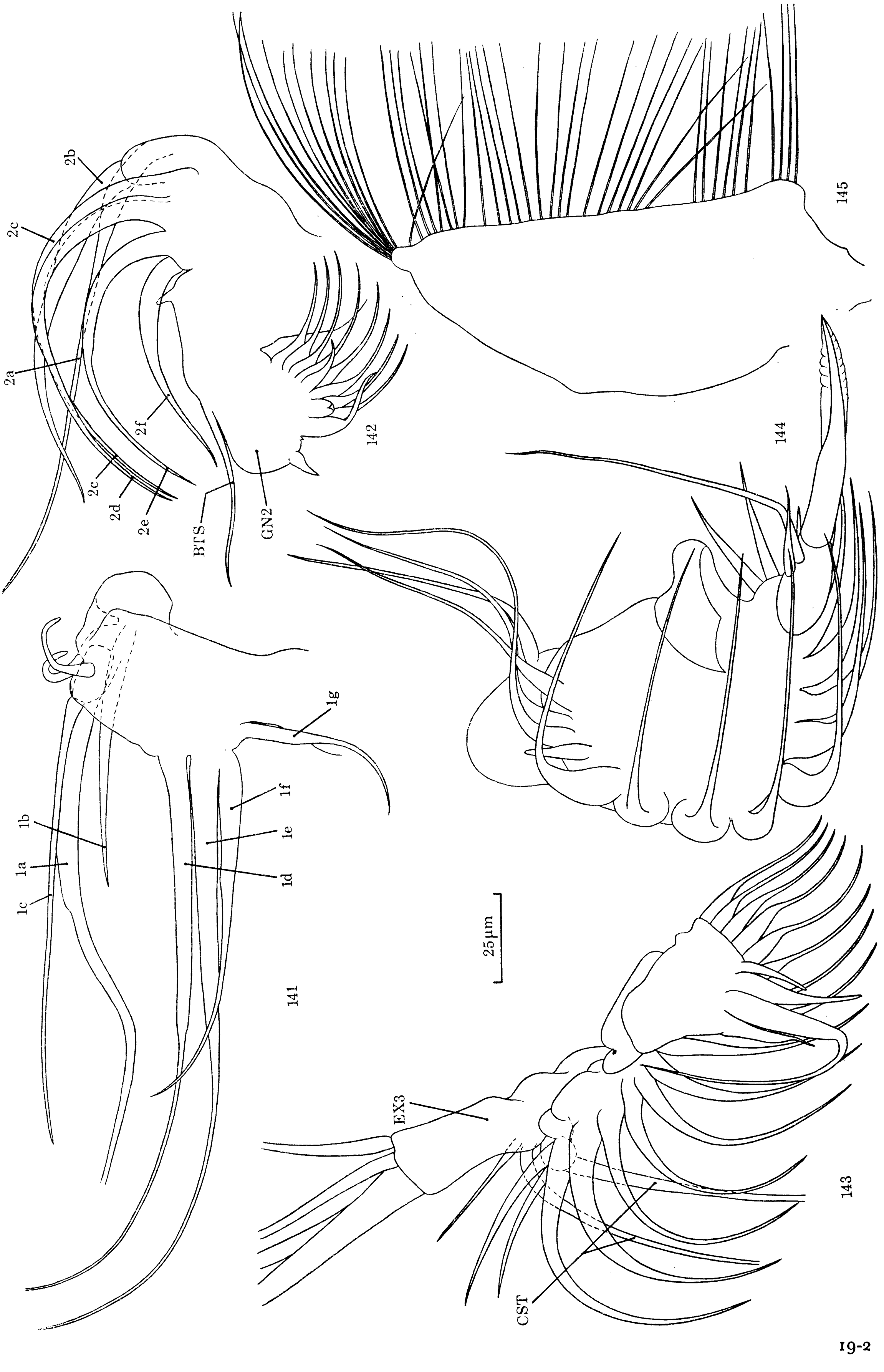


FIGURE 140. *Ilyocryptus sordidus*. The filter chamber and associated structures as revealed by dissection. As indicated by the overlay the sixth trunk limb lies nearer to the observer than do the filtering setae of trunk limb 4 and helps to seal the filter chamber (filtering basket) posteriorly. The position of the masticatory region of the mandible, dislodged during dissection, and indicated by a dotted outline, is added from a longitudinal section. To avoid unnecessary confusion the filtratory setules of many filter setae are omitted. The labrum has been removed and the distal portion of seta 2c is omitted. The limits of individual appendages are most easily appreciated by reference to figures 141–145. Of the distal setae of the first trunk limb, 1a, 1d and 1e are the major contributors to the screening sieve across the entrance to the filtering basket. 1f is the posterior ejector seta. In life setae 1d and 1e are both curved as shown for seta 1d (see also figure 141). As a result of dissection in a viscous medium, seta 1e has here straightened distally – which enables its full length to be shown. Its true course is indicated by dashed lines.



Figures 141–145. For descriptions see following page.

developed six long, curved setae (figures 140, 142 and 146, 2a–f) armed with setules so arranged that the entire complex forms a chute, V-shaped in section, and directed posteriorly and dorsally. This plays an important but entirely passive part in food manipulation (§(v)). Its component setae appear to belong to three endites.

The armature of the gnathobase is clearly shown in figures 140 and 142. Particular attention is drawn to the backwardly directed distal spine, here called the beating spine (BTS). This is without counterpart in macrothricids and chydorids but resembles structures to be seen in the Daphniidae, to the corresponding limb of which family that of *Ilyocryptus* exhibits considerable similarity. Movements of trunk limb 2 consist of swings along the plane of the anteriorly directed gnathobasic setae.

Trunk limb 3 (figure 143), while highly specialized, is readily recognized as having the same basic structure as a macrothricid such as *Acantholeberis* (figure 8) or a chydorid such as *Eurycercus* (Fryer 1963, figure 32). The gnathobase bears eight setae (GP3) – partly obscured by the gnathobasic plate of trunk limb 2 in figure 140 – which serve both for filtration and pushing. These are functionally continuous with a wall of seven massive filter setae borne by the more distal endites (OFP3) so that the limb presents an enormous filtering surface along much of the length of the filter chamber. All these setae are curved so that the opposed filtering surfaces are V-shaped in transverse section, their tips lying in two rows between which is a very narrow gap in the vicinity of the food groove (figures 148 and 149).

Details of the heavy gnathobasic armature are shown in figures 140, 143, 148 and 149 (GA3) but particular attention is directed to the recurved nature of the largest element (DVS3). The remaining armature of the corm, which includes two long setae (CST) which clean the inner surface of the carapace, is shown in figure 143. Only a small portion of their proximal regions can be seen in figure 140. Their great development is related to life in a muddy habitat and the necessity of maintaining scrupulous cleanliness within the carapace chamber.

The exopod (figures 140, 143 and 146, EX3) is armed with highly specialized spines and setae most of which curve towards each other as they extend backwards over the anterior part of the pumping apparatus. One spiniform structure, the innermost of the distal group (figures 140 and 146, MVS), however, extends inwards and somewhat ventrally towards the mid-line and thus towards its partner on the opposite limb.

The corm of trunk limb 3 swings through a wide arc along the plane of its wall of filter setae, whose gnathobasic members sweep along the food groove. The exopod has an independent

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DESCRIPTIONS OF FIGURES 141–145

FIGURES 141–145. *Ilyocryptus sordidus*. Outlines of trunk limbs 1, 2, 3, 4 and 6 respectively. In order to facilitate understanding of figure 140, trunk limbs 1 to 4 are here shown in approximately the same position as in that illustration. (The general form of trunk limb 5, minus the exopod, is readily ascertained from figure 140 and is not drawn separately.)

FIGURE 141. Trunk limb 1. The ejector hooks curve towards the observer and appear much foreshortened.

FIGURE 142. Trunk limb 2. The full course of seta 2c, partially omitted from figure 140 for clarity, is shown here.

FIGURE 143. Trunk limb 3. Here are shown considerable portions of the two long cleaning setae (CST) which clean the inner wall of the carapace, only basal fragments of which can be seen in figure 140. The exopod has a fifth terminal seta completely hidden by the broadest of those visible.

FIGURE 144. Trunk limb 4. Only that part of the limb concerned directly with the handling of the food is shown here. Posterior to the filter is a flap-like exopod with an area more than twice that of the portion illustrated.

FIGURE 145. Trunk limb 6. Only the anterior margin of this limb is shown in figure 140.

movement, being flexed at the joint which it makes with the corm and moving towards the filtering basket. The tips of its long setae, however, move scarcely at all during this activity and consequently become somewhat bent. They straighten as the exopod moves back. Exopod movements, apart from their contribution to the feeding-respiratory current, swing the cleaning setae (CST) which lie between limb and carapace.

The fourth trunk limb (figures 140, 144, 146–148) is similar in many ways to that of a form such as *Acantholeberis* or *Eurycercus*, but here the continuous filtering surface made up by the setae of the gnathobase and more distal endites is enormously enlarged to form a specialized filtering basket. This basket, curving towards its partner of the opposite limb, close to which it lies in the mid-line (figure 147), forms the posterior and dorsal walls of the filter chamber. Not all the setae of the distal endites are filter setae. Distally (that is towards the ventral aperture of the filter chamber) a conspicuous sensilla (SEN) marks the termination of the filtering basket. Still more distally the setae of the limb extend first anteriorly and then ventrally (figure 140, MPS) to form a median palisade best appreciated from horizontal sections (figure 146, MPS). Of these the outermost (SMPS) is spiniform. The distal portions of the setae comprising the dorsal wall of the basket lie close to the food groove (figures 140 and 148). Two of the heavy gnathobasic elements dominate the rest. Most conspicuous is an enormous tusk-like structure (GNT), curved in two planes (figures 140 and 148) and directed anteriorly along the food groove. Distally, and extending over a third of its length it bears on both dorsal and ventral faces a hyaline blade. Near its base arise three spines of which one (DVS4) is bent near its base and then extends approximately at right angles to the gnathobasic tusk right across the mid-line of the filter chamber (figures 140 and 147). The exopod is an enormous flap-like structure forming part of the pumping apparatus discussed at length by Eriksson (1934).

Movements of trunk limb 4 consist of a swing that carries its posterior filter setae towards each other and forward and the more dorsal setae and the gnathobasic tusk forward along the food groove. Because of their location and the region about which the limb pivots, the distal (ventral) palisade setae move scarcely at all even though the amplitude of swing of the limb is considerable.

The fifth trunk limb represents a specialized version of that of a more generalized form such as *Acantholeberis*. The vertical setae of the corm are represented by only a single, extremely well developed and highly specialized structure (figures 140 and 147, VS) which contributes to the sealing of the posterior end of the filter chamber, but a more proximal structure (H5) directed horizontally along the food groove (figures 140 and 148) is probably the homologue of a vertical seta of certain other genera whose orientation has changed. The gnathobase is produced into two lobes (figure 140) one of which (DGN5), bearing three setae which lie almost on the floor of the food groove, is located a little dorsal to the other (VGN5), which bears two similarly directed setae. The flap-like corm is fringed with setules (CLS) on its anterior face. Their role as cleansers of the filtering basket of trunk limb 4 is clearly revealed in figures 140, 146 and 147. The exopod, basically similar to that of other macrothricids and chydorids that employ currents, has been described by Eriksson (1934). While the corm of the limb fulfils an essentially passive role in food collection, the exopod and that of trunk limb 4 are the prime movers in the pumping device.

The sixth trunk limb (TL6) is relatively large. Its location, form and armature are indicated in figures 140, 147 and 148, which clearly reveal its sealing role.

The filter chamber is divided into anterior and posterior compartments by long setae

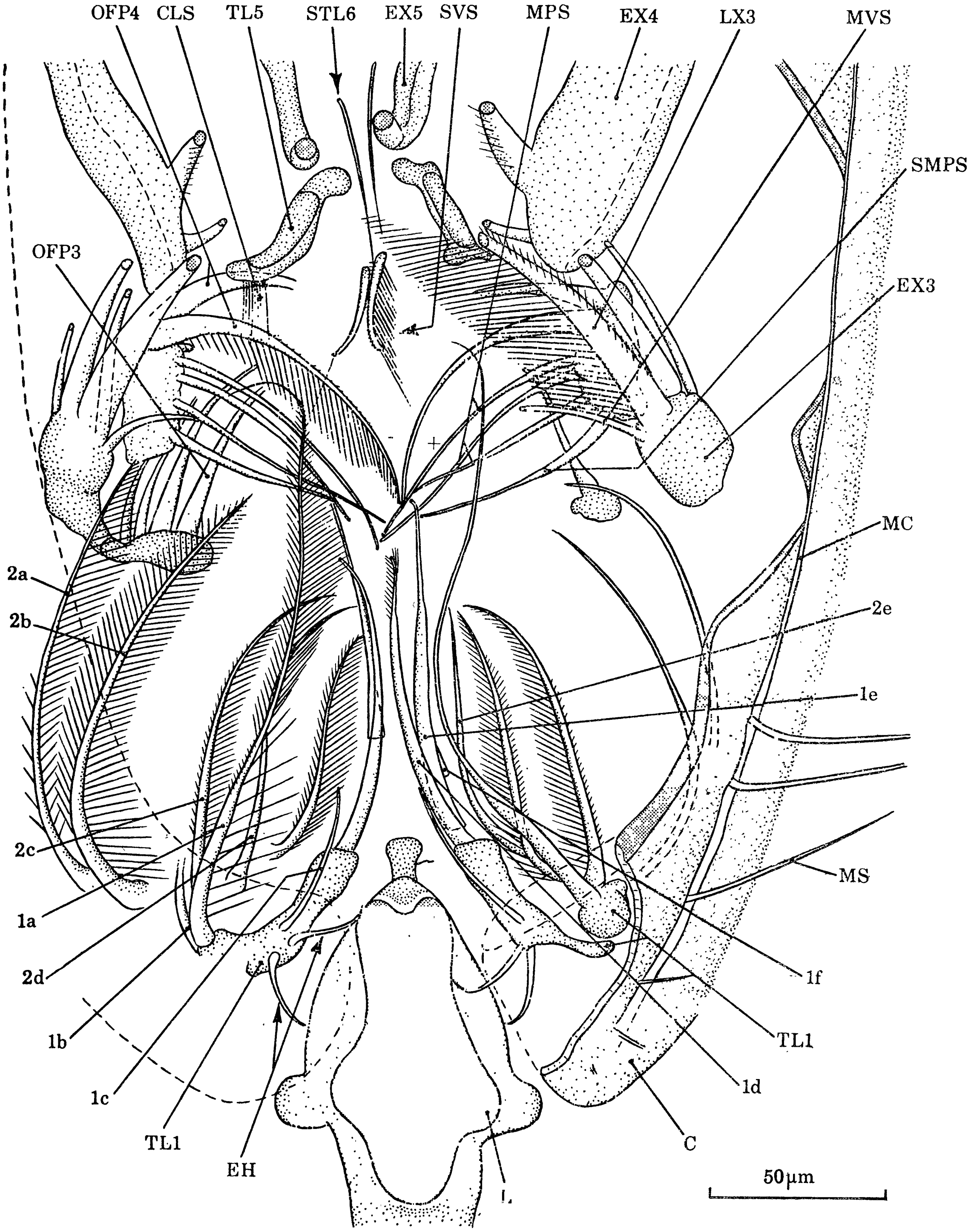


FIGURE 146. *Ilyocryptus sordidus*. Horizontal section, ventral aspect, through the distal portions of the trunk limbs. On the left the position of the carapace, which covers parts of the limbs shown, is indicated by a dashed line, and on the right the extreme anterior ventral portion of the carapace is shown as if cut away to reveal underlying structures. Note on the right that the intact carapace margin is that of the previous instar that has been retained at the moult. Of the guide setae of trunk limb 2 all save the dorsalmost (2a), which lies too deep to be revealed in this slice, are shown. On the right, the two distal endites of trunk limb 1 appear to be separate at the level of the section, and at first glance the outer (more posterior) could be mistaken for trunk limb 2, which, however, lies deeper within the carapace chamber. Setules of some setae are omitted for clarity. All setae on this and the next three figures can be readily related to those on figure 140 by use of similar code lettering. The seta indicated by + is rising towards the observer; that indicated by – descending into the plane of the paper.

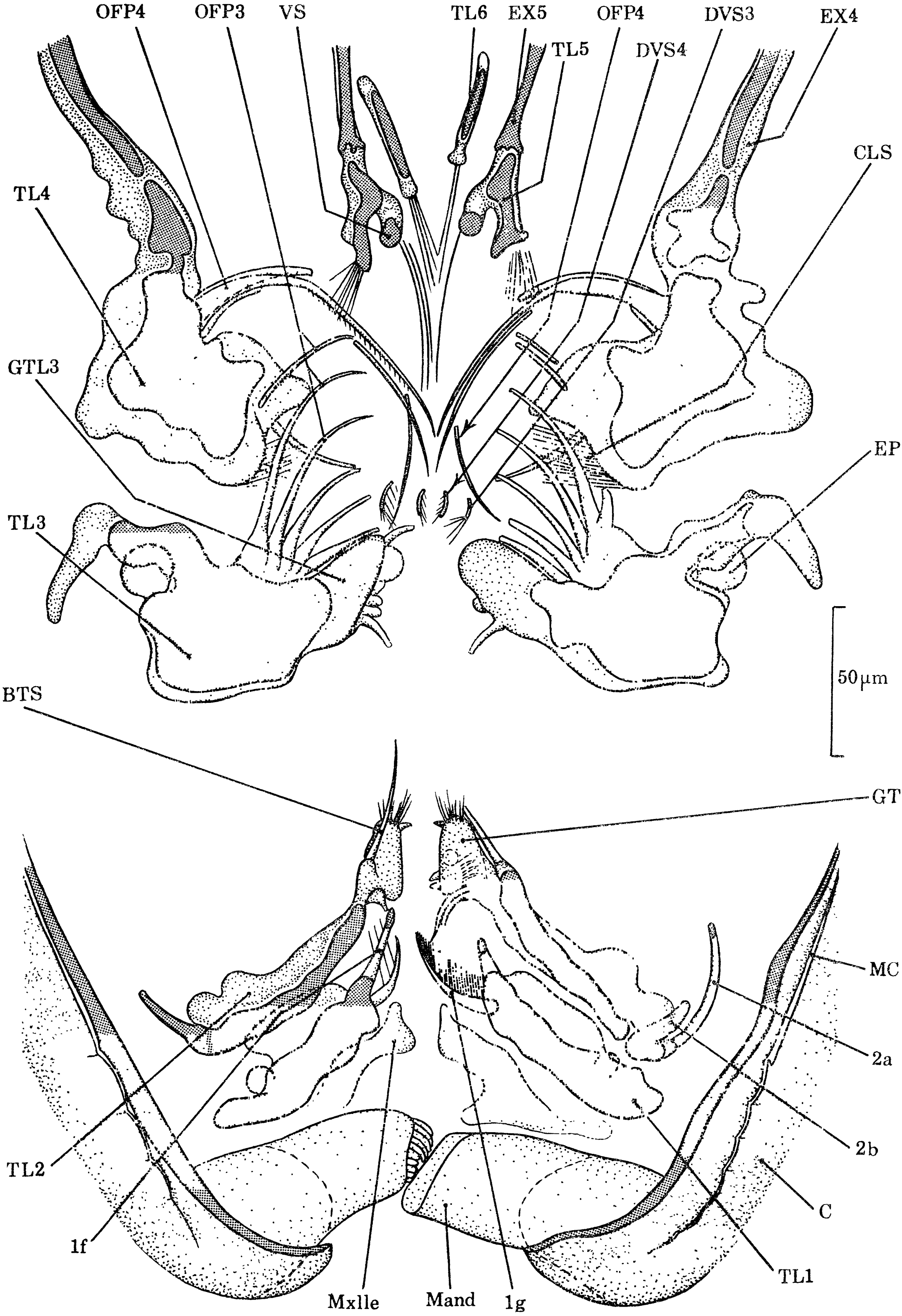


Figure 147. *Ilyocryptus sordidus*. Horizontal section, ventral aspect, more dorsal than in figure 146. Because of the relative positions of limbs 2 and 3 the gap between them appears exaggerated. Note the basket-like arrangement of the more ventral filter setae (OFP4) of trunk limb 4, whose sealing of the filter chamber posteriorly is here clearly seen. In several instances setules are omitted for clarity, and of the long setules of the screening seta (1g) of trunk limb 1 only a few are shown on the left appendage.

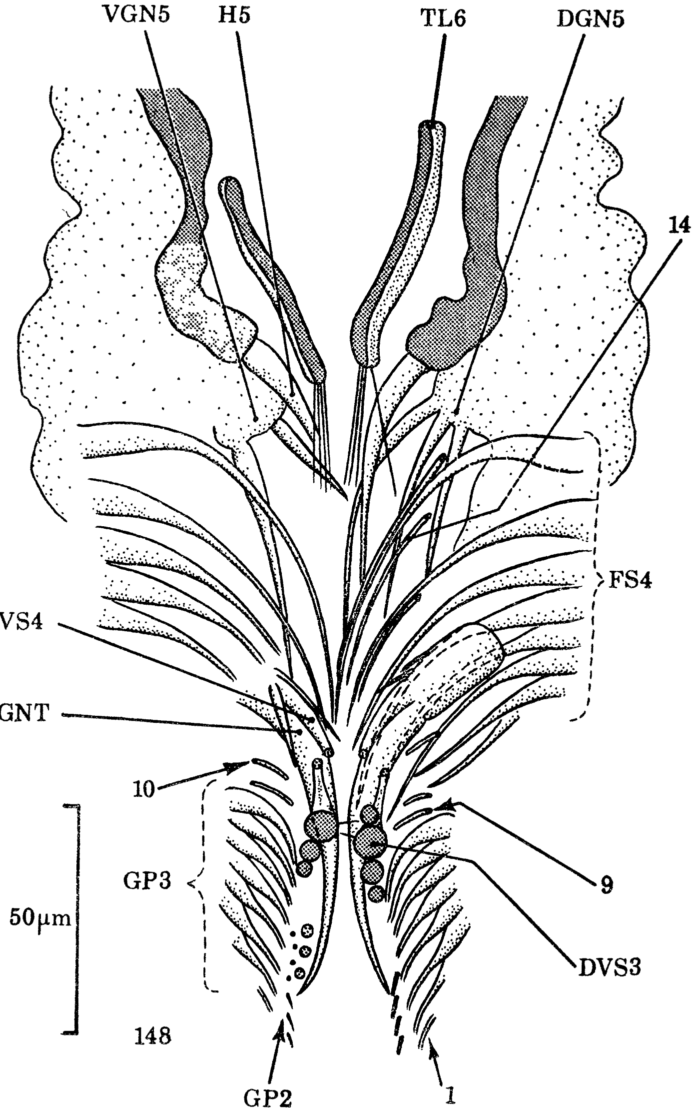
(dividing setae) borne by gnathobases 3 and 4 (DVS3 and 4) that extend dorso-ventrally across it. (See figures 140 and 147 from which the appearance in transverse section can easily be envisaged.) These do not, however, extend into the depths of the food groove.

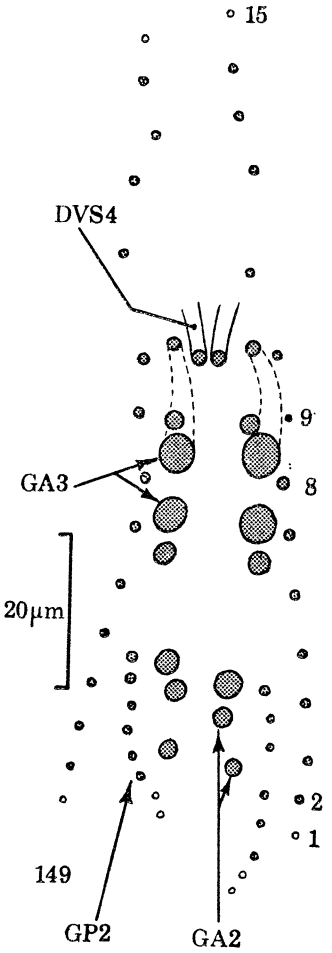
(v) *The feeding mechanism*

Ilyocryptus sordidus frequents similar habitats to chydorids of the genus *Leydigia:* indeed it and *L. leydigii* sometimes coexist in rich organic mud. Life in such oxygen poor habitats probably necessitates the maintenance of a brisk respiratory stream and such is present in both. This stream, however, creates its own problems as it inevitably carries in suspension more fine particles than are required for food. *Leydigia* has solved this problem by diverting the respiratory stream outside the median chamber, which necessitates the abandonment of true filter feeding (Fryer 1968). *Ilyocryptus* has solved the problem in a different way and is a true filter feeder. It is indeed unique among macrothricids (and chydorids) in that all its food is brought within the filter chamber by currents set up by the posterior exopods. None is collected mechanically by any of the trunk limbs, and no limb is ever protruded beyond the confines of the carapace chamber in connexion with feeding, though some of the long armature of trunk limb 1 can be so protruded.

Elucidation of the feeding mechanism of *Ilyocryptus* is fraught with peculiar difficulties as Eriksson (1934) has already discovered. The animal generally feeds only when buried and cannot therefore be watched easily, and its detrital burden makes observation difficult. Although undisturbed individuals may remain stationary for some time while feeding, they seldom do so in situations permitting prolonged observation at adequate magnifications. To restrain an individual so that the depths of the filter chamber can be seen is not easy and can lead to abnormal behaviour. Many disjointed observations, including a few which revealed much of the process, supplemented by the watching of individuals that were restrained, partially narcotized, or immersed in a viscous medium have, however, revealed the essence of the process. Various media – carmine, particles of detritus, small algae or *Lycopodium* spores – have revealed how various sized particles are treated. Eriksson (1934) elucidated certain important features of the feeding mechanism and paid particular attention to the pumping apparatus. While valuable, his account is difficult to follow as it lacks adequate illustrations, and that given here differs from it in certain important respects. More recently Sergeev (1972) has enunciated the general principles involved and drawn attention to the similarities of the mechanisms used by *Ilyocryptus* and *Ophryoxus*. Additional information is given in a paper that has just appeared (Sergeev 1973) (see note added on page 270).

As indicated by figures 134 and 137, the combined respiratory-feeding currents set up by the exopod pump of limbs 4 and 5 draw water from a wide area in front, to the side of, and ventral to the animal. These currents enter the carapace chamber in a restricted antero-ventral region where there is no fence of setae to impede the progress of even large detrital particles which they might carry. The inflowing currents, of which those coming from in front of the animal are particularly powerful, can be tested by the mobile antennules within whose orbits the area involved lies. Water leaves posteriorly. The restricted area of inflow and the unrestricted entry of material into the carapace chamber in this area indicate quite clearly that the elaborate marginal armature of the carapace serves not to prevent the ingress of excessive amounts of food material, or of large particles, but to ensure that such material as enters does so only in the region adapted to deal with it. It is not unwanted food material that is excluded





FIGURES 148 AND 149. *Ilyocryptus sordidus.*

FIGURE 148. Horizontal section, ventral aspect, more dorsal than figure 147. Here the filtering setae (FS4) of trunk limb 4 which form the 'roof' of the filtering basket adjacent to the food groove are clearly seen. These are mostly gnathobasic in origin but as the line of demarcation between the gnathobase and adjacent endite is not apparent the non-committal term 'filtering setae' is appropriate. These are shown in part only on the left, and overlying setae are omitted. In order more clearly to show the course of the largest of the heavy gnathobasic setae of trunk limb 3, the most posterior member of this series is omitted on the left (cf. GA3 in figure 149). The armature of the gnathobase of trunk limb 5, which lies at two levels (figure 140), is shown at the more dorsal level (i.e. deeper within the filter chamber) on the right, at the more ventral on the left. The position in the series of setae (15 in number) of the gnathobasic–outer filter plate continuum of trunk limb 3 is indicated in certain cases by simple numbers.

FIGURE 149. Horizontal section, ventral aspect, more dorsal than in figure 148, through the setae of another individual whose limbs are in a slightly different position, simplified to show only the narrowness of the filter chamber adjacent to the food groove. Of the setae of trunk limb 3 numbers 1–8 belong to the gnathobase, the rest to more distal endites. Numbers 1 and 15, and the first two setae of the gnathobase of trunk limb 2, are not in fact present in this section which is too dorsal to slice their tips, and their position, a little more ventrally, is indicated by open circles. Of the gnathobasic armature of trunk limb 3 (GA3) the third seta from the front, whose curved dorsal course is indicated by a dashed line, is the dividing seta, labelled DVS3 in figure 148. This is cut through twice at this level.

by the carapace setae but material through which the animal crawls which, were it to enter the carapace chamber posteriorly, would clog or impede the working of the delicate apparatus within. Thus the armature of the ventral carapace margins serves an entirely different purpose from that of other macrothricids (and chydorids) in which it is used to facilitate resting on, or intimate association with, a variety of substrata. It is particularly noteworthy that the burrowers *Streblocerus* and *Drepanothrix* have no comparable detritus-excluding device ventrally – a feature related to different burrowing habits from those of *Ilyocryptus* and entirely different feeding mechanisms.

Water that has entered the carapace chamber passes posteriorly and somewhat dorsally to enter the filter chamber through the narrow gap between the screen of setae of trunk limb 1, then through the V-shaped channel formed by the distal setae of the second pair of trunk limbs (figures 140 and 146). These setae, although armed with a double row of setules, are not true filter setae as Eriksson (1934) supposed but serve as a chute to guide particles borne by the inhalent current into the more posterior, and truly filtering, region of the food-collecting apparatus. Particles occasionally adhere to these setae, as Eriksson observed, but this does not mean that their function is filtration, and indeed the rapid passage of particles down the chute is readily observed.

Some current-borne particles continue posteriorly and pass directly into the filtering basket of which the filter setae of trunk limb 4 comprise the posterior and dorsal walls – assisted in the make-up of the latter by those of trunk limb 5 – the large filter setae of trunk limb 3 the lateral (figures 140, 147 and 148). Here they are entrapped. Particles destined for the filtering basket but with a tendency to pass somewhat ventrally are assisted towards their destination by a comb of spinules (CSP) borne on endite 2 of the corm of trunk limb 3 (figure 140), perhaps assisted by a more distal, less prominent comb (DCS).

Both the proximal comb and the long, posteriorly directed beating spine (BTS) of trunk limb 2 automatically help to sweep or beat particles towards their initial destination as their respective limbs swing through well-defined arcs. It is clear from its location that the action of the beating spine is confined to the region lying anterior to the dividing setae (DVS3, 4) that cross the filter chamber. The dividing setae lie beneath the sieve of trunk limb 1 and are extremely difficult to see in the living animal. In spite of much effort it has not been confirmed by direct observation that they prevent the backward drift of any clumps of material that have negotiated the initial sieve provided by the first trunk limbs and impinge upon them. From their structure and arrangement, however, this would appear inevitable. Because of the phase difference between trunk limbs 3 and 4 as they swing, the relations of the dividing setae to each other are not always the same, but they can scarcely do other than provide a barrier to even small clumps of material whatever the relative positions of the two limbs. It is clearly the larger of the entering particles that will be restrained by these setae and swept directly towards the food groove by the beating spine of trunk limb 2, assisted by the long setules on the posterior face of the gnathobase of that limb. Ample confirmation that some larger particles follow this route is provided by the arrangement of the heavy gnathobasic armature of trunk limbs 2 and 3 which clearly serves to transport material towards the food groove and forward as in many anomopods whether filter feeders or mechanical handlers of particles. Because small particles passing forward from the filtering basket lie deep in the food groove, and thus out of reach of some of the heavy gnathobasic armature, the latter would have no function unless it served to deal with material in the way just described.

In addition to the particles mentioned, however, yet others pass more ventrally and do not enter the filtering basket. These, which may be more numerous than those which enter the basket, though this is difficult to assess quantitatively, are collected by the long, posteriorly directed setae of trunk limb 1, and particularly by setae 1d and 1e which make up a simple screening sieve of which seta 1a forms the lateral wall. While relatively large, discrete particles can pass into the posterior filtering basket – spores of *Lycopodium* (diameter *ca.* 30–37 μm) sometimes did so when supplied – the aperture leading to this basket is restricted by the armature of trunk limb 1 (figure 146) which excludes flocculent clumps of material such as often enter the carapace chamber. While the critical size of such clumps cannot be defined precisely – and must vary with the size of the animal – figure 146 shows that most irregular-shaped clumps with a width of more than about 25 μm must be so excluded. In nature most of the material collected is flocculent or of very small dimensions: compact objects as large as *Lycopodium* spores are probably seldom brought in. Such sieved material, plus some of very small dimensions that would not in any case have entered the filtering basket but would have passed backwards in the ventral region, accumulates on the sieve. Because setae 1d and 1e are curved (figures 140 and 146) the material piles up at their distal ends, that collected last gradually pushing that already accumulated towards their tips. Eventually trunk limb 1 is swung forward so that these setae swing ventrally towards the ventral aperture of the carapace chamber. The post-abdomen is now swung so that its distal armature wipes between these setae, efficiently removing from them their accumulation of material, and conveying it outside the carapace chamber. The same swing cleans accumulated detritus from the setae of the ventral carapace margins. Backward flow of particles in the vicinity of the curved tips of setae 1d and 1e is also impeded by the ventrally extending palisade of distal setae of trunk limb 4 (figures 140 and 146, MPS) but it is on the sieve of trunk limb 1 that the largest accumulations can be seen. The inwardly directed spiniform seta of the exopod of trunk limb 3 also arches over into this region (figure 146, MVS) possibly granting stability to the slender palisade setae at times, and itself contributes to the barrier formed here. I cannot, however, confirm the clip-like function of this seta shown diagrammatically by Eriksson (1934) who, however, made useful observations on the screening setae of trunk limb 1. When trunk limb 1 is swung forward as described the action requires no movement of the seta of exopod 3; the tips of the swinging setae simply flick past this alleged clip. (In narcotized individuals at least they sometimes rest against it anteriorly.)

While exclusion from the filtering basket of embarrassingly large clumps of material is one function of the sieve, another (and more important?) is to prevent such larger clumps as would in any case never have entered the basket from drifting backward. The presence of such material in the vicinity of the pumping mechanism is highly undesirable. Small particles pose no problems. They pass freely through this region and are discharged with the exhalent current, many probably being deflected ventrally by the long setules of the largest distal seta of the exopod of trunk limb 3 (figures 140 and 146, LX3) though this is difficult to observe.

As in several filter-feeding anomopods, filtered material accumulates posteriorly and has to be conveyed anteriorly along the food groove. A wealth of cleansing areas – on trunk limb 5 to clean the filters of trunk limb 4, and on trunk limb 4 to clean those of trunk limb 3 – is present, some of these being clearly shown in figures 140, 146 and 147, CLS. These, in conjunction with brisk swings of wide amplitude by trunk limbs 3 and 4, ensure that material is carried towards the food groove. Here the tips of the filter setae of trunk limb 3 and the gnathobasic tusk of trunk limb 4 sweep material forward, a process continued by the gnathobasic armature of trunk limbs 3 and 2, and ultimately by the maxillules, as can easily be envisaged from figure 140 (see also figures 148 and 149). While the proximal parts of the gnathobasic setae of trunk limb 3 are filtratory their tips are used for pushing as in many anomopods. The gnathobasic setae of trunk limb 2 are specialized for pushing and sweeping only. Curiously, Eriksson (1934) held that forward movement along the food groove was by means of currents, but admitted that he had no evidence to prove this and stated that the power of this current must be very small. In his just published paper Sergeev (1973) (see note added on page 270) agrees that food is moved mechanically but makes no reference to the important gnathobasic tusk of trunk limb 4.

The posterior setules of the screening seta (1g) of trunk limb 1 guard the gap between trunk limbs 1 and 2 as in several anomopods (Fryer 1963 and this paper), but are here extremely long (figure 140). This is perhaps in part associated with the need for very effective screening at all times in a mud-frequenting species, but is also related to the movements of wide amplitude performed by trunk limb 1 when material is removed from the posterior parts of the food-collecting apparatus as described below. That the gap is left exposed when trunk limb 1 tilts forward to allow the sieve setae to lift material towards the ventral carapace aperture is doubtless associated with a momentary cessation of food collection as the post-abdomen swings to remove the accumulation of material.

Individual food particles collected in the filtering basket often remain there while the posterior limbs complete many cycles of movement, and material frequently accumulates there before its passage along the food groove. Should this accumulation become excessive it can be removed either by the curved spiniform setae (1f) of the first trunk limbs which reach into the basket and sweep it ventrally before removal from the carapace chamber by the post-abdomen, or directly by the post-abdomen, though the latter method has seldom been observed.

Individuals that had trapped *Lycopodium* spores in the filtering basket evidently experienced considerable difficulty in ridding themselves of these objects, which were unsuitable as food. Cells of *Scenedesmus* also appeared to present difficulties. These observations, and those on the feeding mechanism, suggest that in nature, food consists essentially of fine particles and flocculent clumps of detritus such as can be dealt with easily by the filtering, cleansing and transporting systems. The gut contents suggest likewise but these have conceivably been comminuted. The use of labral gland secretions has not been proved. By analogy with other species any such secretions would drift posteriorly to facilitate the agglutination of food masses in the basket, but here it seems unlikely that the dividing setae would permit this. Secretions possibly accumulate against the dividing setae but no evidence of this has been obtained.

(vi) *The evolution of* Ilyocryptus

While *Ilyocryptus* occupies an isolated position among the Macrothricidae and represents the end-point of a highly specialized and successful evolutionary line, it is possible to visualize the route by which its specializations were derived. *Parophryoxus* is in no way interpreted as ancestral to *Ilyocryptus*, but nevertheless reveals in both structure and habits certain incipient *Ilyocryptus*-like attributes. The progenitors of *Ilyocryptus* may be visualized as filter feeders with a straight antennal protopod which, instead of developing their potentialities for swimming, began to row over and penetrate into soft bottom deposits by use of the antennae. *Parophryoxus* exhibits this grade of organization today and shows how, in relation to such habits, the ventral carapace setae may become modified into a screening device. The ventral setae of *Parophryoxus* and *Ilyocryptus* are indeed similar in many respects. *Parophryoxus* also shows how, at a relatively unspecialized stage of association with detritus, the habit of collecting a detrital burden could have been acquired. This has been taken farther in *I. agilis* and to its apparent limits in *I. sordidus* where it is associated also with the retention of old carapaces. Although the post-abdomen of *Parophryoxus* is certainly not specialized for pushing it has an attribute, lacking in many macrothricids but a pre-requisite for the successful development of *Ilyocryptus*-like habits – mobility. *Parophryoxus* also has very efficient and elaborate filter-feeding equipment and, while this is not made too much of, the outer filter plates of trunk limb 4 make up a basket-like structure whose nearest parallel is in *Ilyocryptus*. That trunk limb 3 moves with a steady rhythm is also perhaps significant but further observations are desirable. Certainly, however, the stage is set in *Parophryoxus* for the collection by filtration alone of material already in suspension in the inhalent stream or stirred up by the antennae. It and *Ilyocryptus* are the only burrowing macrothricids that use filtration. Such filtration would release the first two pairs of trunk limbs from any obligation to collect food or to pass it into the filter chamber (exactly as in the Daphniidae) and would free their distal portions for other purposes – in *Ilyocryptus* for use as chutes and strainers. Such an evolutionary trend meets the requirement of functional continuity, as do gradual changes and specialization of the antennae, post-abdomen, headshield and posterior carapace margins, all of which are easily visualized. The small size of the compound eye of *Parophryoxus* is probably also related to burrowing habits, as it is in *Ilyocryptus*.

Although one of the most specialized anomopods, *Ilyocryptus* retains several primitive features, clearly for functional reasons. These include a straight antennal protopod, a two-segmented antennule, the retention of the sixth trunk limbs and of a gnathobasic plate on the fifth.

(vii) *Conclusions*

Ilyocryptus sordidus is a non-swimming, crawling and burrowing animal which extracts all its food from currents set up by the exopods of the posterior limbs. The antennae and post-abdomen are used for burrowing. Specializations of the ventral carapace margins serve to exclude debris from the carapace chamber. Old carapaces are retained at each moult and provide a highly specialized, hedgehog-like array of defensive spines posteriorly. Other specializations for life in mud include shape, a broad headshield, the collection of a camouflaging burden of detritus on headshield and carapace, the habit of shamming death, and the development of abundant haemoglobin in the blood. Given suitable deposits it is tolerant of a wide range of environmental conditions.

Currents bearing suspended particles pass through a sieve made up by spines of trunk limb 1. This, regularly cleaned by the post-abdomen, prevents large clumps of material from entering the filter chamber or from clogging the pumping device. Material to be used as food passes down a chute made up by the second trunk limbs and is either trapped in a large posterior filtering basket and subsequently conveyed mechanically along the food groove to the mandibles, or beaten towards the groove more anteriorly and thence conveyed mechanically forward. In its limb structure, and to some extent its feeding mechanism, *Ilyocryptus* stands closer to the daphnids than do other macrothricids.

XVII. ADAPTIVE RADIATION AND PHYLOGENY OF THE MACROTHRICIDAE

(i) *Morphological radiation and phylogeny*

The antiquity of the Macrothricidae is attested by the magnitude of its radiation, its geographical distribution, and its evolutionary relationships to other families. The last point is not, however, discussed here. Phyletic relationships of its component genera are not easy to recognize. As indicated by the functional analyses presented here, extant forms often represent end points of widely divergent and mutually incompatible trends, and a given species may exhibit a mosaic of specialized and primitive features, the latter sometimes having been retained for functional reasons. Some 75 % of the recognized genera are monotypic, which adds to the difficulty of determining affinities.

TABLE 1. SUMMARY OF CERTAIN CHARACTERISTICS OF SOME INVESTIGATED MACROTHRICIDAE

Indications in parentheses are probably correct but not proven with certainty. Data for *Bunops* are mostly from Merrill (1893). A mobile post-abdomen is one which is capable of vigorous swings and may or may not be used for pushing. The post-abdomen of species listed as negative in this respect are often capable of feeble swings.

	antennal protopod straight (s) or flexed (f)	post-abdomen mobile	trunk limb 1: no. of elements on inner distal lobe	trunk limb 3: gnathobasic plate	trunk limb 3: outer grid filtratory (+), non-filtratory (−) or absent (a)	trunk limb 4: gnathobasic plate	trunk limb 4: outer grid filtratory (+), non-filtratory (−) or absent (a)	trunk limb 5: gnathobasic plate	trunk limb 6
Acantholeberis curvirostris	f	−	3	+	+	+	+	+	+
Ophryoxus gracilis	s	+	3	+	+	+	+	+	+
Streblocerus serricaudatus	f	−	3	+	−	+	a	−	−
Drepanothrix dentata	f	−	3	−	−	+	−	−	−
Macrothrix laticornis	f	−	3	−	−	+‡	−	−	−
M. triserialis	f	−	3	+†	−	−	−	−	−
Onchobunops tuberculatus	f	+	3	+	+	+	+	−	−
Bunops serricaudata	f	?	3	+	(+)	+	(+)	−	−
Lathonura rectirostris	f	−	4	+†	a	−	a	−	−
Pseudomoina lemnae	(f)	?	4	+	+	+	a	−	−
Guernella raphaelis	(f)	?	4	+	−	+†	a	−	−
Neothrix armata	(f)	(−)	4	−	−	−	a	−	−
Grimaldina brazzai	f	+	3	+	+	+	+	−	−
Parophryoxus tubulatus	s	+	3	+	+	+	+	+	+
Ilyocryptus sordidus	s	+	*	+	+	+	+	+	+

* Homology of lobes uncertain. † Much reduced. ‡ Reduced to 1 seta.

Some attributes have arisen more than once during the evolution of the family. Thus the abandonment of filtration (or at least of the extraction of particles from suspension) by the ancestors of *Lathonura* probably arose in connexion with habits very different from those that led to such loss in *Drepanothrix*, *Streblocerus* and *Macrothrix*. Likewise the habit of grasping by trunk limb 1 certainly evolved independently in *Onchobunops* and *Macrothrix triserialis*.

Comparative studies suggest that the primitive macrothricid, and therefore the primitive anomopod, possessed the following attributes:

(1) a relatively elongate trunk;
(2) a non-pushing post-abdomen;
(3) no headshield;

(4) simple setation of the ventral carapace margins;
(5) long, probably two-segmented, antennules;
(6) large antennae with a straight (unflexed) protopod, and probably with five setae on each ramus;
(7) locomotion restricted to swimming by means of antennae;
(8) six pairs of trunk limbs;
(9) ability to collect food by trunk limbs 1, 2 and, probably, 3;
(10) gnathobasic plates on trunk limbs 2–5; filtratory on at least the last three and possibly on trunk limb 2;
(11) trunk limbs 2–5 with flap-like exopods, particularly well developed on limbs 4 and 5;
(12) trunk limbs 4 and 5 used for creating 'respiratory'-feeding currents;
(13) a non-coiled gut, probably with no diverticulum;
(14) an ephippium employing a but slightly modified carapace and containing a variable number of eggs;
(15) benthic, but not burrowing, habits.

Many, but not all, these attributes are exhibited by *Acantholeberis* and *Ophryoxus*. Contrariwise many extant species have departed widely from these primitive conditions.

Changes in the method of locomotion have clearly played an important part in macrothricid evolution. The primitive method can hardly have been other than swimming over the substratum by means of antennae which had a straight protopod. This conclusion, arrived at from comparative studies, is in accord with ideas on the origin of the group that will be developed elsewhere. Such a method is retained by some present-day forms, for example *Ophryoxus*. Nevertheless an early acquired attribute was a marked flexure of the antennal protopod (which is not usually divided into coxa and basis as it is in the Chydoridae). Throughout their history macrothricids have been bottom dwellers and the initial advantage of a flexed protopod, even in forms using their antennae for swimming, was probably that when at rest the antennae were held clear of the substratum. The alternative, in certain respects more advantageous, strategy exploited by chydorids such as *Peracantha* and *Alonella* which tuck their antennae within the carapace chamber (Fryer 1968), is here precluded because large antennae are retained.

What is probably the primitive arrangement of setae on an antenna with a flexed protopod is that of *Lathonura* (figure 91), though here other specializations preclude the use of the antennae for persistent swimming and the setae themselves are specialized. Similar armature is present in *Pseudomoina* which almost certainly, and *Guernella* which probably, have flexed antennae in life (only preserved material of these has been available), and in what is probably another genus recorded from Sinkiang (see below). Although it has lost the swimming seta of the basal endopod segment, *Grimaldina* exhibits what in form and function is probably otherwise a primitive type of antenna with a flexed protopod. Here – probably in part because such antennae are less efficient for this than those with a straight protopod – swimming abilities, while superior to those of levering macrothricids, are weaker than those of most chydorids, and the antennae are used only for short periods at infrequent intervals.

Flexure brings the armature of the antennal rami into a relation with the substratum that permits propping and levering and, by suitable modification of the appropriate setae and an increase in robustness of the protopod, appendages used primarily for these purposes have been evolved, for example in *Acantholeberis*. This feature, which does not prohibit the use of the antennae for at least slow swimming, has played an important part in the adaptive radiation of the family. Such usage is, however, incompatible with their employment for sustained swimming, though in some cases the powerful thrusts of which they are capable can be used for rapid, indeed violent, take-off which serves as an escape reaction, e.g. *Acantholeberis*.

Specialization for levering leads naturally to burrowing in soft deposits. One route to this habit has been exploited by forms with a flexed protopod, notably *Streblocerus* and *Drepanothrix*. To some such burrowers the disadvantages accruing from the possession of a seta on the third exopod segment perhaps outweigh the advantages conferred during rare bouts of swimming, and this seta has been lost in *Drepanothrix*. Specializations enhancing burrowing abilities – such as the burrowing spines of *Drepanothrix* – are described under the species concerned.

Flexure lends itself also to quite different specializations. The unique method of crawling exploited by *Lathonura* makes no demands on the antennae – which have in fact to be kept clear of the substratum – and these appendages have been able to specialize in another way by the utilization of primitive features. They may indeed have begun to do so before the present method of crawling was evolved. Here, specialized swimming setae, five on each ramus, are used for the transmission of a powerful initial thrust, and also serve incidentally as a parachuting device.

While efficient, though never rapid, swimming along an essentially straight course can be accomplished by forms with a flexed protopod, long slender antennae with straight protopods of relatively small diameter appear to be better suited to this and are best exemplified by *Ophryoxus*. Even in these forms, however, swimming is seldom, in nature probably never, sustained for more than a few seconds. As it is hoped to demonstrate elsewhere, this route led eventually to the swimming Daphniidae, where again sustained antennal activity is not practised.

The evolutionary potentialities of an unflexed antennal protopod are not restricted to swimming, and macrothricids have exploited other possibilities. The antennae of *Parophryoxus* have a straight, not paricularly robust, protopod. With them females row into soft detritus in a manner indicative of the way in which the highly specialized *Ilyocryptus* probably embarked on the route to its present means of burrowing. Males have a long swimming seta on each of the two basal endopod segments, lacking in females, which indicates that they can swim more actively than females (an aid to the finding of the latter?), but I have seen no males and nothing is known of their habits. Certainly, however, the antennae of *Parophryoxus*, basically of the swimming type, indicate how the route to alternative and incompatible ways of life – swimming and a specialized type of burrowing – lay open to their possessors. Progression by levering as practised by *Drepanothrix* and others could not have been derived via either of these routes.

The specialized antennae of *Ilyocryptus*, used for rowing through mud, were derived by reduction in length, increase in girth (partly to house powerful muscles), use of slow rather than rapid muscular contractions, and the requisite modifications of the armature. *Parophryoxus* indicates in both structure and function the way in which such antennae could have evolved, functional continuity being maintained throughout.

Primitively the post-abdomen is no more than a reflexed termination of the trunk, and in many macrothricids plays no part in locomotion. In this the family stands in marked contrast to the Chydoridae to whose evolutionary success the development of a trunk/post-abdominal joint and use of the post-abdomen for pushing has contributed greatly. Certain genera, however – *Grimaldina*, *Onchobunops*, *Ilyocryptus* and *Iheringula* – have developed a pushing post-abdomen, probably independently. In view of its known habits, the perfection of the pushing device in *Grimaldina* is somewhat unexpected for this animal swims over deposits, which suggests that pushing is largely restricted to take-off. Further observation may, however, reveal that this ability is used more frequently than hitherto suspected as the animal moves over the bottom, to which it is largely confined. The same may also be true of *Iheringula* which, while able to swim slowly, and to crawl (§VIII), can also push with its post-abdomen (Sars 1900). While the value of pushing to *Onchobunops* is easily appreciated, its use is again less expected than in a burrower. In *Ilyocryptus* levering with the post-abdomen combines with antennal rowing to grant propulsion through deposits in a manner unique within the family. Burrowers such as *Streblocerus* and *Drepanothrix* evidently never developed such a device. Had they done so it is scarcely conceivable that it would later be lost. In some genera the post-abdomen is in process of reduction, e.g. *Lathonura*, though here it not only still fulfils the primitive function of serving as the site of the anus but is involved in the production of a secretion used to anchor the ephippium (Fryer 1972) and houses part of a gland apparently involved in ephippium formation (Makrushin 1970). In *Neothrix*, a deposit frequenter and probably a burrower, it plugs the posterior end of the carapace chamber, is probably immobile, and has even lost its claws.

A further method of locomotion – crawling by means of the first trunk limbs – is discussed in an evolutionary context below.

Changes in the means of locomotion have gone hand in hand with changes in the method of food collection. The morphology and behaviour of extant forms suggests that, in the ancestral macrothricids, which swam over and rested on the bottom, food, certainly consisting of detrital particles, would be whisked or dragged into the filter chamber by means of the distal portions of the first and second, and possibly also the third, trunk limbs. Increased efficiency of the distal, food collecting, armature of trunk limb 1 would lead to the kind of device seen today in *Acantholeberis* and several other genera but would have another, inevitable, consequence. Such an appendage, making contact with any but loose clumps of material, would pull the animal against the food mass/substratum, thereby facilitating the application to it of scraping devices on trunk limb 2 (and perhaps 3). Such a condition is to some extent approximated by *Ophryoxus* which has, however, advanced beyond it, and has begun to use the hook-like distal armature of trunk limb 1 to give firm anchorage to the substratum, a tactic exploited to a more striking degree by *Bunops* and *Onchobunops*. This specialization has been carried to its logical conclusion by *Iheringula* and *Macrothrix triserialis*, which use such hooks for intermittent attachment as they crawl by appropriate movements of the first trunk limbs, as do many chydorids.

Increased intimacy of association with the bottom would confer certain advantages on swimming, detritus-eating macrothricids. Energy expenditure would be reduced, food made more readily available, and conspicuousness to predators possibly reduced. Selection for such association would therefore be favoured. In species frequenting bottoms covered with flocculent organic detritus relatively large clumps of food would be acquired easily and this would obviate the need to filter. Indeed such conditions would present problems to a filter feeder. Loss of filtration, especially by forms that began to burrow, would therefore be a logical (but not the only possible) evolutionary step. That the original currents probably had little to do with respiration is clear from the ability of several macrothricids (and chydorids) to survive without them. Feeding currents have also been lost, probably independently, in association with quite different habits in *Lathonura*. Here hyper-development of certain epipodites may compensate for this.

An alternative strategy is shown in incipient form by *Parophryoxus* and carried to exquisite perfection in *Ilyocryptus*. Here the feeding current is retained and unwanted particles excluded from the carapace chamber by modification of the setae of the ventral carapace margins into a screen. This, in animals which, like *Ilyocryptus*, live surrounded by food renders the anterior trunk limbs redundant as collectors and frees them to specialize as strainers and chutes (§XVI).

It so happens that *Parophryoxus*, which shows how the specialized rowing into detritus by *Ilyocryptus* could have been initiated, also exhibits hyper-development of the outer filter plates of the fourth trunk limbs, thereby illustrating the way in which the filtering basket of *Ilyocryptus* evolved. It has also begun to collect detritus on its carapace, but it is doubtful whether there is any direct phyletic affinity between it and *Ilyocryptus*. *Ilyocryptus*, the only genus to feed exclusively by filtration, has the largest filtering area of any macrothricid. Here the currents set up may also serve a respiratory function. Such would be advantageous to animals living in what is often foul mud. The quest for oxygen is also indicated by the presence of abundant haemoglobin in the blood, especially in *I. sordidus*.

One group of genera – *Lathonura*, *Pseudomoina*, *Guernella* and an animal from Sinkiang referred to as *L. rectirostris* by Chiang (1964) but which may well represent a distinct genus – may possess true phyletic affinity. All have very similar antennae with the same arrangement of natatory setae, and the first three each have four spines on the outer distal lobe of trunk limb 1 (the condition in the animal from Sinkiang is unknown); these being attributes of no other genus save that *Neothrix* has four spines distally on trunk limb 1. The animal from Sinkiang, well illustrated by Chiang (1964) whose figures of other species are excellent, bears an overall similarity to *Lathonura*, including the presence of what appear to be similar, otherwise unique, setae of the ventral carapace margins. It also has a conspicuous dorsal organ, as have *Lathonura* and *Guernella*. Its body is, however, much shorter than that of *Lathonura*, its antennules quite different, being somewhat as in *Guernella* and, most striking, of two segments as illustrated and mentioned in the brief description (kindly translated by Dr Teo Leng Hung). The antennae have a distal seta on the protopod not found in *Lathonura*, and again very similar to that of *Guernella*, and the post-abdomen is completely different from that of *Lathonura*, being again *Guernella*-like. This animal is also much smaller than *Lathonura*, the size being given as 0.45–0.51 mm and the embryo-carrying female illustrated being a little less than the smaller of these dimensions. From the available information it combines features of *Lathonura* and *Guernella* and is perhaps nearer to the latter. However, we know nothing of those features that would establish its real relationship to these genera which, while sharing several attributes (e.g. accessory sweepers of trunk limb 2), have diverged along widely differing adaptive paths.

Pseudomoina not only bears an overall resemblance to *Lathonura* but also shares certain features that do not appear to be necessary correlates and which seem best explained by common ancestry (§XII), but these genera today stand far apart.

Although the literature reports only that the habits of *Pseudomoina* 'are rather sluggish' (King 1853) it has clearly adopted a very different way of life from *Lathonura*. Its feeding mechanism involves filtration – not employed by *Lathonura* – and it is certainly unable to crawl in the manner of the latter. One suspects that it settles on the ventral carapace margins as does *Lathonura* and that the antennae are used to enable it to 'hop' from place to place. (*Guernella* may well move likewise.) This does not attribute ancestral status to *Pseudomoina* though this genus exhibits several incipient *Lathonura*-like features. It does, however, indicate that the

Lathonura type of antennae, which are primitive in certain respects, could have been acquired before the specialized locomotory-feeding habits which this genus exhibits today.

Neothrix may be related to this group of genera but the evidence is not strong. It is the only other genus with four spines on the inner distal lobe of trunk limb 1, it possesses a distinct dorsal organ, and its post-abdomen has certain features in common with that of *Lathonura*. It also shares with *Lathonura* the distinction of having an extra, ninth, element in the scraping armature of trunk limb 2. Its divergent adaptations, however, are such as to make its relationships difficult to elucidate.

Bunops and *Onchobunops* are obviously related in a phyletic manner and probably represent the end-points of divergent evolution from a common ancestor or stock in widely separated geographical regions.

Other affinities suggest themselves but until more information is available on the structure and habits of the various species of *Macrothrix* and allied genera speculation is unlikely to be very profitable.

(ii) *Geographical and ecological features of macrothricid evolution*

Some groups of the Macrothricidae, notably the species currently embraced by *Macrothrix* and allied genera such as *Drepanomacrothrix*, are in need of taxonomic revision but certain features relevant to the evolution of the family are evident from the taxonomic grouping of its members. Very striking is the high proportion of monotypic genera of which, if *Iheringula* be recognized and *Wlassicsia*, *Echinisca* and *Gurneyella* are allocated to the '*Macrothrix* complex', 12 are described. In addition it is probable that the animal assigned to *Lathonura* by Chiang (1964) belongs to a distinct genus. By contrast, only four described genera contain two or more species, but *Macrothrix* may eventually be split, possibly to include at least one additional monotypic genus. Of the validity of all the monotypic genera save *Iheringula* there is little doubt, and on the available evidence *Iheringula* appears to merit such status. These genera exhibit distinctive patterns of geographical distribution, summarized as follows, the number of species being indicated in parentheses. Precision rather than rigid adherence to a particular system is the aim of the terminology employed, and the monotypic genera are arranged on a geographical basis.

Ophryoxus (1). Holarctic, particularly northern. Palaearctic and nearctic races or subspecies of *O. gracilis* are probably recognizable.
Parophryoxus (1). Nearctic. Known only from a restricted region in the eastern U.S.A.
Acantholeberis (1). Holarctic.
Drepanothrix (1). Holarctic.
Bunops (1). Holarctic (including N. Africa) and oriental.
Lathonura (1). Holarctic, including N. Africa.
Grimaldina (1). Circumtropical and southern nearctic.
Guernella (1). Old world tropics.
Iheringula (1). Neotropical. Known only from Brazil.
Onchobunops (1). Southern neotropical. Known only from Argentina.
Pseudomoina (1). Australia and New Zealand.
Neothrix (1). Australia and New Zealand.
Streblocerus (2). Both species holarctic and neotropical.
Drepanomacrothrix (2). Both species Asiatic palaearctic.

Ilyocryptus (perhaps 9). Cosmopolitan.
Macrothrix (30–40). Cosmopolitan.

That the family has a world-wide distribution is suggestive, but not proof of, its antiquity but is in keeping with other attributes clearly indicative of such antiquity. The preponderance of monotypic genera suggests that, while a particular grade of organization may be highly successful in a particular habitat, it offered little scope for subsequent radiation. This is in accord with the ecological distribution discussed below and is quite different from the pattern of speciation shown by the Chydoridae, Daphniidae, Moinidae and Bosminidae. Although the distribution of some monotypic genera is extensive it is always confined either to one hemisphere, and sometimes to a restricted portion of that hemisphere, or to the tropics and subtropics. In no case is it so wide as that of many chydorids. Even widely distributed species often show marked ecological restrictions or are rare. Only the genera *Ilyocryptus* and *Macrothrix*, whose success is indicated also by their relative richness in species, include species with a near world-wide distribution. *I. sordidus* is virtually cosmopolitan while *M. laticornis* and *M. hirsuticornis* Norman & Brady, although unknown in Australia, are both also extremely widespread, the range of the latter including even Antarctica. By contrast, several chydorids are cosmopolitan and others more widely distributed than any macrothricid belonging to a monotypic genus.

The pattern of six northern, three tropical and three southern monotypic genera is indicative of climatic restriction. This is supported by the holarctic distribution of several northern genera some of which, such as *Acantholeberis* and *Drepanothrix*, can remain active in winter, and by the wide, in one case circumtropical, distribution of two of the tropical genera, which indicates that there have been few geographical barriers to dispersal within a restricted latitudinal range. The three southern genera are more restricted but two are common to Australia and New Zealand. There is little evidence for ecological replacement from zone to zone so the simplest hypothesis to explain present distribution is that the various genera originated in isolation in the zones in which they occur today, but this is unproven. Certainly the tropical belt appears to have been an absolute barrier to the monotypic genera, notwithstanding their possession of drought resistant ephippia, for it is difficult to believe that habitats suitable for animals like *Acantholeberis*, *Drepanothrix* and *Lathonura* do not exist in places like southern South America where ecological equivalents are unknown. Relevant here is the recent observation that ephippia of several of these genera are attached to fixed objects and appear to be adapted more for ensuring survival in an already colonized habitat than for dispersal (Fryer 1972). Their dispersive role is not denied but may be secondary.

Ecologically several macrothricids are confined to specialized habitats, and some – *Bunops*, *Onchobunops*, *Parophryoxus* and probably others – appear to be genuinely rare and either restricted or sporadic in distribution. *Acantholeberis* is an excellent example of a species confined to a restricted range of habitats, in this case acidic pools or *Sphagnum*-filled hollows on moors and heaths (§III). Here it is often unaccompanied by possible competitors and, while not exactly what Hutchinson (1951) would call a fugitive species, is an occupant of refugia. Although it occurs in *Sphagnum* mats at the fringe of even large bodies of water it is not a member of the littoral fauna of lakes. For example, although common in many places in the English Lake District, it is not recorded from any lake. This apparent inability to colonize lakes is shared to a considerable extent by several other macrothricids. Even species such as *Macrothrix laticornis* and *M. hirsuticornis*, which on the criterion of wide distribution are successful species, are rare in the littoral zone of lakes. The success of *Ophryoxus gracilis* in this respect is noteworthy. A lack of competitors in northern latitudes or advantages conferred by its powers as a swimmer may be involved.

In the tropics *M. triserialis* – perhaps on account of morphological and behavioural attributes (§VIII) – appears well able to participate in communities that include a diversity of other small crustaceans, but this is not the impression given by temperate zone species as a whole. It is in the warmer parts of the world that the *Macrothrix* complex is best represented, but more information, both taxonomic and ecological, is needed before the significance of this can be appreciated. *Ilyocryptus sordidus*, a highly successful species, clearly avoids competition from any but congeneric species by its specialized burrowing habits and appears to be restricted largely by the nature of the substratum. Less widely distributed members of the genus are similarly specialized and equally unaffected by competition from most other crustaceans. *I. acutifrons* Sars penetrates to considerable depths, where competition is minimal; in Italian lakes to at least 100 m (Corbella, Della Croce & Ravera 1956), and in Lake Ladoga to 198 m (Nordquist 1888). Investigation of the profundal region revealed its presence in ten lakes in the English Lake District, from which area it was previously unrecorded (Smyly 1968). Obermayer (1922) and Muckle (1942) found that in sub-alpine lakes it is most abundant in the sublittoral region and penetrates to greater depths than *I. sordidus*. Likewise in Lake Maggiore, Smyly (1964) showed that while it coexists with, but is less abundant than, *I. sordidus* at 20 m, it is more common than that species at 30 m and occurs alone at 40 m and 50 m, which suggests different depth (substrate?) preferences and possible competition.

The general picture of macrothricid evolution is that of an old group that has produced a number of solutions, based on complex mechanical devices, to the problems posed by the environment to organisms endowed with the attributes of primitive anomopods. However, many of these solutions appear to have been such as to offer few opportunities for further radiation and tend to impose restrictions on range of either a geographical (climatic) or ecological nature, or both. Exceptions are the genera *Ilyocryptus* and *Macrothrix*. The former has exploited a specialized way of life with few competitors; the latter, whether or not it represents one or more genera, exemplifies a successful combination of attributes to some extent comparable with those of the Chydoridae.

The great differences in structure and habits between many monotypic genera indicate that interspecific competition has played little part in their recent evolution and that the factor of overriding importance has been refinement of those aspects of morphology and behaviour that lead to ever more efficient adaptation to particular ways of life. Competition with chydorids may, however, have been of importance and one suspects that such competition, either now or in the past, goes some way at least to explaining the present ecological restriction of certain macrothricids. A somewhat subjective impression, which may nevertheless enshrine an issue of importance, is that on the whole the macrothricids are less active than the chydorids, and certainly the deliberate swimming from place to place which at least enabled crude estimates of swimming speeds of chydorids to be given (Fryer 1968) is much less practised by macrothricids.

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Since this paper was submitted Sergeev (1973) has published a further contribution which briefly summarizes his earlier work on *Ophryoxus*, *Lathonura* and *Ilyocryptus*, makes available in English some of the information on the last two, previously given in Russian, and adds extra details of the feeding mechanism of *Ilyocryptus*. The widely differing habits of these animals are compared and it is emphasized that during food collection both mechanical scraping and filtration are employed by *Ophryoxus*, mechanical processes only by *Lathonura*, and filtration only by *Ilyocryptus*.

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List of abbreviations used on figures

A1	antennule
A2	antenna
AD	apodeme
ADM	apodeme of mandible
AF	anterior flange of carapace
AGP	anteriormost element of the gnathobasic plate of trunk limb 2
AGS	anterior gnathobasic seta of trunk limb 2
AM	adductor muscle of carapace
A1 MUS	antennular muscle
A2 MUS	antennary muscles
A1N	antennular nerve
ASW (1, 2)	accessory sweepers (1, 2) of trunk limb 2
ATL1	armature of trunk limb 1
AVC	anterior ventral corner of carapace
AVS	anterior ventral spike of labrum
BBPT	bases of blade plates
BG	brushing seta of gnathobase of trunk limb 2
BP	brood pouch
BPT	blade of plates
BR	basal brush of posterior seta of gnathobasic plate of trunk limb 2
BSP	burrowing spine of antenna
BTS	beating spine of trunk limb 2
C	carapace
CC	carapace cuticle
CCH	carapace chamber
CCL1, 3	crawling claw of trunk limbs 1, 3
CEX3	cleaning seta of exopod of trunk limb 3
CG	cerebral ganglion
CH	crest of headshield
CL4	cleaning lobe of trunk limb 4
CLC	cleaning comb of trunk limb 3
CLS	cleaning setules
COC	circum-oesophageal commissure
CS	carpet of setules of posterior outer face of gnathobase of trunk limb 2
CSP	comb of spinules of trunk limb 3
CST	cleaning setae of trunk limb 3
CT	curved tips of blade plates
D	distal seta of outer filter plate of trunk limb 3
DAO	dilator muscle of atrium oris
DASW	distal accessory sweeper of trunk limb 2
DC	dorsal ridge (or crest) of carapace
DCL	distal claw
DCS	distal comb of spinules of trunk limb 3
DDS	dorsalmost distal spine of trunk limb 1
DE	double eye of embryo
DG	duct of labral glands
DGN5	dorsal portion of gnathobase of trunk limb 5
DIV	diverticulum
DLM	dorsal longitudinal trunk muscles
DMG	duct of maxillary gland
DPS	defensive posterior spines of definitive carapace
DPS′	defensive posterior spines of old carapace(s)
DS3	distal spine (scraper) of trunk limb 3
DS4	distal spine(s) of trunk limb 4
DVM	dorso-ventral trunk muscles
DVS3, 4	dividing setae of gnathobase of trunk limbs 3, 4
E	compound eye
E1, 2, 3, 4	endite 1, 2, 3, 4 (endite 4 = inner distal lobe of trunk limb 1)
EA	endite armature of trunk limb 3
EC	exhalent canal
EH	ejector hooks of trunk limb 1
EMB	embryo
EMG	end sac of maxillary gland
END	endoskeleton
ENP	endoskeletal plate
EP	epidermis
EP1, 2, 3, 4, 5	epipodite of trunk limbs 1, 2, 3, 4, 5
ER	extension of reservoir of labral gland
ES3, 4	endite spines of trunk limbs 3, 4
ESS	external sensory setae of trunk limb 2
EX2, 3, 4	exopod of trunk limbs 2, 3, 4
EXS4	exopod seta of trunk limb 4
FG	food groove
FIB	fibrils
FM	food mass
FMS	fine setae of carapace margin
FP3, 4, 5	gnathobasic filter plate of trunk limbs 3, 4, 5
FPT	food particles
FS3, 4	filtering setae of trunk limbs 3, 4
G4	fourth element of gnathobasic plate
GA2, 3, 4	gnathobasic armature of trunk limbs 2, 3, 4
GC, GC′	gland cells of secretion-filled reservoirs of trunk limb 1
GCL	gland cells of labrum
GDS	guard seta of trunk limb 2
GES	guarding endite spines of trunk limb 1
GNT	gnathobasic tusk of trunk limb 4
GP2, 3, 4, 5	gnathobasic plate of trunk limbs 2, 3, 4, 5
GRS	grooming setae of carapace margin (on definitive and old carapaces)
GS2, 3	gnathobasic setae of trunk limbs 2, 3
GSL	guard setules
GT	glandular tissue
GTL2, 3, 4, 5	gnathobase of trunk limbs 2, 3, 4, 5
H5	horizontal seta of trunk limb 5
HDL	hook-like spine of inner distal lobe of trunk limb 1
HP	head pore
HS	headshield
HSS	hyaline setules
HT	heart
I3	inner spine of endite 3 of trunk limb 1
IC	inner cuticular lining of carapace
IL	inner lobe of trunk limb 1
IS1	inner spine of trunk limb 1
ISL	inner spine of inner distal lobe of trunk limb 1
IVS	inner vertical seta of trunk limb 5
K	keel of labrum
L	labrum
LB	lateral bulge of carapace
LDS	long distal setae of outer distal lobe of trunk limb 1

LGC	labral gland cell(s)
LM	levator muscle of labrum
LPS	long posterior setules of gnathobase of trunk limb 2
LS3	long seta of gnathobase of trunk limb 3
LSA	levering spines of antennal protopod
LSE	levering spines of endopod of antenna
LSH	lateral spinules of headshield
LX3	longest distal seta of exopod 3
Mand	mandible
MC	margins of old carapaces
MG	mid-gut
MPS	median palisade setae of trunk limb 4
MS	marginal seta
MSH	muscle sheath
MVS	medio-ventrally directed spine of exopod 3
Mx	maxilla
Mxlle	maxillule
NC	nerve cord
O	ocellus
OC	outer cuticular lining of carapace
OCS	outer cleaning setae of trunk limb 2
OCM	oesophageal constrictor muscles
ODL	outer distal lobe of trunk limb 1
ODM	oesophageal dilator muscles
OE	oesophagus
OFP3, 4	outer filter plate of trunk limbs 3, 4
OGS3, 4	outer grid of setae of trunk limbs 3, 4
OMS	outwardly directed setae of carapace margin
OV	ovary
OVS	outer vertical seta of trunk limb 5
PA	post-abdomen
PAL	post-abdominal lamella
PAS	post-abdominal seta
PC	posterior dorsal crest of carapace
PDS3	penultimate distal spine (scraper) of trunk limb 3
PF	posterior flange of carapace
PG	posteriormost gnathobasic seta of trunk limb 2
PGC	parenchymatous gland cells
PL	posterior limit of labrum
PLS	pre-labral spines
PP	posterior projection of labrum
PSA1	proximal sensory seta of antennule
PT	plate in face view
R1	reservoir of trunk limb 1 containing entangling secretion
RE	rectum
RLG	reservoir of labral gland
RS	rostrum
S	sensory seta of coxal region of antenna
S′	distal sensory seta of antennal protopod
S1a, e	setules of setae 1a, e
S3	sensilla of endite 3 of trunk limb 1
SA1	sensory setae of antennule
SCC	supplementary crawling claw of trunk limb 3
SCM	setule covered mound
SE2, 3	spines (scraper-like) on endites 2, 3 of trunk limb 1
SEN	sensilla
SG	spiniform gnathobasic seta of trunk limb 4
SIDL	spines of inner distal lobe of trunk limb 1
SIL	setae of inner lobe of trunk limb 1
SMPS	outermost (spiniform) median palisade seta of trunk limb 4
S Mxlle	spines of maxillule
SO	labral gland secretions in oesophagus
SP1–8	endite spines (scrapers) 1–8 of trunk limb 2
SPS	endite spines (scrapers) of trunk limb 2
SS	screening seta of trunk limb 1
SSG	setose seta of gnathobase of trunk limb 4
SSS	supplementary hyaline setules
SST	supernumerary seta of trunk limb 2
STL6	setules of trunk limb 6
SUS	suspensory ligament of mandibles
SVS	setules of vertical seta of trunk limb 5
TIS1	trident-like inner spine of trunk limb 1
TL1, 2, 3, 4, 5, 6	trunk limbs 1, 2, 3, 4, 5, 6
TLS	trunk limbs
TMM	transverse mandibular muscle
TMT	transverse mandibular tendon
VCS	ventral carapace setae
VGN5	ventral portion of gnathobase of trunk limb 5
VLM	ventral longitudinal trunk muscles
VMS	ventrally directed setae of carapace margin
VS	vertical seta of trunk limb 5
VSA1	ventral setae of antennule
VSH	ventral surface of head
X3, 4	exopod segments 3, 4 of antenna
1, 2, 3, 4, 5, 6	trunk limbs 1, 2, 3, 4, 5, 6
1a–f	distal armature of trunk limb 1
1g	screening seta of trunk limb 1
2a–f	chute setae of trunk limb 2
4′	remotor roller muscles
5c	transverse muscles of mandible
5b, d	minor transverse muscles

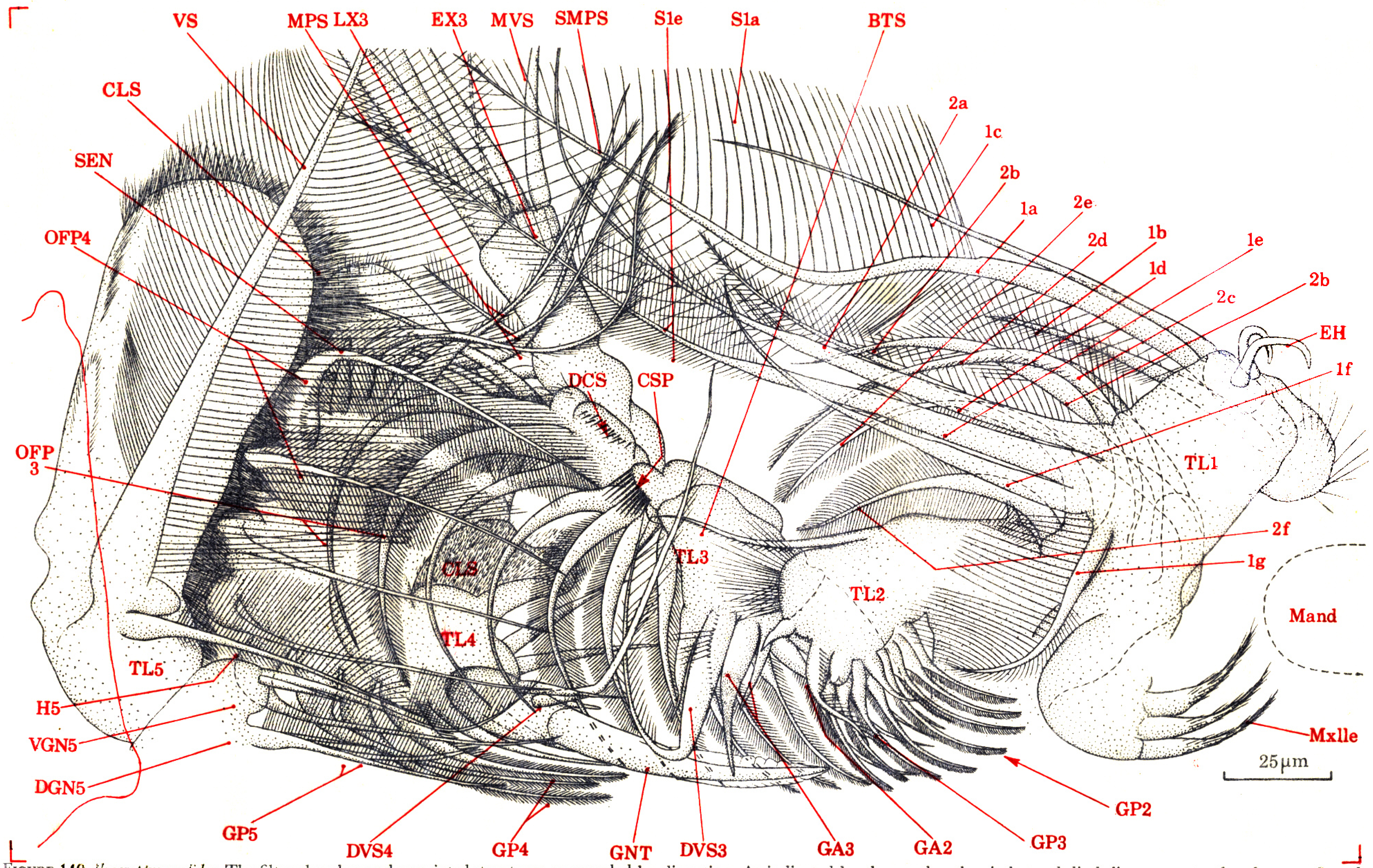

FIGURE 140. *Ilyocryptus sordidus.* The filter chamber and associated structures as revealed by dissection. As indicated by the overlay the sixth trunk limb lies nearer to the observer than do the filtering setae of trunk limb 4 and helps to seal the filter chamber (filtering basket) posteriorly. The position of the masticatory region of the mandible, dislodged during dissection, and indicated by a dotted outline, is added from a longitudinal section. To avoid unnecessary confusion the filtratory setules of many filter setae are omitted. The labrum has been removed and the distal portion of seta 2c is omitted. The limits of individual appendages are most easily appreciated by reference to figures 141–145. Of the distal setae of the first trunk limb, 1a, 1d and 1e are the major contributors to the screening sieve across the entrance to the filtering basket. 1f is the posterior ejector seta. In life setae 1d and 1e are both curved as shown for seta 1d (see also figure 141). As a result of dissection in a viscous medium, seta 1e has here straightened distally – which enables its full length to be shown. Its true course is indicated by dashed lines.

FIGURE 140. Overlay.